NATIONAL UNDERSEA RESEARCH PROGRAM Research Report 89-2

North Carolina Coastal Oceanography Symposium

R. Y. George and Alan W. Hulbert, Editors

December 1989

DEPARTMENT OF COMMERCE
UNITED STATES OF AMERICA

FOREWORD

The National Oceanic and Atmospheric Administration (NOAA), under the aegis of its Undersea Research Program (NURP), directly assists a large cadre of marine research scientists to conduct their scientific activities under the sea. This research is accomplished using manned submersibles, remotely operated vehicles, and compressed-air scuba, mixed-gas, and saturation mode diving. Additionally, the NURP assists all divers of the nation through research undertaken in accordance with the terms of Sec. 21(e) of the Outer Continental Shelf Lands Act of 1978 (PL 95-372; 43 USC 1331 et seq.). This statute requires NOAA, under the authority delegated by the Secretary of Commerce, to "... conduct studies of underwater diving techniques and equipment suitable for protection of human safety and improvement of diver performance."

The Research Report series published by NURP is intended to provide the marine community with results of undersea research, often presented at NURP-sponsored symposia and workshops, in a timely fashion. In the majority of instances, participants at symposia or workshops are reporting on results of NURP-sponsored research. In such instances, the printing of their papers meets report requirements of grantees to the Office of Undersea Research. In other instances, the topic is of direct interest to NURP and could represent a framework for future research if published and distributed to the science community.

The papers presented in this volume are the result of a symposium held at the National Undersea Research Center at the University of North Carolina at Wilmington on September 30 to October 2, 1987. The purpose of the symposium was to establish and describe the current status of coastal oceanography in the Carolina Capes region of the South Atlantic Bight. Because of continued intense interest following the symposium, participants were asked to rewrite their oral presentations to include extensive literature reviews and the latest data available. The papers, as presented, represent the status of oceanography in the region as of late 1989. Accordingly, proposals to conduct in situ research in the Carolina Capes region will find reference to this symposium to be useful background.

Papers are printed as presented, and publication is in partial fulfillment of requirements under Grant No. NA80-AA-H-00081. Comments on the report are welcome. They should be directed to:

Director
National Undersea Research Program
NOAA
6010 Executive Blvd., Room 805
Rockville, MD 20852

Rockville, Maryland
December 1989

David B. Duane
Director

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U.S. DEPARTMENT OF COMMERCE
Robert A. Mosbacher, Secretary
National Oceanic and Atmospheric Administration
John A. Knauss, Under Secretary
Oceanic and Atmospheric Administration
Alan R. Thomas, Acting Assistant Administrator
Office of Undersea Research
David B. Duane, Director

PREFACE

The National Undersea Research Program of the National Oceanic and Atmospheric Administration (NOAA) conducts oceanographic research utilizing a variety of systems including manned submersibles, saturation habitats, remotely operated vehicles (ROVs), and air and mixed gas SCUBA. There are currently five National Undersea Research Centers, located at Universities, which operate under grants from NOAA and constitute the national program. The centers are located at the Caribbean Marine Research Center, Lee Stocking Island, Bahamas, the University of Connecticut at St. Croix, USUI, the University of Hawaii at Manoa, and the University of North Carolina at Wilmington.

The National Undersea Research Program conducts research on regional and national objectives in the broad areas of: global oceanic processes, pathways and fate of materials in the ocean and great lakes, coastal oceanic and estuarine processes, ocean lithosphere and mineral resources, biological productivity and living resources, diving safety and physiology, and ocean technology.

The papers presented in this volume are the result of a symposium held at the National Undersea Research Center at the University of North Carolina at Wilmington on September 30 to October 2, 1987. The purpose of the symposium was to establish the current status of coastal oceanography in the Carolina Capes region. Because of intense interest, the symposium volume authors were asked to rewrite their papers to include extensive literature reviews and the latest data available. The papers, as presented, represent the status of oceanography in the region as of January 1990. The volume is organized into three major parts: I. Land/Sea Interaction, II. Studies on the North Carolina Continental Margin and III. North Carolina Marine Policies and Programs.

We wish to acknowledge Ms. Gloria Crowell who typed the final papers into camera ready copy and also provided significant organization. Ms. Jo-el Spader assisted in the final proof reading and organization of the volume.

Dr. R.Y. George
Professor of Oceanography
University of North Carolina
at Wilmington

Dr. Alan W. Hulbert
Center for Marine Science
Research
National Undersea Research
Center
University of North Carolina
at Wilmington

TABLE OF CONTENTS

Page

INTRODUCTION AND ACKNOWLEDGMENTS

The Marine Expo '87 Symposium volume contains research papers and presentations that give an overview of ongoing research projects along the North Carolina coast and also provides a vivid impression of the various marine programs in North Carolina. This volume entitled "North Carolina Coastal Oceanography" current as of January, 1990 will serve as a source of reference for researchers and students in the field of marine science for years to come. The volume includes three parts. The first part deals with interaction between the seashore and the estuaries with emphasis on pathogenic organisms and biotechnology-aquaculture potentials. The second part primarily addresses questions of continental shelf-slope dynamics with foci on the gulf stream, geologic history, air-sea fluxes, slope processes and biota, of the Carolina Capes. The third part is unique since it is probably the first time all marine related program managers and policy makers from the different institutions and agencies have assembled to succinctly assess "the state of the art" with reference to the various activities that are currently in progress in North Carolina.

An important coastal process along the shores of North Carolina is the erosion problem which has a profound influence on the morphology of the coast. There were two research papers on this subject; unfortunately these papers are not included in the symposium proceedings. Similarly, a research paper on the status of aquaculture in North Carolina state was also presented in the symposium but this paper was not submitted for inclusion in this volume. Nevertheless, an extensive discussion on marine biotechnology and aquaculture potentials in North Carolina became an integral part of the workshop proceedings that constitute the final chapter of the volume. We are thankful to Mrs. Mimi Cunningham of the University Advancement Office for her help in the organization of the symposium and her colleague Mrs. Renee Brantley for her contributions in the preparation of the symposium announcement and the design of the symposium logo.

As conveners of the conference and co-editors of the symposium volume, we are extremely grateful to the sponsoring organizations and in particular to certain individuals who gave us, not only moral support, but also constant encouragement to make the event a success. Dr. William H. Wagoner, Chancellor of the host institution, the University of North Carolina at Wilmington, gracefully supported the concept of the symposium and addressed the delegates. The co-sponsors of the symposium are (1) the North Carolina Biotechnology Center which gave a grant for conducting the conference and meeting part of the publication cost; (2) the National Undersea Research Center at UNCW; (3) the UNC Marine Science Coordinating Committee; (4) the Center for Marine Science Research and the Department of Biological Sciences at UNCW; (5) the Duke-UNC Oceanography Consortium. We are very thankful to the sponsors for their generous support.

Dr. Rita Colwell graciously delivered the Key Note address on marine biotechnology that is so relevant to the theme of the symposium which bridges a link between the oceanographers and the molecular biologists. For her unique contribution in bridging the gap between field research and laboratory studies, this volume is dedicated to Dr. Colwell. It is appropriate that we discuss general oceanography projects with a broad and open outlook and make the best use of the seas for the betterment of mankind. Dr. Charles L. Cahill, Provost of UNCW, welcomed the delegates at the symposium banquet, held in honor of Dr. Rita Colwell. Dr. Daniel B. Plyler, Dean of the School of Arts and Sciences and Dr. Paul Hosier, Associate Vice Chancellor of Academic Affairs gave their support to the symposium by making contributions at several symposium events. Dr. James Merritt, Director of the Center for Marine Science Research, showed keen interest and helped in various phases of the preparation of the symposium volume.

We are indeed indebted to the Honorable Congressman Charles Rose for taking the time to come from Washington, D.C. to attend the policy session and for his valuable suggestion to promote a dialogue between congressmen, state legislative representatives from coastal counties in North Carolina and marine scientists in educational institutions to discuss coastal issues and for a mutual exchange of knowledge. The Honorable Secretary Thomas Rhodes of the N.C. Department of Natural Resources addressed the delegates and eloquently explained the state's policies and programs. We are much beholding to the following individuals for their help: Dr. Jasper Memory, Vice President, UNC; Dr. John Costlow, Director, Duke Marine Laboratories; Dr. B. J. Copeland, Director, UNC Sea Grant; Dr. Dirk Frankenberg, Director, UNC Marine Science Program; Dr. Earl R. MacCormac, Science Advisor to Governor James Martin; Dr. Charles E. Hamner, President, N. C. Biotechnology Center and Dr. William Hogarth, Director, N.C. Marine Fisheries. We also wish to thank the members of the Symposium Advisory Council and Symposium Organizing Committee and all those individuals who chaired the different symposium sessions.

We thank the participants and the authors for their contributions. We are grateful to the numerous reviewers of the papers of the symposium. Although the reviewers remain anonymous, we wish to acknowledge the key role they played in the process of compilation of the symposium volume. During the symposium and in the preparation of the volume Ms. Gloria Crowell helped enormously, particulary in getting the manuscripts in camera-ready format. We are thankful to Gloria for her help and enthusiasm. Ms. Jo-el Spader helped with the final preparations of the manuscripts.

One inevitable outcome of the symposium exercise is the awareness among N. C. marine scientists and policy makers that we have more questions than answers. The marine scientists in North Carolina are, therefore, bound to face more scientific challenges, greater cooperation and coordinated efforts for prudent management of North Carolina's natural resources along our coast. Let us now summarize our feelings in simple words!

The Ocean is abundant with all

sorts of things,

The Oceanographers know that the future is full

of fascinating things.

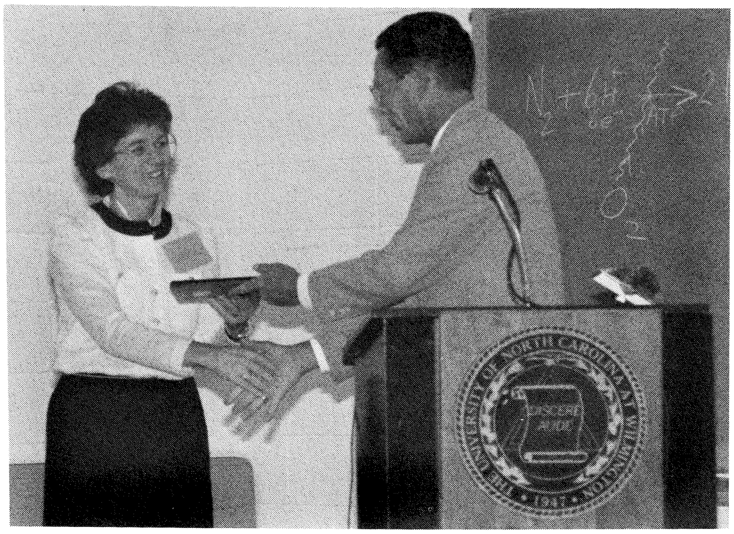
Robert Y. George & Alan W. Hulbert
Symposium Conveners and Co-Editors

"Symposium Group Photograph of Participants"
In Front of the University Union
The University of North Carolina at Wilmington
September 30, 1987

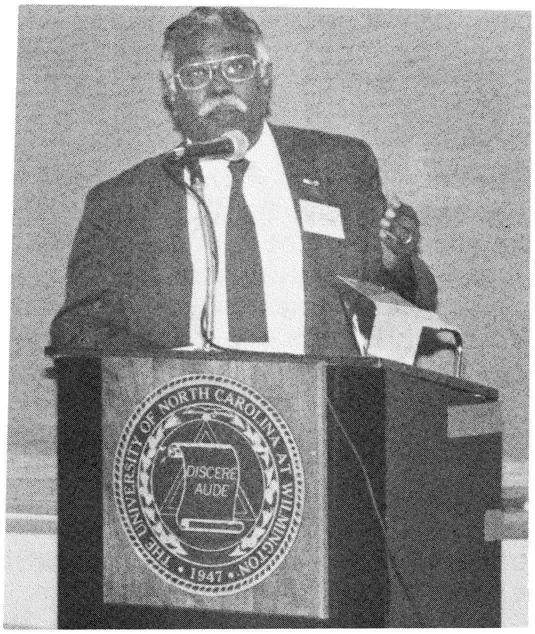
DEDICATION

This Symposium Volume is dedicated to Professor Rita Colwell for her outstanding contributions in the area of Marine Biotechnology and Coastal Oceanography.

Prof. Rita Colwell delivering the Symposium "Key Note Address" on Sept. 30, 1987.



Provost Dr. Charles Cahill of the host Institution (UNCW) presenting the Marine Biotechnology Award to Dr. Rita Colwell.



Prof. Robert Y. George, Symposium Convener delivering the "Symposium Opening Statement" on Sept. 30. 1987.

Provost Dr. Charles Cahill presenting "Sir George Deacon Award" in Oceanography to Dr. Leonard J. Pietrafesa.

Symposium Motto:	"Support of Basic Marine Research is vital if we are to understand the global oceans, to predict the behavior of marine environment, to exploit (wisely) the sea's resources" ...from 'Our Nation and The Sea,' 1969.

SYMPOSIUM OPENING STATEMENT

Robert Y. George
Symposium Organizer
Center for Marine Science Research
University of North Carolina at Wilmington

We have gathered here for participating in the North Carolina Coastal Oceanography Symposium. This year - 1987 - is the 40th anniversary of the University of North Carolina at Wilmington. It is a major milestone in the history of this Institution. This Oceanography Symposium is, therefore, conducted in honor of the celebration of the 40th anniversary of this youthful, vibrant and growing University in the UNC-system. As you know, this University is fondly labelled as the "UNC - By the Sea" since the campus is located adjacent to the western edge of the Atlantic Ocean and marine science is offered as an integral part of the overall curriculum.

"Marine science", by definition, is an interdisciplinary academic field wherein basic subjects like Chemistry, Physics, Geology, Biology and Biotechnology merge with some measure of equilibrium that leads toward a sound understanding of not only what is there in the coastal environment but also in terms of what is going on with reference to coastal processes and what impact 'MAN' has on this resourceful environment. The quotation in the Symposium announcement clearly points out "Support of Basic Marine Research is vital if we are to understand the global oceans, to predict the behavior of the marine environment, to exploit (wisely) the sea's resources." In North Carolina we have a strong marine educational and research program on the University campuses, in the Federal and State Fisheries Laboratories and in industry-sponsored centers of research such as the Marine Corrosion Laboratory at Wrightsville Beach. Our strength in marine science is really remarkable if we take into account the manpower, productivity and facilities in the various academic marine programs in NCSU, UNC-Chapel Hill, Duke University, ECU and UNCW. Many of the active marine scientists in North Carolina have assembled here today to report on what we are doing and what direction we are going during this symposium. It is pleasant that we have chosen to hold this conference in the autumn when the weather is much more conducive and those of you who drove from the western part of the state also had a chance to see the colors of the trees.

Let me at this point inform you how the idea of holding the Coastal Oceanography Symposium came about. About two years ago, soon after the Marine Expo '85, I was at the Duke University Marine Laboratory at Beaufort to attend the annual meeting of the North Carolina Oceanographers. This meeting was coordinated by the Duke-UNC Oceanography Consortium which is also one of the co-sponsors of this symposium. I found in this meeting that

North Carolina Oceanographers are conducting research all over the World Oceans - off Peru in South America, in Alaskan, Norwegian and Swedish Fjords, in the Indian Ocean, in the Great Lakes, and in the African Lakes and in the frigid waters of Antarctica, apart from investigating the North Carolina waters. The idea of conducting a symposium, exclusively dedicated to North Carolina waters, came up in my discussions with some of the scientists. Subsequently, Provost Dr. Charles Cahill of the University of North Carolina at Wilmington appointed me to serve on the UNC-Marine Science Coordinating Committee that is chaired by Dr. Jasper Memory, Vice President for Research at the University of North Carolina. I received full support from this committee to make plans for this symposium. On a pleasant afternoon, Dr. Pietrafesa of North Carolina State University, and I drove up to the UNC General Administration in Chapel Hill where we met with Dr. Memory who gave his enthusiastic endorsement of the symposium program. I pursued this idea further and as a consequence, a plan was proposed to bring together not only academic marine scientists and students in the University campuses but also managers and scientists from the State and Federal Fisheries Laboratories in North Carolina, and representatives from Research Triangle Institute, N. C. Aquarium, private foundations and corporations such as 'Maricultura' at Wrightsville Beach. Today, this dream has come true and the event is now real and, therefore, we are here to spend three days of activities revolving around scientific presentations, discussions, and dialogues all for the uplift of our knowledge about the rivers, estuaries, marshes, beaches, barrier islands, bays and the open ocean along the vast stretch of the coast of North Carolina. We have appropriately selected a "logo" for this Oceanography Symposium a satellite photograph of North Carolina with the Gulf Stream flowing along the coast. This satellite picture is portrayed on the front page of this Symposium volume.

In recent years, the impact of man's activities has endangered not only the aquatic environment but also led to depletion of the ozone-layers twelve miles up in the Earth's atmosphere. Thanks to the new International Treaty that will hopefully help us to reduce the ozone-eating chemicals almost in half by the year 2000. We, the marine scientists, should move in this direction to take appropriate measures to reduce pollution in North Carolina waters in excessive running of storm waters and dumping of wastes (sewage, hydrocarbons, heavy metals, even low-level radioactive waste) that threaten the breeding areas of fin fishes and shell fishes such as oysters, shrimps and blue crabs. Marine seafood industry contributes significantly to the economy of the State of North Carolina. With the advent of marine biotechnology and genetic engineering, we are examining the possibility of producing new marine-based pharmaceutical, innovative methods to clean up marine pollution and possibly new anti-fouling techniques to protect marine vessels from biodeterioration. There are enormous potentials for aquaculture. Let me give one example of the application of biotechnology. Commercially important fishes such as salmon, trout and bass produce millions of eggs in captivity. These eggs hatch and develop only in the right environmental conditions. When the fertilized fish eggs are exposed briefly for a few minutes to high hydrostatic pressure or abnormal temperature, the mitotic division takes place only in the nucleus (a phenomenon known as Karyokinesis) but not in the cytoplasm (cytokinesis). Therefore, we are able to produce polyploid eggs. When these eggs develop, they grow much faster and attain significantly larger final size. However, these fishes become sterile. This culture method increases cultivated biomass for human food. Our Key Note Speaker, Dr. Rita Colwell from the University of Maryland will speak on this theme of marine biotechnology during the Symposium Banquet this evening.

The Symposium has brought under one roof both the coastal marine scientists and policy makers to review the state of the art in the field of coastal oceanography in North Carolina. The proceedings of this Symposium incorporates researches along the shoreline, studies in the Continental Shelf and continental margin and research in the field of biotechnology. The Symposium Volume, containing the presentations of several North Carolina marine scientists, will undoubtedly serve as a reference book for students, researchers and program managers in the coastal environment of North Carolina, and may also serve as a stimulus for other coastal states to make a similar approach to review their current activities in Coastal Oceanography.

SYMPOSIUM KEYNOTE ADDRESS

"Marine Biotechnology: Its Scope in National Perspectives"

Rita Colwell
Director, Maryland Biotechnology Institute
University of Maryland
Adelphi, Maryland 20783

I am delighted to be here tonight to talk about my favorite topic, marine biotechnology, and the future of marine science, which I think is really very exciting. In the past couple of hundred years, marine scientists and especially marine biologists, have amassed fantastic amounts of information and literature. Marine biologists in general are the type of individuals who spend time at the seashore, not just counting clam shells, looking or thinking great thoughts. They are people who make very precise observations and record in literature various kinds of activities of sea animals and behavior, as well as the physiology and some very interesting phenomena with regard to chemical inhibitors and various kinds of pharmacological substances. We now find ourselves, in 1987, at the point where we can, with genetic manipulation, take advantage of the opportunities of the substances produced by marine plants and animals in a way that is environmentally protective and actually commercially productive. I will explain tonight, as I go along, some of the areas where molecular genetics and the development of genetic engineering will change marine biology in a very positive way. Let us harvest the sea so that we will not deplete the resources but perhaps make use of genome. I will talk about what I call a new era in biotechnology, mainly, the marine biotechnology aspect.

What really changes everything is the ability to recombine genes; that is, you take the chromosome of DNA, whether it is from plants, seaweed, or from the seasquirt or coral. To purify the DNA with specific enzymes, one can cling to DNA and then introduce the DNA into plasmid DNA, which is extra-chromosomal DNA carried by a bacterium, and introduce these genes (from whatever source) into a bacterium whereby the expression of the gene successfully permits them the production of whatever compound the original genes code; that is, whatever enzyme or enzyme activity. We have such things as the insulin produced, in the case of medical biotechnology, in pancreas cells coded by the DNA group. We can then put those genes into plasmids, into a bacterium or, as has been done in the past several years, we can have production in the test tube or in flasks or in culture, in this case, insulin.

In marine systems, there are fascinating compounds; for example, the tunicates, one group of which I will discuss a little bit in more detail. The didemnins produce a compound which turns out to have a anti-leukemic potential. So, it means that we now can extract DNA from these tunicates and insert, by appropriate cloning, the genes into bacteria and produce large amounts of what may be a very powerful agent against human leukemia.

Let me cover several areas. First of all, the applications of biotechnology in marine science cover such wide topics or wide subareas as the application in aquaculture, or in fish farming. I will describe, using examples of shellfish, the potential of genetic engineering in the marine sciences. Another area is in marine pharmacology, to which I alluded very briefly, and the ability to clone genes for the production of specific compounds, antibiotics, anti-leukemic and anti-viral agents. Another area is in the application of molecular genetics through the production of bacteria capable of degrading toxic chemicals in their release to the marine environment. One would want to use marine bacteria into which the genes for degradation of toxic chemical have been introduced. So, these are areas that are just now being exploited, just now being considered and represent some very exciting, new potentials for the marine biologists.

Let us look at the work of Dan Morris and his colleagues in Santa Barbara, on Abalone. What Dan has done with the Abalone is to control the series of events such that he and his crew will be able to probe Abalone in laboratory culture. The first step is to get a laboratory culture of the larvae. What Dan and his group discovered was that the addition of a drop or two of catalase to an adult Abalone would induce spawning. What it does is synchronize the release into the water of the eggs and sperm, which subsequently are fertilized and the larvae then can be further studied. What it means is that you can have a group of larvae in essentially the same stage of development. Now, one of the things that they observed is that the Abalone always seem to be in association with crusts of coral and he found that, in fact, the production of a compound attractive to the Abalone larvae was gamma acid; he and his crew found that the release of the gamma served as an attractant to the larvae so that they would settle and then metamorphose. This group has been able to track down the important initial steps in the development of the Abalone. Subsequently, they are in the process of cloning the genes which code for the growth hormone in mollusks (in this case, the Abalone) so that the ability to introduce multiple copies of the growth hormone, either through multiple copy or through production externally of bacteria and then apply it to be able to grow larger or a combination of larger and faster growing Abalone. This means we have come closer and closer to a technological approach to the culture, at least, of this particular shellfish.

We at the University of Maryland have been working with the oyster <u>Crassostrea</u> <u>virginica</u>, which has a very interesting life cycle, in that the fertilized egg goes through a swimming larval stage and development stage and then eventually settles. It settles to the surface and then develops into an oyster. In the Chesapeake Bay, we harvested perhaps 10 to 15 million bushels of oysters at the turn of the century; it is down this year half a million bushels of oysters. The irony is that the price has gone up so that we are collecting fewer bushels and consequently, the oysters are worth more. It is a steady state, but this can not go on for long. The difficulty is that we don't quite know why the oyster harvest is declining. However, we are suspicious that it may be related to pollution. The interesting thing is that we are now moving in our knowledge of the development of the oyster that we may, in a few years, be able to produce oysters entirely in the laboratory, entirely in closed culture and under very safe and sanitary conditions so that we would indeed have, maybe in four to five years, oysters that are truly safe to eat because they will be entirely free of virus and potential _vibrios_ and pathogens. But what have we learned?

Let me share this with you tonight. We have found that the stages of an oyster are controlled by a variety of chemicals. The oyster becomes a competent larva then undergoes searching behavior. They will crawl along a surface or swim and eventually, by some trigger, settle, cement themselves to the surface and then undergo metamorphosis. We know that the initial stages are controlled by L DOPA which is a compound that sounds very familiar because, indeed, it is a neurotransmitter and is used to treat Parkinsonism in humans. In the first few stages the competent larvae extend the foot and search; during the cementation stage the L DOPA plays a role. In the medical approach to this, epinephrine and norepinephrine are important and we also know that tyramine and some derivatives are effective in inducing settling behavior. What we have discovered is that there is a bacterium on the surface to which the oyster is attracted, adheres and develops on the surface. The larvae are attracted to that surface by the chemical compound L DOPA released by the bacterium. This is the sensory organ on the oyster and it is able, by chemotactile capabilities, to sense the L DOPA. This is very dramatic when you observe this under a microscope. We are producing a video which, is going to be very interesting, where you can actually see the larvae swimming about. The L DOPA is released into the water, the larvae pause for a moment, begin to settle down, then search for the surface, fix themselves to become a staff, and then settle on the bacteria on the surface. What we have been able to do is work out the system in determining the bacterium playing this major role in the development of the oyster. We discovered that the bacteria were always associated with successful oyster settlement and development; bacteria, then, produce the pigment melanin. We were also able to, by UV irradiation, produce mutants. By a series of experiments, we were able to show that the L DOPA and its relatives were produced by bacteria, the melanin. These are intermediates in the production of melanin and are produced by the bacteria but, in fact, L DOPA is active in producing larvae settlement. The experiments we did were simply to add them to flasks with glass slides or sterilized oyster shell surfaces then dip into the bacterial culture, into L DOPA, into the melanin sucrinate from the bacterium. We used a variety of bacterium. We were able to determine by the experiments that we can get as many as 30 to settle in 24 hours on a surface coated with the pigment from this bacterium.

I am leading up to the fact that we have been able to work out a mechanism for controlling the developmental cycle of the oyster. We know that the larvae sense the L DOPA and get the cue from bacteria on the surface; the larvae begin to swim, crawl and search for a surface and the biofilm polymers cue that the surface is suitable for attachment and settlement to the surface and, ultimately, for metamorphosis. We have done experiments in the field and some of the things that we have learned in the laboratory do not work in the field. Initial experiments were done a couple of years ago in Washington state, where they have very active closed-culture oysters and these oyster shells were coated with a bacterium. You can see the electron micrograph of an oyster shell surface with the bacterium, the LST, which we know produces the dopamine - this is after about three days on the surface; that is just about right or ready for oyster attachment. We added the shell then, to the tanks to which the oyster larvae were present. We were able to increase settlement by 30 to 50%; that means we were able to induce the larvae to settle and to move to the next stage in the development of the staff. At the University of Maryland this past summer, we took these results out into the field because we were very much encouraged; we were able to show these tests in the Chesapeake Bay. Within 40 or 50 minutes, we can induce almost 100% of the larvae to go from the simple swimming stage to the search stage and settlement. We were able to obtain a settlement onto the LST film within a matter of 72 hours. We had several thousand larvae to settle onto the surface and undergo further development. We were able to prove that, in fact, two factors were very important: pigment, that is the dopamine, and what we call the polysaccharide adhesive viscous ethylpolymer. This is very important in the further development because it appears that epinephrine and norepinephrine concentrate in that surface. What we were able to show in the field is that the number of staff per shell, using the LST sucrinate, was very much increased over a given period of time. Therefore, there is no question that we can attract the larvae, capture them and improve the settlement. We hope to be able to increase the number of adult oysters for a given area in the Chesapeake Bay.

What does this have to do with biotechnology? First of all, we are in the midst of cloning the genes that are involved in the tyrosine so that we can produce abundant amounts of the attractive, so that we can provide this in the oyster beds in the Chesapeake Bay. Secondly, the adhesive material itself has turned out to be fascinating. It is produced by the bacterium as it adheres and glues itself to the surface. It turns out to be a "super glue" and, in fact, we have patented it. We are in the process now of developing this adhesive for use in patching up fiberglass and other structures that are exposed to seawater. This adhesion to surfaces is very interesting because there are several steps that occur. First, there is the cloning of organic matter to which the bacteria, like the LST, is attracted. This is the other side of biofouling or surface attraction, where we want to enhance attraction to the larvae. On the other hand, we want to know the steps in biofouling and maybe interfere with those steps so that we can prevent the attachment of barnacles. This is a selective kind of settlement and attachment, as it were, to use biotechnology on the one hand to attract oyster larvae specifically and on the other hand to figure out the steps in biofouling so that we can perhaps engineer a bacterium which doesn't produce the attractive larvae so that we can coat the surface of a sailboat with this material to prevent biofouling. From a scanning EM picture on a slide dipped in seawater for just a minute or two, you can see immediately that there is an organic film which forms, followed by bacteria which produces a polysaccharide and glue the bacteria and LST. We find other species of algae produce a very high alginic acid content; about 50% of the polysaccharide material produced by this bacterium is an alginate. The characteristics are very interesting because it turns out that the viscosity of the LST is very high. This particular LST is polysaccharide; it remains as a gel up to about 50° or 60° C, which is quite good because either melt at about 30° C, and gelatin melts at about 20° C. So, it has some very interesting properties other than simply being a "super glue".

We are using the techniques of genetic engineering to clone the genes for the production and to get multiple copies of genes and speed up the production so that we can move into commercial production of the polysaccharide.

Let me switch gears for a minute. I talked about one aspect; that is biotechnology applied to aquaculture. Then, I talked a little bit about seaweed and seaweed culture because there is a commercially very lucrative area for the individual who is able to control the genetics of seaweed. There are algae, either alginates and carrageena, which are very important as foodstuffs because they are the extenders and blenders of puddings and ice cream. They represent essentially a billion-dollar-a-year industry, in the food industry. It is collected by the old-fashioned technique of raking it over the side and singularly by pulling it up by dredges. It would be very nice if we could, in culture, grow the seaweed under controlled conditions for abundant production of alginates, using the techniques that are used in agriculture; that is, either by the tea plasmin that is well known for introducing genes, including the "lux" gene - the gene that causes production of light and we now have tobacco plants in light and dark. Using those techniques we can also, in seaweeds, be able to protoplast, fuse or introduce genetically. Fusions of protoplasts in plants have been done whereby the cell wall is removed and by the addition of polyethyleneglycol (what we use in automobile antifreeze) that causes the membrane to coalesce. One can then get fused genomes of two different plants into a single cell. This has been done in the case of higher plants, as in the tomato.

Let us discuss what is being done with seaweed. You can take seaweeds of two different types, remove the cell walls, fuse the econoclasts and develop a hybrid. This is a wild type seaweed. This is the work of Don Chaney, where protoplasts have been produced. This is the green mutant and shown here in the lower right is the fusion of the two: the wild type and the green mutant. Other scientists working in fronds have been able to carry the protoplast yields to a much greater extent and have been able to get a large number of protoplasts and to get protoplast division. This is the work recorded at the Roscoff Laboratory in France. We are moving to a capability of producing seaweed adequately in the laboratory and eventually in the field and to be able to select, with genetic engineering, seaweeds producing large amounts of carrageena, which may be commercially valuable.

In the hydrothermal vents of the deep sea, there are bacteria that will tolerate very high temperatures and very high pressures. These bacteria will probably provide enzymes of unusual specific activities, activities against such things as yet untested. There are potentials for new genes or genetic material that code for production of enzymes that are stable at perhaps 160°, particularly, proteases, for production of compounds in commercial procedures. There is a whole series of enzymatic mechanisms, enzyme potential for commercial application. In fact, what we are doing now is to determine whether we can transfer plasmids from one bacterium to another under pressure using bacterium grown only under high hydrostatic pressure and low temperature, but eventually under high temperature as well. You may say, "Well, what is the point of this?" There are a variety of bacteria that have been isolated from the deep sea which grow only under high hydrostatic pressure and if we are going to harvest the functioning enzymes, that is, the genes that code the enzymes and to clone those genes into bacteria we need to have a high-pressure system. We are in the process of developing the bacteria system into which these genes can be cloned or subsequently used.

Let me focus on yet another area, marine pharmacology, a fascinating area which I think immediately poses tremendous commercial potential. How does one go about harvesting from the sea potential antibiotics, anti-virals and anti-leukemics? A sensible way would be to look for those organisms which demonstrate, as in this case, the clown fish, the ability to withstand the toxins of the stinging anemones. There are two reasons: first is to understand the toxin that is produced; the second is to understand how the fish withstands it. Is it a specific antibody or some mechanism by which the fish is immune to the toxin? Either way, there is a commercially important compound to be studied.

The halitoxins produced by the octopus have some potential because of the activities they induce in mammals. The halitoxin blocks the nerve/muscle junction, that can potentially be a great analgesic if modified. Saxitoxin and tetrotoxin are interesting toxins. Tetrotoxin is particularly interesting and I will discuss that in a moment. First, let me point out one of the really bizarre toxins produced by the palythorn. The palytoxin is a very complicated molecule and a very, very large molecule which is highly toxic. It is known to be more lethal than the clostidium marginitis toxin so that micrograms of it, theoretically, could "do in" a small city perhaps the size of Wilmington, if deposited in the water supply. Palytoxin was first known because the natives in Hawaii and the outer islands would dip their spears into the polyp and if invaders came onto the island, they would find that one slip of the spear was always instantaneous death. The interesting thing is that recently the group (Moore and his colleagues) have been collecting the polyps and they were told that the legend was that they really ought not go near those reefs where those particular kinds of sea organisms lived because bad things would happen to them. Well, they went anyway and the natives were very upset about this. Mysteriously, the laboratory in the shack burned down and they were told by the natives, "See, you really ought not to have gone there." Of course, we think it is probably because the natives did not want them there. But, in any case, the palythorn and the playtoxin offer the potential because, if it is modified, it could possibly be a very powerful analgesic, much like the tetrotoxin produced by the puffer fish. The tetrotoxin is actually produced by a family of the tetrotoxin fishes. What is very interesting is that the tetrotoxin not only acts on the nerve endings, but also directly on the heart and the actions are very similar to those of local anesthetics. It is like procaine and cocaine in that it selectively blocks the sodium ion transport. We have found that the Japanese have reported and we have confirmed that it is the bacterium on the puffer fish which actually produces the tetrotoxin. We just recently published that marine vibrios produce this tetrotoxin, which turns out to be a sodium-channel blocker. So the tetrotoxin has been used, actually, in Japan as an anesthetic for the treatment of neurotrophic leprosy and also in terminal cancer cases. Raw applications of tetrotoxin are very effective in pain killing. Much caution must be used,as the Japanese have found from those who use tetrotoxin as a recreational drug (which I do not recommend). If you eat puffer fish that has tetrotoxin, a little bit too much and it is "Sayonara!". In any case, the tetrotoxin is one of the interesting potential toxins, the genes for which could be cloned and now that we know that tetrotoxin-like compounds are produced by marine vibrios. We can now go after cloning the genes for the production of this compound.

The structure of tetrotoxin is very much like saxitoxin. It is suspected that bacteria also produce saxitoxin. We now have the potential of being able to deal with some of these compounds in a way that can be beneficial to man.

From tunicates there are a variety of didemnins that produce structures as fairly complicated but have been confirmed as being active against the leukemia agent, the leukemia virus. The result of some in vitro activities of didemnins A and B against P38 leukemia in mice is of interest. They have been able to get some kind of survival and actually cause regression of tumors. The didemnins have an anti-viral activity against the Herpes simplex virus. The didemnins are now in clinical trial at the National Cancer Institute. The potential of cloning the genes for the production of didemnins is complicated but, at least, now it is possible.

There are other toxins. the ecclesium which grazes on algae which produces the compound, ecclesiopsin. The ecclesiopsin is noted, along with retsin and lariatin, as potential drugs of value. Lopatoxin is another one of the toxins, produced by the seawhip, which has been carried to some pharmacological use and application. Some of the algae produce these compounds. These beautiful organisms also produce pharmacologically reactive substances.

The important point to make is that, up until now, to go out and actually harvest great masses on a continual, perpetual, constant, reliable basis was not possible. Therefore, to utilize the marine drugs really was not within the realm of the practicum until the advent of genetic engineering. Now, we do not want to harvest and deplete our whole resource. We simply want to gather some of the animals, some of the coral, some of the seawhips, etc.; extract the DNA, clone the genes, introduce them into yeast or bacterium and produce ad lib in the amounts that we need.

One of the actually effective and commercially productive compounds is amarosponsin produced by a marine amarosponsin which is active against flies. It was first discovered that it was active against insects because the Japanese fishermen who used the compounds as bait noticed that when the dead worms lay in the floor of the boats and flies landed on them, they were killed almost instantly. In fact, the amorosponsin was extracted by some of the biologists who were interested in this phenomenon and subsequently it was shown that the amorosponsin is very active against the larvae and those treated with amorosponsin reacted. The amorosponsin under the grand name of cartabhydrochloride is used effectively in Japan. It does not seem to induce tolerance and it also does not seem to be effective or active against mammals. Therefore, it is a very good insecticide to use.

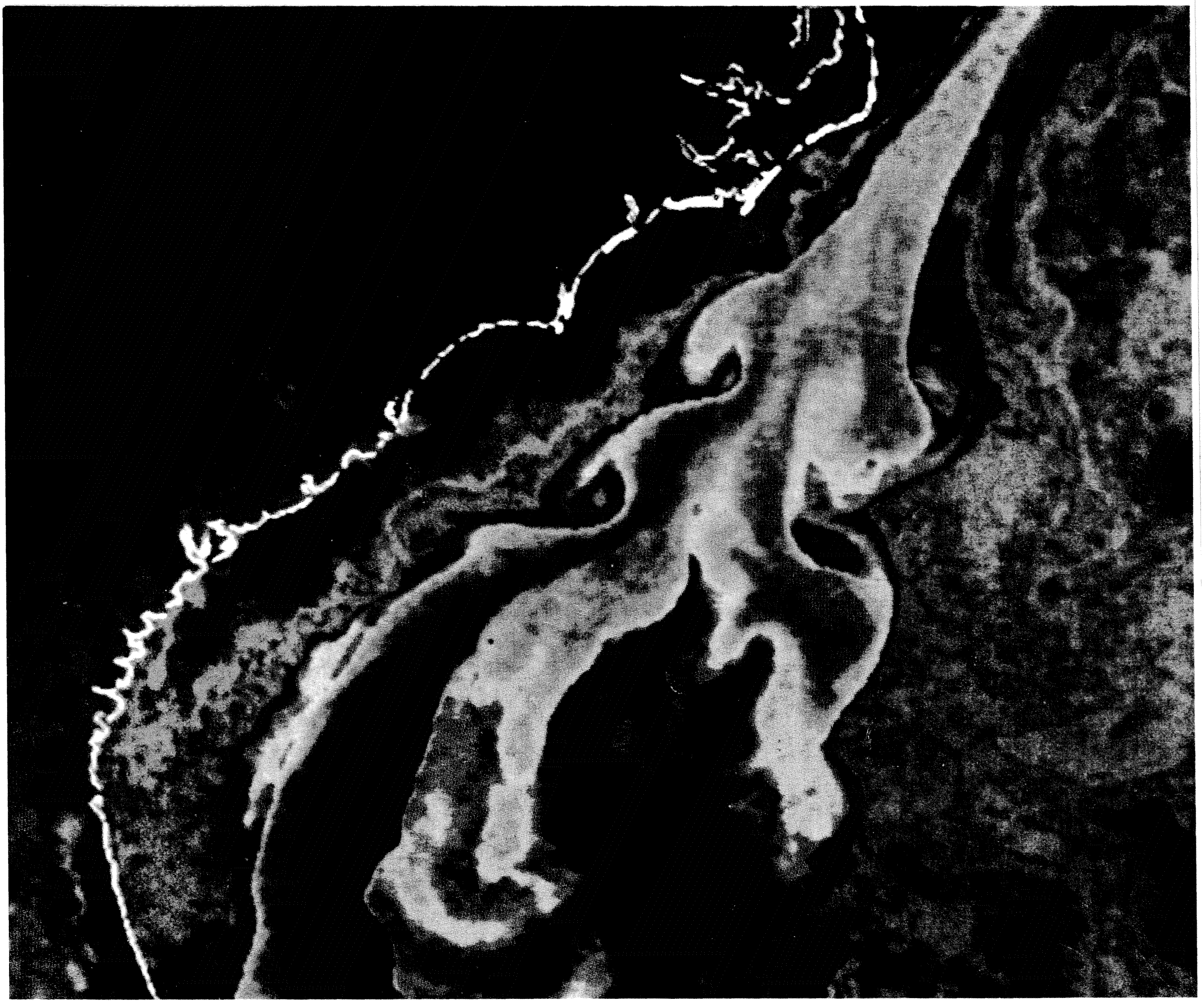
Halitoxin is another one of the compounds that is particularly interesting because it allows me, then, to go to another aspect of biotechnology. Some of the very unusual chemicals that are produced in the sea: chlorinating compounds, ruminative compounds, terpines, suspaterpines, etc., may have some value commercially in the chemical industry. These are produced by a variety of interesting invertebrates. We now have applications of biotechnology in the pharmaceuticals, industrial chemicals, as biodegradation agents, in aquaculture and as application and prevention in biofouling. The chemicals include the alginates, carrageena, chitin, adhesives, emulsifiers, enzymes, etc. These are already in some way, shape or form, industrial chemicals that are produced from marine sources; though as yet in small amounts, they represent potential large industries. The Calgon Company does produce the alginates and carrageena and they are very busy developing a biotechnological approach to the production of those compounds.

There has been, perhaps, an overselling of the capacity of biotechnology, at least in this early stage and certainly in marine biotechnology. What we need to have is a long-range perspective, that is, to understand that the payoff really, genuinely, unequivocally is there; but, whether it is immediate, mid-term or long-term is really not clear. The research we need to do has to be a good mix of applied and basic so that we can understand the fundamental mechanisms. First of all, we have to find the chromosomes in seaweeds. Then we must do some fingerprinting of the DNA to understand the relationship of the DNA within the seaweeds. We can eventually be able to produce the compounds that we will bring to market and make the commercial capability a reality. What we do not want to do is misuse the capability of genetic engineering so that we get an end result we did not expect and one that we may not want to live with. Therefore, we want to do our cloning in a sensible, effective way and do our direct applications in a meaningful way.

I would say that there is no question that the marine environment offers to those of us who are interested scientifically, an absolutely beautiful time to be working, especially in the genetics of marine organisms; to understand how they function, how they are able to survive and metabolize in the regions of the deep sea, and to find suddenly marine biology, which we went into because we love the beauty of the sea useful in a very environmentally protective way, can provide us with new drugs to cure cancer, new antibiotics to cure disease, new commercial chemicals, potential for enhancing the protein production of shell fisheries, and even to deal with some of the pollution problems and all the messes that we have already gotten ourselves into. I always say that the investment in marine biotechnology is a sensible one. I am not sure that it is wise to move very fast with the tremendous amounts of money as such an effort was made for the production of insulin and some of the "tumor necrotic" factories. I would certainly say that a wise investment and a reasonable level that allows the training of molecular geneticists capable of dealing with marine systems, is certainly an investment in the future of the United States.

There are several points to be made before I close. First, the Japanese are investing $18 to $36 million in marine biotechnology, in everything from mariculture to deep sea hydrothermal vents, to molecular biology. They have done their market analysis and know the future is there. This is a country that depends on the sea for the source of their food. I would say that in the United States we should be investing much more funds than we presently are. The National Science Foundation has started appropriating about a million dollars in marine biotechnology. North Carolina is certainly one of the states that should be putting together a program in marine biotechnology for a center of excellence. I think it makes good sense because, much like the state of Maryland, the fisheries are very important. In the Chesapeake Bay in Maryland, the fisheries represent a billion dollars a year to the state income from a variety of aspects of the marine resources. Clearly, this is a great investment and it makes good sense for the state.

We have a very serious problem. You <u>cannot</u> take a marine biologist and say, "Do biotechnology.". What you have to do, what we all <u>have</u> to do is train a new kind of molecular biologist, someone who understands marine systems. Again, you cannot just take a molecular biologist, throw him into seawater and say, "Fine, now you can do molecular biology in seawater." As we all know very well marine systems are different. DNA is coded the same and the enzymes behave the same. However, to get marine organisms to grow you must know and do much more. We need to train the molecular biologist who can deal with marine systems. At the University of Maryland we are, in fact, actively involved in doing just that through the University Research Initiative for turning out the molecular biologists who are trained in marine biotechnology.



This AVHRR image, taken from the orbiting NOAA-6 Satellite on April 23, 1980, was chosen as the symposium logo for the Marine Expo '87 Coastal Oceanography Symposium at UNC Wilmington and is a mesoscale view of the Carolina Capes and the South Atlantic Bight. Identifiable are the capes of the Carolinas at the top, the Outer Banks and the chain of barrier islands, Pamlico Sound, Cape Fear River, cold waters (purples) in the North Carolina bays, and the warm Gulf Stream (reds) with filaments protruding over the Carolina Continental Shelf. The path of the Gulf Stream resembles Ben Franklin's original charts, printed for the General Post Office 200 years ago and now accurately pictured in infrared with the advent of modern satellite oceanography. The impact of the Gulf Stream on the biological productivity, larval recruitment, and coastal fisheries of the Carolinas and the South Atlantic Bight poses new challenges for discovery and research. While the photo shows the Gulf Stream in two dimensions, it is in fact three dimensional. Research in the sea using manned submersibles, remotely operated vehicles, and scuba will permit measurements, experiments, and observations that can define the third dimension.

-- R. Y. George and A. W. Hulbert

PART I. STUDIES ON NORTH CAROLINA SHORELINE

Chapter 1. Land/Sea Interaction

Chairperson - Dr. Douglas Rader

RAINWATER-SURFACE WATER INTERACTIONS IN SOUTHEASTERN NORTH CAROLINA

Joan D. Willey, John R. Kucklick and G. Brooks Avery, Jr.
Department of Chemistry
University of North Carolina at Wilmington
Wilmington, North Carolina 28403-3297

ABSTRACT

Southeastern North Carolina has a diversity of surface water types which receive rainwater with widely varying chemical composition. Lakewater types range from alkaline hard water to acidic blackwater with high organic content. River waters include a turbid piedmont river, organic rich coastal plain rivers, and almost pure water sandhills streams. Seawater is another distinct water type in this area. Rainwater composition varies from almost pure or slightly salty water in coastal storms ($pH \geq 4.8$), to very acidic ($pH \leq 4.0$) high nitrate and sulfate rain from continental storms and local thunderstorms. Because of the diversity of water types and the variability of rainwater composition, comments about rainwater impacts must be made with a specific water type in mind. Three possible impacts include pH decrease (to $pH < 5.4$), which laboratory experiments indicate could result from an 8% dilution by rainwater of some surface waters, nitrate input from rainwater which can significantly increase this nutrient in surface waters; and deposition of sea salt. Deposition of large amounts of seasalt is restricted to within 10 km of the surf zone; catastrophic storms like Hurricane Diana can contribute the equivalent of several years of salt deposition in a single storm.

INTRODUCTION

Southeastern North Carolina has many different types of surface waters which greatly enhance the quality of life in this region. In part, because of this resource, Southeastern North Carolina has enjoyed extensive industrial and population growth during the last decade, which brings with it increased challenges with respect to environmental protection. One of the principle threats to water quality in the Northeastern United States is acidification, which probably results from the sulfuric acid in acid rain (Galloway, 1984). Southeastern North Carolina at times receives very acidic rain with high sulfate and nitrate concentrations (Willey et al., 1988). The most acidic rain in this geographical region in 1983-1987 was summer rain from two types of storms: continental frontal or low pressure systems (average pH = 4.00) and local thunderstorms (average pH = 3.99). This area also received much less acidic rain (average pH = 4.84) with high salt content from coastal storms (Willey et al., 1988). There is therefore reason to consider possible impacts from rainwater on surface water quality in this geographical region.

Anthropogenic emissions of SO_2 and NO_x into the atmosphere exceed those emissions from natural sources by at least a factor of ten (Galloway and Whelpdale, 1980; Robinson, 1984), so it is not surprising that this large addition would eventually have some impact. The exact timing of the onset of this increase in anthropogenic sulfur emission is uncertain; estimates vary depending on method of determination from 1900 (Fay et al., 1986; Mayewski et al., 1986) to 1930 (Holdren et al., 1984). Atmospheric deposition of sulfate is often the primary source of sulfate to surface waters in North America (Galloway, 1984; Sullivan et al., 1988). Nitrate is also a significant and increasing component of rain in North America and Western Europe (Galloway and Likens, 1981; Brimblecombe and Stedman, 1982).

There are some indications of change in the rain and surface waters in the Southeastern United States, although this region has not been as extensively studied as the Northeastern United States or Western Europe. The pH of rainwater has probably decreased (Likens and Butler, 1981; Hansen and Hidy, 1982), and sulfate and nitrate concentrations in rainwater have probably increased over the last several decades (Brimblecombe and Stedman, 1982; Galloway et al., 1984). The concentrations of dissolved sulfate and nitrate in streams and rivers in the Southeastern US may be increasing also (Brezonik et al., 1980; Burns et al., 1981; Galloway et al., 1983; Smith and Alexander, 1983; Turk, 1983; Smith et al., 1987). These historical changes are difficult to prove because of the differences in analytical methods used to generate data several decades ago (Church, 1984), and the lack of a long term data base. The Eastern Lakes Survey recently conducted by the US Environmental Protection Agency (Landers et al., 1988) included two Southeastern regions: the Southern Blue Ridge Province, which is geologically very different than Eastern North Carolina, and Florida. The Florida lakes showed a great diversity in chemical composition (Eilers et al., 1988), similar to the diversity observed in the current North Carolina study. No coastal plain North or South Carolina lakes were studied in the EPA Survey.

Several chemical parameters are useful in evaluating surface water or rain water. The pH of water in equilibrium with CO_2 in air is approximately 5.6; natural sources of acidity lower the pH of uncontaminated rainwater to approximately 4.8 to 5.0 (Charlson and Rodhe, 1982; Galloway et al., 1982). Alkalinity is a measure of buffering capacity, or resistance to a pH decrease, because a primary component of alkalinity in natural waters is bicarbonate. Alkalinity is an important indicator of change in natural waters because alkalinity decreases often precede pH decline (Schindler et al., 1985). The predominant acids in most rainwater are sulfuric acid (H_2SO_4) and nitric acid (HNO_3), which come from the gaseous precursors SO_2 and NO_x. Measurement of hydrogen ion, sulfate and nitrate concentrations, followed by ion balance calculations, indicate the presence of these strong acids. Sulfate concentrations in coastal areas must be corrected by subtracting the sulfate that is contributed by seaspray. This process is accomplished assuming that all the chloride in coastal rainwater comes from seaspray, and seasalt sulfate occurs in a constant ratio to chloride in rainwater (Gambell and Fisher, 1966; Cogbill and Likens, 1974; Gorham et al., 1984). Rainwater is often quite acidic, however it is usually very poorly buffered. The impact of sulfate versus nitrate ions on natural water systems is different because nitrate is a nutrient which tends to be quickly utilized in soils and surface waters, and does not accumulate (Galloway, 1984). Sulfate is not utilized as extensively as nitrate. Soils have a limited capacity for retaining sulfate; when this limit is exceeded, sulfate accumulates in natural waters (Galloway, 1984).

Three possible impacts of rainwater on surface water are considered in this study:

1. Acidification is one threat; when surface water pH values fall below 5.4, survival of many fish populations becomes threatened although primary productivity does not always decrease (Schindler et al., 1985). Certain fish are able to tolerate lower pH water in naturally acid lakes (Patrick et al., 1981). Invertebrate communities change below pH 6.0 in acid sensitive regions of North America (Schindler, 1988). Transitory pH decreases have been reported in a South Carolina Piedmont watershed and lake system after individual storm events, although soil buffering prevented permanent changes over the three year time period of the study (Elzerman, 1983). A study of five South Carolina Piedmont lakes also found soil buffering to be sufficient to prevent pH decrease below 7.0 in lake waters (Talbot and Elzerman, 1985).

2. Nutrient addition is also a possible impact. Enhancement of primary productivity has been observed as a result of the addition of rainwater nitrate to coastal North Carolina surface seawater (Paerl, 1985). Nitrate input from rain is an important source of this nutrient for many surface waters (Likens and Bormann, 1974; Gorham et al., 1985), including rivers and sounds in Eastern North Carolina (Smith et al., 1987), and the Chesapeake bay (Fisher et al., 1988).

3. Transport of seasalt by rainwater also poses a potential impact on fresh surface waters in coastal regions (Gorham et al., 1985).

These three potential impacts from rainwater have been evaluated using the following approaches in this work:

1. Possible pH changes have been investigated through laboratory experiments in which synthetic rainwater was mixed with actual surface water samples. Because the

maximum possible impact is of interest, the most acidic rainwater likely to be encountered (pH = 3.0) was used in these mixing experiments. Rainwater with pH < 3.0 has been received in both Wilmington and Morehead City, NC, so pH 3.0 rain is not unrealistic. Deposition of acid is episodic in nature, and not evenly distributed throughout all the storms of a year (Summers et al., 1986). These experiments simulate the most acidic events. Separate experiments were run with nitric and sulfuric acids to determine if pH changes were different for either of these predominant acids in acidic rain.

2. Nutrient impacts have been investigated by calculating the contribution of rainwater nitrate from individual storms to surface water nitrate concentrations assuming complete mixing, and also assuming mixing limited to an 8 cm surface layer. Eight cm was observed to be the average depth of penetration of colored drops falling from 3 m into a 60 cm column of water (10 cm diameter). This 8 cm mixed depth was maintained for only approximately 8 minutes in the absence of wind, so this is an indication of very short term mixing.

3. Transport of salt by rain has been studied by calculating salt deposition from rainwater chloride concentration and rain volume during intense storms and by plotting deposition as a function of distance from the coast.

The surface waters selected for this study (Figure 1) demonstrate the range of chemical compositions and reactivities that occur in this geographical region (Table 1). A surface seawater sample (salinity = $35^{o}/oo$) was collected 20 km southeast of Wrightsville Beach, NC. Three lakes were also sampled. Greenfield Lake is a small (0.51 km^2, maximum depth 3.7 m), eutrophic lake in the city of Wilmington which has contact with limestone. Greenfield Lake is the only lake sampled in this study which undergoes summer stratification. It is heavily utilized for recreational purposes and receives runoff water from the city of Wilmington, including several small ponds on a golf course. Lake Waccamaw is a large (36.2 km^2, maximum depth 3.3 m) mesotrophic lake, which is also used for recreation. Lake Waccamaw has a limestone outcrop along the northern shore and receives water from coastal swamps in addition to runoff from land used for agriculture and timber. Singletary Lake (2.3 km^2, maximum depth 2.7 m) is an acidic brownwater lake (dystrophic) located in an undeveloped area of the Bladen Lakes State Forest. No oligotrophic lakes occur in Southeastern North Carolina. Lake data were obtained from Witzig (1982). Three permanent streams were also sampled in this study. The Cape Fear River, the largest river sampled, is a piedmont river with high sediment load. The Black River is a coastal plain, high-organic black water river. Jordan Creek is a sandhills stream with low organic, low mineral, slightly acidic water. Millipore Milli-Q deionized water was also used as a sample for comparison.

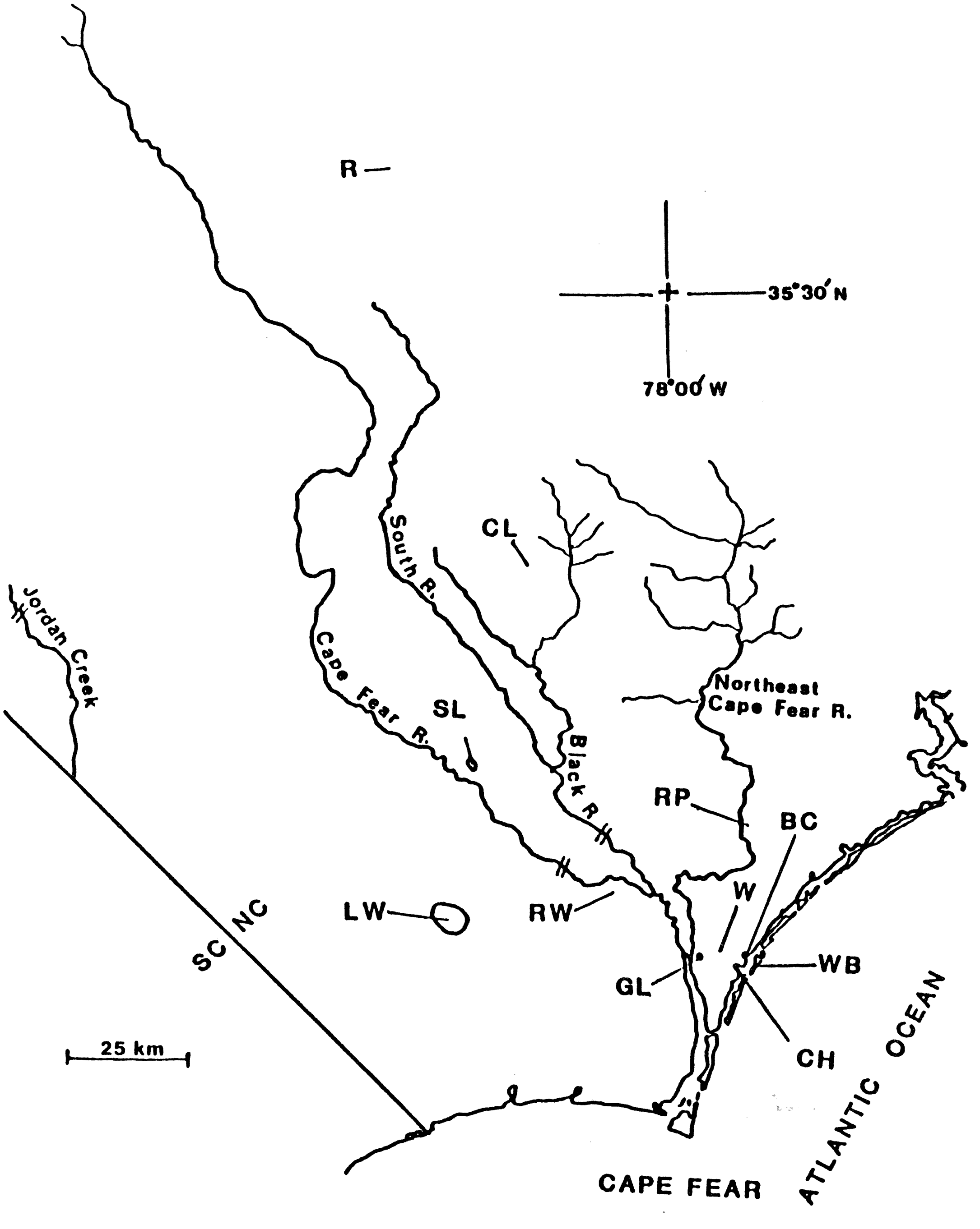


Figure 1. Southeastern North Carolina study area. Rainwater sampling sites are as follows: WB = Wrightsville Beach (two locations, one ocean side and one sound side); CH = Channel Haven; BC = Bradley Creek; W = UNC-Wilmington; RP = Rocky Point; RW = Riegelwood; CL = Clinton; R = Raleigh. The river or stream sampling sites are indicated by //. The three lakes sampled are SL = Singletary Lake; LW = Lake Waccamaw; and GL = Greenfield Lake.

Table 1. Water samples used in experiments and in calculations. Initial pH values are given, along with alkalinity in meq/L (titrated to pH 4.5). The percent of dilution required for pH 3 rainwater to lower the water sample pH to 5.4 is also given (% Rain to pH 5.4); these data are obtained from Figure 2. NR indicates not relevant.

Water Samples	Origin or type	pH	Alkalinity	% Rain to pH 5.4
Cape Fear R.	Piedmont	6.10	0.14	8
Black R.	Coastal Plain	6.27	0.20	11
Jordan Creek	Sandhills	4.50	0.00	NR
Greenfield L.	Eutrophic	7.49	1.38	50
L. Waccamaw	Mesotrophic	6.67	0.20	12
Singletary L.	Dystrophic	3.84	0.00	NR
Seawater	Coastal Surface	8.14	2.33	62
Deionized	Milli-Q	5.60	0.01	1

METHODS

Surface water samples were bucket samples collected from bridges, small boats, or long docks. Samples were collected in the daytime between March and July in 1985 and 1987, stored, refrigerated, and placed in the dark until titrated soon after collection. The rainwater samples collected at Lake Waccamaw were obtained using an automatic Aerochem Metrics Wet-Dry sampler, which opens only during rain events. The rainwater samples collected for the salt transport study were collected using plastic basins set out several hours prior to the rain event; these samples may therefore contain some dry deposition along with the rain sample. pH measurements were made using a Fisher gel-filled electrode standardized with buffers at pH 4 and 7, and checked at pH 3. The chloride measurements used to calculate deposition in Figure 3 were made using an Orion chloride electrode set up for low concentrations. Precision was 9% and the detection limit was 3 uM. Nitrate and sulfate concentrations were determined using ion chromatography. Analytical methods used since 1986 are discussed in more detail in Willey et al. (1988). Titrations were performed by adding mL aliquots of pH 3.0 synthetic rainwater to 100mL of stirred surface water. pH equilibration was achieved within minutes after each addition. Separate titrations were performed using sulfuric and nitric acids, and on filtered (0.45 um pore size) and unfiltered samples. Several titrations were run in duplicate to check reproducibility. Each titration was complete within one hour.

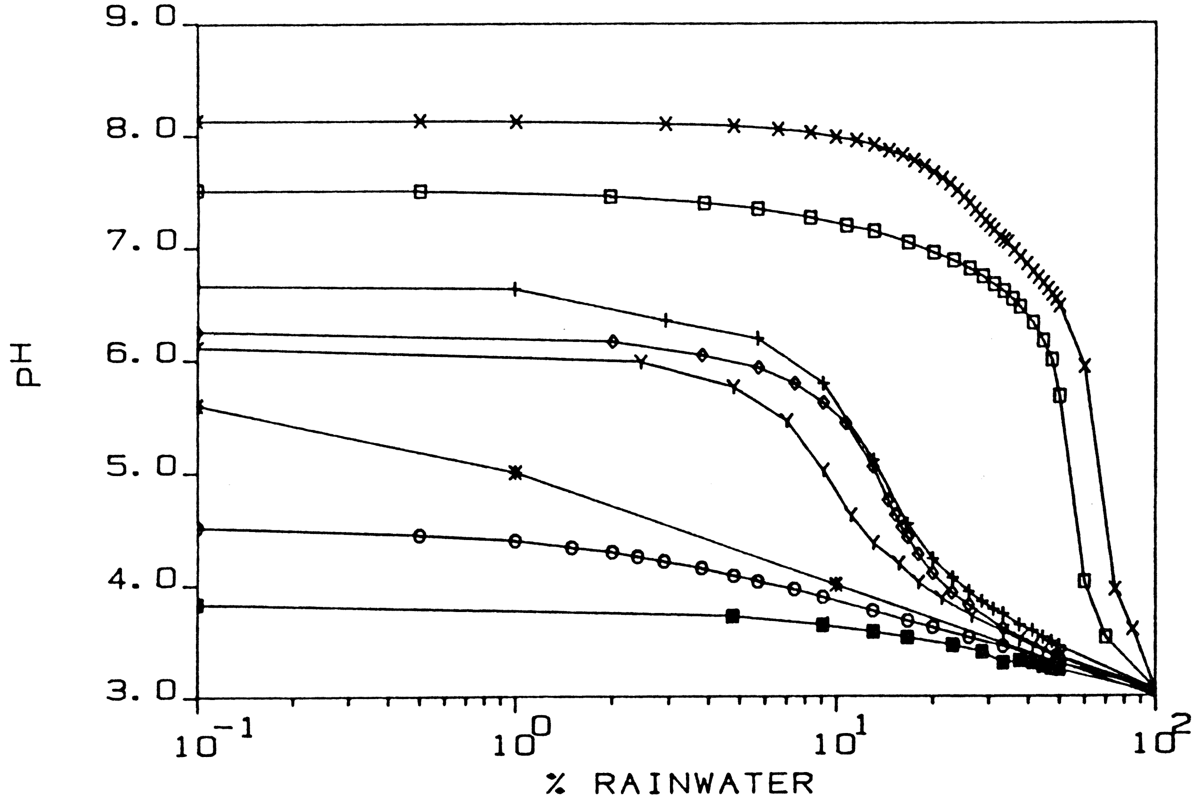


Figure 2. River, lake or seawater pH as a function of amount of synthetic rainwater (pH 3 H_2SO_4) added. The water samples are as follows: X = seawater, ◻ = Greenfield Lake, + = Lake Waccamaw, ◊ = Black River, Y = Cape Fear River, * = deionized water, O = Jordan Creek, and ■ = Singletary Lake.

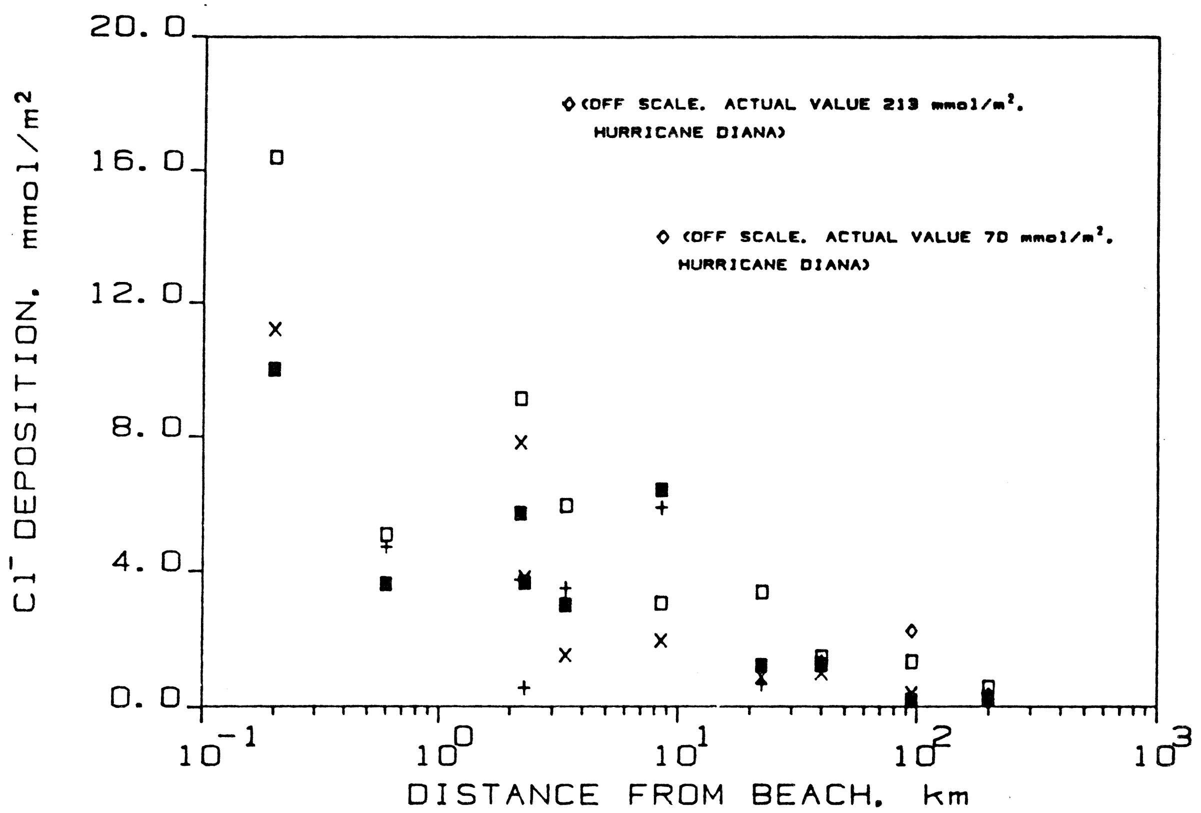


Figure 3. Chloride deposition (mmole/m^2) per storm event plotted as a function of distance from the beach in km. The sampling locations going away from the beach are (as defined in Figure 1) WB 1 and 2, CH, BC, W, RP, RW, CL and R. The storms are: + = 9/13-14/83; X = 10/11/83; □= 10/23/83; ■= 11/9/83; ◇ = 9/11-18/84 (Hurricane Diana). Note the offset for two of the four Hurricane Diana data points.

RESULTS AND DISCUSSION

Addition of synthetic rainwater to a surface water sample while monitoring pH produces a titration curve that shows how surface water might respond to the addition of acidic rain during a rain event. This titration is similar to an alkalinity determination except that the concentration of acid used is more dilute so that it better simulates rainwater. Results for the Southeastern North Carolina river, lake and seawater samples are shown in Table 1 and Figure 2. The Jordan Creek and Lake Singletary samples had essentially no buffering capacity, so the curves produced are similar to but offset from the simple dilution shown for deionized water. The Lake Waccamaw, Black River and Cape Fear River samples had limited buffering capacity; these waters could have pH reduced to 5.4 by a 12, 11, or 8% dilution by rainwater, respectively. Seawater is of course very well buffered and large pH decrease did not occur until the seawater sample volume was less than the volume of rainwater added. The Greenfield Lake sample was also very well buffered. The chloride concentration in Greenfield Lake water was 0.45 mM, so this was not brackish water. No pH impacts from rain would be expected for either of these waters. Identical results were obtained for each surface water, whether pH 3.0 sulfuric acid or pH 3.0 nitric acid was used as titrant, which indicates that the predominant reaction occurring in these titrations was an acid-base reaction. Filtration of samples caused an initial pH increase, but no change in the shape of the titration curve, which suggests that suspended sediment is not the major component of the buffering system.

These experiments show that there is much variation in the response of the various types of surface waters to rainwater addition in Southeastern NC. Jordan Creek and Singletary Lake were very acidic when sampled and had virtually no buffering capacity. Seawater and Greenfield Lake water were very well-buffered and would not experience pH changes due to rainwater input. Other surface waters were sensitive to the addition of acid (with alkalinity values less than 0.200 meq/L, sensitivity as defined by Hendry and Brezonik, 1980; and Church, 1984) and could perhaps experience short term pH changes during extremely acidic rains until thorough mixing with water at depth occurs. The intermediate types in this study were Lake Waccamaw, the Black River and the Cape Fear River.

Nutrient inputs into surface waters in Southeastern North Carolina may be a significant rainwater impact. Paerl (1985) showed that primary productivity, as indicated by C-14 uptake and chlorophyll-a production, was significantly enhanced in surface seawater 1-5 km off Morehead City, North Carolina, after acidic rain. The primary productivity response time after these rain events was very rapid which indicates that the enhancement of productivity was due to direct input from rain rather than from terrestrial runoff which takes longer to reach the sampling location. Bioassay experiments showed that the productivity enhancement was a response to nitrate addition rather than to pH changes, sample dilution, or phosphate addition. Similar productivity response to rainwater nitrate was observed in bioassay experiments using Lake Waccamaw water collected near the limestone outcrop (Kucklick, 1988). Preliminary experiments with Greenfield Lake water also suggest a productivity increase from nitrate addition in acid rain (L. Cahoon, 1987, UNCW, personal communication).

Lake Waccamaw has been described as incipiently eutrophic (Casterlin et al., 1984), so any nutrient additions to this lake could be particularly important. Calculations indicate that nitrate addition from rainwater could be very significant for this lake. Analysis of rainwater collected at Lake Waccamaw from September of 1986 through November of 1987 shows that occasional storms do deposit relatively large amounts of nitrate in this lake. Two particularly large nitrate deposition events occurred on September 28, 1986, when 1.3 cm of rain with 59.8 uM NO_3^- fell, and April 15, 1987, when 6.1 cm of rain with 11.6 uM NO_3^- was received at Lake Waccamaw. Assuming whole lake mixing, these two storms would increase the concentration of nitrate in lakewater by 0.34 and 0.31 uM, respectively. If these rains mixed with the top 8 cm rather than with the whole lake, the concentration of nitrate in the resulting surface layer would be 13.3 and 12.4 uM NO_3^-. This concentration compares with an average background concentration of approximately 2.8 uM (Casterlin et al., 1984), so these additions could be very significant in surface water for a short time.

Concentrations of phosphate in Eastern North Carolina rain are generally low, comparable to the 0.2 uM average in Lake Waccamaw (Casterlin et al., 1984). So, direct addition of phosphate from rain is not expected to have as large an impact on nutrient concentration as nitrate addition from rain. Rainwater may, however, indirectly cause the addition of phosphate to Lake Waccamaw water. Many of the limestones in eastern North Carolina contain some phosphate; the limestone that outcrops at Lake Waccamaw contains approximately 0.1% phosphate. Limestone, as calcium carbonate, is much more soluble in acidic rain than neutral rain, and as the limestone dissolves the phosphate contained within it is released. Sediment composition indicates enhanced productivity in the area of Lake Waccamaw near the limestone outcrop (Kucklick, 1988). Three Lake Waccamaw bioassay experiments conducted during May, June and September of 1987 also indicated that the lake water near the limestone was more nitrate limited than the lake water at the southern part of the lake away from the limestone outcrop. Lake Waccamaw water away from the limestone required addition of both nitrate and phosphate to stimulate productivity; near the outcrop only nitrate was necessary. Phosphate addition alone did not stimulate productivity at either location. Productivity was estimated in these bioassay experiments by either chlorophyll-a concentrations or ^{14}C uptake measurements (Kucklick, 1988). The limestone at Lake Waccamaw is not unique; if this proves to be a significant source of phosphate to this lake, it may also be an important source in many other areas in eastern North Carolina.

Sulfate addition from rainwater to surface waters in Eastern North Carolina could be of interest because sulfate is the major anion in most rainwaters. However, many of these lakes have been high in sulfate for decades. Frey (1949) reported results of analyses of lake water for several of the bay lakes in North Carolina. These lakes, which included Singletary Lake and Lake Waccamaw, had sulfate concentrations between 63 and 82 uM SO_4^{2-} in the summer of 1948. Recently measured sulfate concentrations (spring of 1987) were 118 and 46 uM respectively. Sulfate concentrations in NC rivers and streams from 1943-1967 were also high although quite variable (Wilder and Slack, 1971). Concentrations from the 1940's do not represent background levels (Patrick et al., 1981); anthropogenic emissions of SO_2 and NO_x began increasing between 1900 and 1940 (Holdren et al., 1984; Gschwandtner, 1985; Fay et al.,1986; Mayewski et al., 1986). Harned (1982) reported that concentrations of sulfate have increased in the Neuse River in central eastern North Carolina, and Turk (1983) reported an increase in many streams and rivers in the Southeastern US, all attributed to deposition from rain. Talbot and Elzerman (1985) found no evidence for increased sulfate concentrations in five South Carolina Piedmont lakes; their lakewater compositional data indicates sufficient retention of sulfate by soils. An increase in sulfate concentration can be an important early indicator of change for a river or lake, because, like an alkalinity decrease, it precedes the pH decline (Galloway et al., 1983; Perry et al., 1986; Schindler et al., 1986).

The ocean is a significant source of seasalt to rainwater (Cogbill and Likens, 1974; Gorham et al., 1984) and surface water in coastal areas (Beck et al., 1974; Gorham et al., 1985). During 1983, the maximum chloride deposition occurred in the autumn and was associated with storms that had wind off the ocean, usually from the northeast. In Figure 3, chloride deposition from the storms which gave the largest salt deposition is plotted versus distance from the beach. This Figure shows that during these storms chloride deposition from rain decreased rapidly with distance from the beach. In Wilmington, the 1983 value for chloride deposition was approximately twice the average annual value of 20 meq/m^2-yr calculated for the Southeastern United States (Munger and Eisenreich, 1983). Figure 3 indicates that in coastal regions, individual storm events often deliver significant amounts of chloride relative to the annual average. This large coastal effect is restricted to a rather narrow zone approximately 10 km wide along the coast. Although seasalt is very important in chloride transport and deposition in coastal locations, it is a minor source of sulfate (Gambell and Fisher, 1966). At the Wilmington site (8 km from the surf zone) the maximum contribution by seasalt to the total sulfate concentration occurred during coastal storms, however, even in these storms only approximately 30% of the sulfate on the average came from seasalt (Willey et al., 1988).

The most severe storm during this study was Hurricane Diana, which deposited approximately ten times more chloride than any other storm during this study (Figure 3). Hurricane Diana brought approximately 37 cm of rain and winds in excess of 50 m/sec to the Wilmington sampling site. It made landfall 25 km south of Wilmington on September 12, 1984. Salt deposition, assuming that all the chloride occurred as NaCl, was 12.5 g NaCl/m^2 at a site 3 km from the beach, and 4.1 g NaCl/m^2 at the Wilmington site (8 km from the beach). Rainwater during this storm, at the time of maximum wind intensity was 0.3% seawater at the site 3 km from the beach. Based on data from four locations (Figure 3), the effect of Hurricane Diana with respect to salt deposition was apparent as far inland as Clinton (95 km), but not at Raleigh (200 km inland). Both places received rainfall from this Hurricane. The observation that the rainwater extends farther inland than does the salt deposition indicates that the rainwater and seasalt are not completely mixed throughout the storm system.

CONCLUSIONS

1. Rainwater has the potential to affect certain surface waters in Southeastern North Carolina through pH change (acidification) and through nitrate addition. Some surface waters are very well buffered and unlikely to change in pH; some surface waters are already as acidic as most rain. Any changes in sulfate concentrations would be difficult to detect because of high variability in surface water sulfate concentrations; also many of the lakes and rivers have had high sulfate concentrations for decades.

2. Most of the salt added to rainwater from seaspray is transported only a short distance inland (10 km). Individual catastrophic storms can deposit as much salt in one storm as several average years of rain.

ACKNOWLEDGMENTS

This work was supported in part by NSF Grant ATM-8512537 to J.D. Willey and by a North Carolina Department of Natural Resources and Community Development Fellowship to J.R. Kucklick.

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INFLUENCE OF NUTRIENT LOADING ON THE NEUSE RIVER ESTUARY, NORTH CAROLINA

Robert R. Christian, William M. Rizzo & Donald W. Stanley
Biology Department & Institute for Coastal and Marine Resources
East Carolina University
Greenville, North Carolina 27858

ABSTRACT

Selected data from a two year study are presented which describe patterns of inorganic nitrogen and phosphorus loading to the Neuse River Estuary and the role of the estuary as a trap, or "filter" of these nutrients. The Neuse River was found to be the major source of nutrient loading to the estuary when compared to local point sources and the Trent River. Loading to the estuary from the rivers is flow dependent, so that most of the total annual nutrient load comes during the late winter when flow is highest. Concentrations of ammonium (NH_4), nitrate plus nitrite (NO_3 + NO_2), and filterable reactive phosphorus (FRP) were consistently higher at the head of the estuary than at its mouth. NO_3 + NO_2 was the predominant form of dissolved inorganic nitrogen entering the estuary, but in water leaving the estuary NH_4 was more abundant than NO_3. The decreases in concentrations within the estuary were due in part to dilution of nutrient-rich river water by nutrient-poor Pamlico Sound water, but processes other than conservative mixing also played roles in decreasing the nutrient concentrations. Therefore, the estuary can be considered to be a major "filter" of freshwater nutrient inputs from the Neuse Basin, and thus, it most likely helps prevent eutrophication in Pamlico Sound.

INTRODUCTION

Estuaries represent a major interface between land and sea. As freshwater runs over and percolates through watersheds, it accumulates a large variety of dissolved and particulate substances from both natural processes and man's activities. These substances are transported along rivers toward the estuarine interface. At this interface, the substances are subject to new processes or modified rates of processes which alter their concentrations within the water. These processes are physical, chemical, and biological, resulting from the mixing of fresh and seawater and from the geomorphological forces of the juxtaposition of land and sea. Therefore, estuaries play an important role as "filters" which modulate the impacts of land runoff to the ocean (Kennedy, 1984). Understanding the nature of the filtering mechanisms is an important goal of estuarine scientists and is essential to sound management practices for estuaries.

For the past several years, we have studied the nutrient dynamics within the Neuse River Estuary and its major tributary, the Neuse River. The Neuse system drains a watershed that accounts for 12% of the area of North Carolina. While nearly two-thirds of the watershed is forest and wetland, most of the nitrogen and phosphorus inputs to the Neuse River are derived from agricultural activities and the 31 industrial and municipal point sources (N.C.D.N.R.C.D., 1984). Resultant inputs of nutrients are such that the Neuse River is hypereutrophic during most of the year, i.e., nutrient concentrations exceed the needs of primary producers (Paerl, 1987; Christian et al., 1986).

If the estuary is to act as a nutrient filter, concentrations must diminish, to an extent greater than can be explained by dilution alone, as water passes from the river to Pamlico Sound at the estuary's mouth. Christian et al. (1984) found such decreases in nitrate plus nitrite and filterable reactive phosphorus concentrations within the upper Neuse River Estuary during four dates in the summer of 1982. Further, yearly average concentrations of nutrients decline from river to estuarine mouth (e.g., Stanley, 1983). Such trends are also found in other estuaries and appear to be a common feature of many drowned river valley estuarine ecosystems (Stanley, 1986; Harding et al., 1986).

Estuaries possess gradients of features which could affect nutrient concentrations. Gradients of salinity, turbidity, sediment type, surface area to volume ratio, and taxa exist. In many studies, water quality is indexed against the salinity gradient as a dominant feature of an estuary (Christian et al., 1984; Harding et al., 1986). However, in the Neuse River Estuary, the salinity gradient is highly dependent upon river flow and does not always reflect the geomorphological features of the estuary. At high river flow, much of the upper estuary may be fresh, while at low flow, salinity may intrude upriver (Hobbie and Smith, 1975). Various attributes of the estuary may be inherent in their geomorphological position rather than their position relative to the salinity gradient. This feature may be especially true for attributes associated with sediments or surface area to volume ratios. Nutrient concentrations and water quality may be affected by both salinity and geomorphological related features.

In this paper we evaluate the ability of the Neuse River Estuary to act as a nutrient filter. We concentrate on the dissolved inorganic nutrients: ammonium (NH_4), nitrate plus nitrite (NO_3 + NO_2), and filterable reactive phosphorus (FRP, primarily PO_4). The estuary acts as a filter in two ways: (1) by reducing nutrient concentrations in the water column and (2) by reducing loading of nutrients into Pamlico Sound. The first process is important to the consideration of productivity within Pamlico Sound, as growth of phytoplankton and other primary producers may be limited by the concentration of inorganic nutrients. The second process is important to long-term processing and storage of nutrients and organic matter within the Sound, but is difficult to estimate based on present data. Here we present information on nutrient concentrations at the Neuse River Estuary's head and mouth, on the relationship of river flow to nutrient processing within the estuary, and on nutrient loading at the head of the estuary. From this information we, evaluate the potential of the estuary as a nutrient filter.

MATERIALS AND METHODS

Study Site and Sampling

In Figure 1 we show the Neuse River Estuary and its position relative to eastern North Carolina. The letters within the estuary refer to stations at which sampling has been conducted since February 1985. For this paper, we describe results from station G (at Cowpen Landing) representing inputs from the Neuse River, Pollocksville (P) representing inputs from the Trent River, Weyerhaeuser pulp mill effluent (WPM), effluent from the New Bern sewage treatment plant (STP), and station A, representing outputs from the estuary into the Sound. We also include nutrient and salinity data from stations A through G.

The distance from station G to station A is 74 km, and the surface area of the estuary is 394 km^2. The Neuse River is the major tributary, with a long-term average discharge more than ten times that of the Trent. River flow dominates the salinity structure of the estuary with astronomical tides being of minor importance and vertical stratification being ephemeral. The average depth is 4.6 m with depth increasing from head to mouth (Matson et al., 1983).

Sampling occurred for more than two years, from winter 1985 through spring 1987. Stations G, P, and STP were sampled on an average of one-week intervals, and stations A to F were sampled at two- to four-week intervals. Surface waters of the rivers and estuary were sampled, as was effluent from the STP immediately prior to entrance to the river. At each sampling we measured salinity and temperature and collected a minimum of four liters of water, which was stored during transit at ambient or sub-ambient temperatures and returned to the laboratory within 1 to 6 hours. Results presented here are part of a larger study of nitrogen cycling and primary productivity within the estuary.

Chemical Analyses

In the laboratory, samples were filtered prior to chemical analysis. The filtered water was either kept refrigerated for analysis within 48 hours or stored frozen. During the two-year period, both manual and automated chemical analyses were conducted. In both cases the basic analytical chemistries for each N and P fraction were similar. Ammonium concentrations

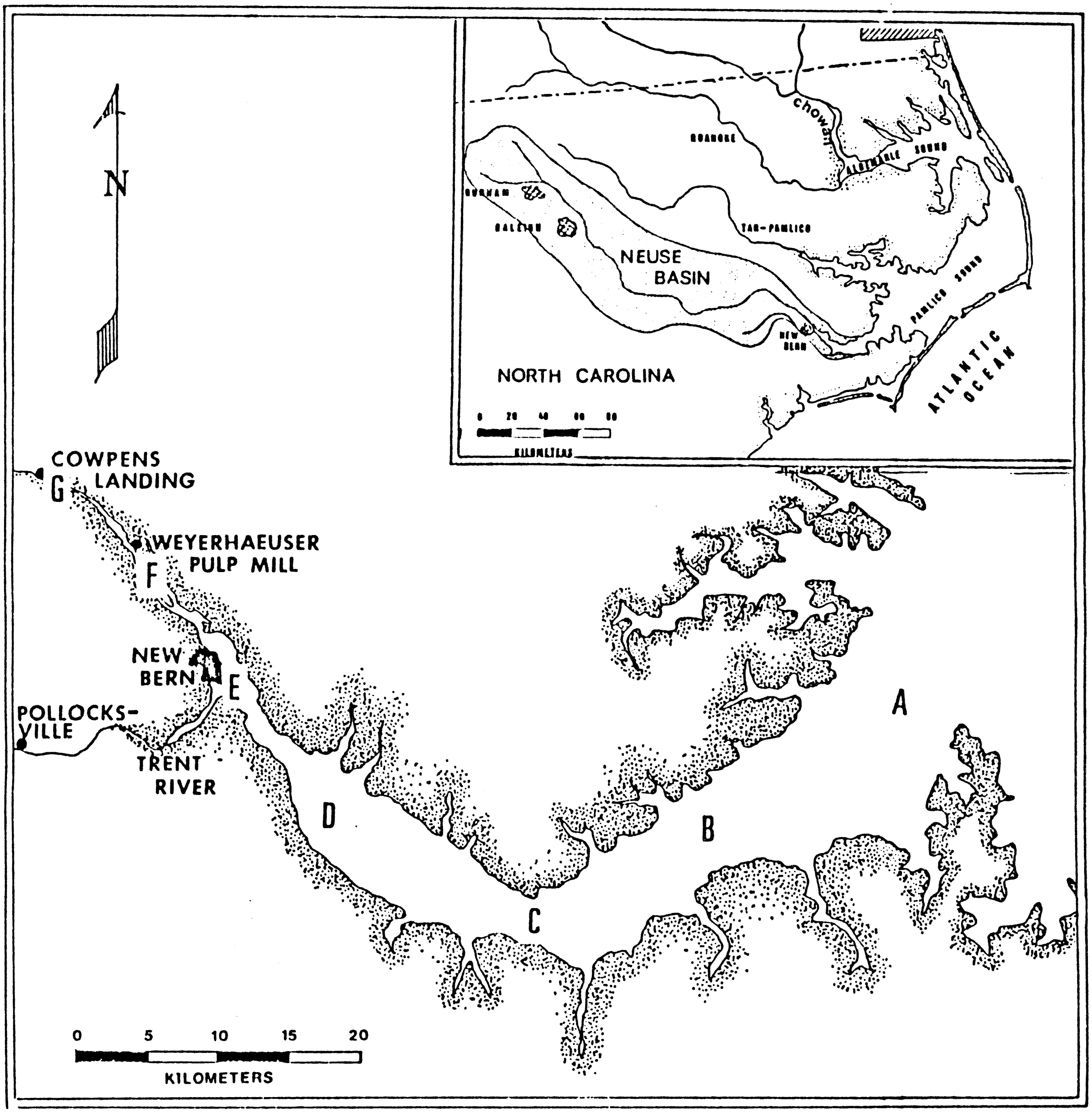


Figure 1. Map of Neuse River Estuary, watershed, and sampling site locations.

were determined by phenate techniques (Strickland and Parsons, 1972, U.S. E.P.A. 1979). Nitrate plus nitrite concentrations were determined after cadmium reduction (APHA) (1980), and filterable reactive phosphorus was determined by the ascorbic acid method (A.P.H.A., 1980). Intercalibrations between the automated and manual methods were done to insure comparability of the results.

Data Manipulation

Concentration data from stations A and G were grouped by month, independent of year, and were averaged to provide a composite annual picture of concentrations of each nutrient.

Loading calculations were made for the period from March 1985 through February 1987. Instream loading was calculated as the product of water discharge at a location times concentration at that location. To do this calculation, certain assumptions were made depending on location. For station G, daily water discharge was estimated by multiplying flow at the nearest gauging station (Kinston) by 1.45 to correct for the ungauged basin area between the two sites. Dissolved inorganic nutrient concentrations from the nearest sampling date at station G were multiplied times water discharge to estimate daily loadings. These loading estimates were summed over two sampling period intervals: 1) from March 1985 through February 1986 and 2) from March 1986 through February 1987. Other loadings were calculated as follows. To obtain loading for the Weyerhaeuser pulp mill, monthly average concentrations of effluent nutrients (Stanley, unpublished data) were multiplied by mean daily water discharge for the month (N.C. Department of Natural Resources and Community Development, unpublished data). For the New Bern sewage treatment plant, our measured concentrations were multiplied times flow data (N.C.D.N.R.C.D., unpublished data). Loading from the Trent River was determined as for the Neuse; i.e., measured concentrations at Pollocksville were multiplied times the gauged flow at Trent, N.C., and the product was then multiplied times 3.09, a correction for the ungauged basin area between the gauging station at Trent and the mouth of the Trent River.

RESULTS

Changes in Concentrations Between Estuarine Head and Mouth

At the head of the estuary (station G) $NO_3 + NO_2$ was present in the highest concentrations of the three nutrients, although NO_2 was only a minor component (unpublished data) (Figure 2). Often nitrite was present at concentrations near the limits of detection. $NO_3 + NO_2$ exceeded 100 µM on some sampling dates and the monthly averages were all >30 µM. The highest $NO_3 + NO_2$ concentrations occurred in winter and late spring, and the lowest were in March and in the summer months.

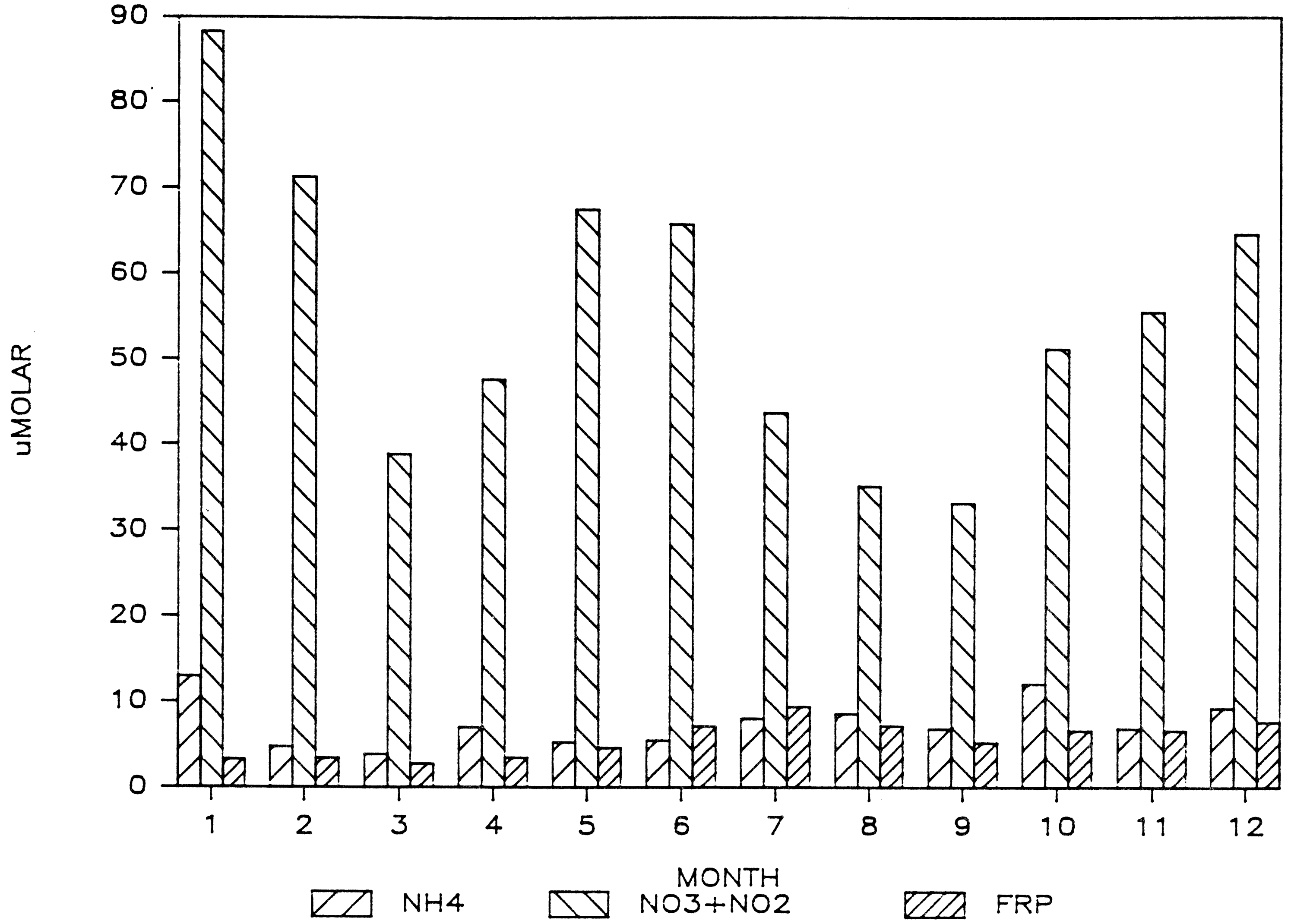


Figure 2. Composite, average monthly mean nutrient concentrations from station G within the lower Neuse River. Samples were from winter 1985 to spring 1987.

NH_4 concentrations varied from 4 to 13 µM. The lowest concentrations occurred in February and March, but there were no obvious seasonal trends. FRP concentrations ranged from 3 to 9 µM and were highest in summer and were lowest in winter. Intra-month variation was considerable for all of the nutrients.

Water at the mouth of the estuary (station A) was largely depleted of NO_3 + NO_2 (Figure 3). Concentrations were often below the limits of detection (0.1 µM) and the highest single concentration was only 9.7 µM. Lowest values were in May and July with high values in March and the fall months. NH_4 dominated the dissolved inorganic nitrogen pool, with a peak ammonium concentration for a single date of 16.2 µM. Highest concentrations were in spring, late summer, and November. Monthly mean FRP concentrations varied ten-fold over the composite year from 0.46 to 4.50 µM. The lowest values were found in spring and highest in summer and fall.

Differences in the annual mean N and P levels at stations G and A show that concentrations of all three nutrients decreased between the head and mouth of the estuary (Table 1). The rows for "total" represent measured concentrations at each station and are considered here. Later we discuss a correction for sound water nutrient contributions. Both NH_4 and FRP levels fell about 50% as water passed through the estuary, but the "filtering capacity" for NO_3 + NO_2 apparently was even greater, since concentrations of this nutrient declined by about 97%. Consequently, the molar ratio of N:P in the inorganic nutrients changed dramatically. At the head of the estuary it was 11.0, whereas at the mouth it was >3.2. The "greater than" sign must be used because of the frequency at which NO_3 + NO_2 concentrations were below the limits of detection.

Relationship of River Flow to Nutrient Processing

Figures 4A and 4B show that, at Station A, NH_4 and NO_3 + NO_2 exhibited similar patterns with respect to salinity. In both cases the highest concentrations were observed when salinity was low. When salinity was greater than 14 ppt, NH_4 was always less than 4 µM, and NO_3 + NO_2 was less than 1 µM. At times when water had below 14 ppt salinity, concentrations varied from near the limits of detection to the highest values measured. FRP concentrations at Station A were most variable at mid-salinities, ranging from the limits of detection to 6 µM (Figure 4C). Variability decreased at low and high salinities.

The relationships between nutrient concentration and salinity described above were used to estimate the contribution of nutrients to the estuary from Pamlico Sound. Water with salinities greater than 14 ppt was assumed to be from Pamlico Sound, and hence nutrient concentrations in this water represented concentrations within the sound. Average concentrations from samples of such water were 17.4 ± 2.3 (X ±

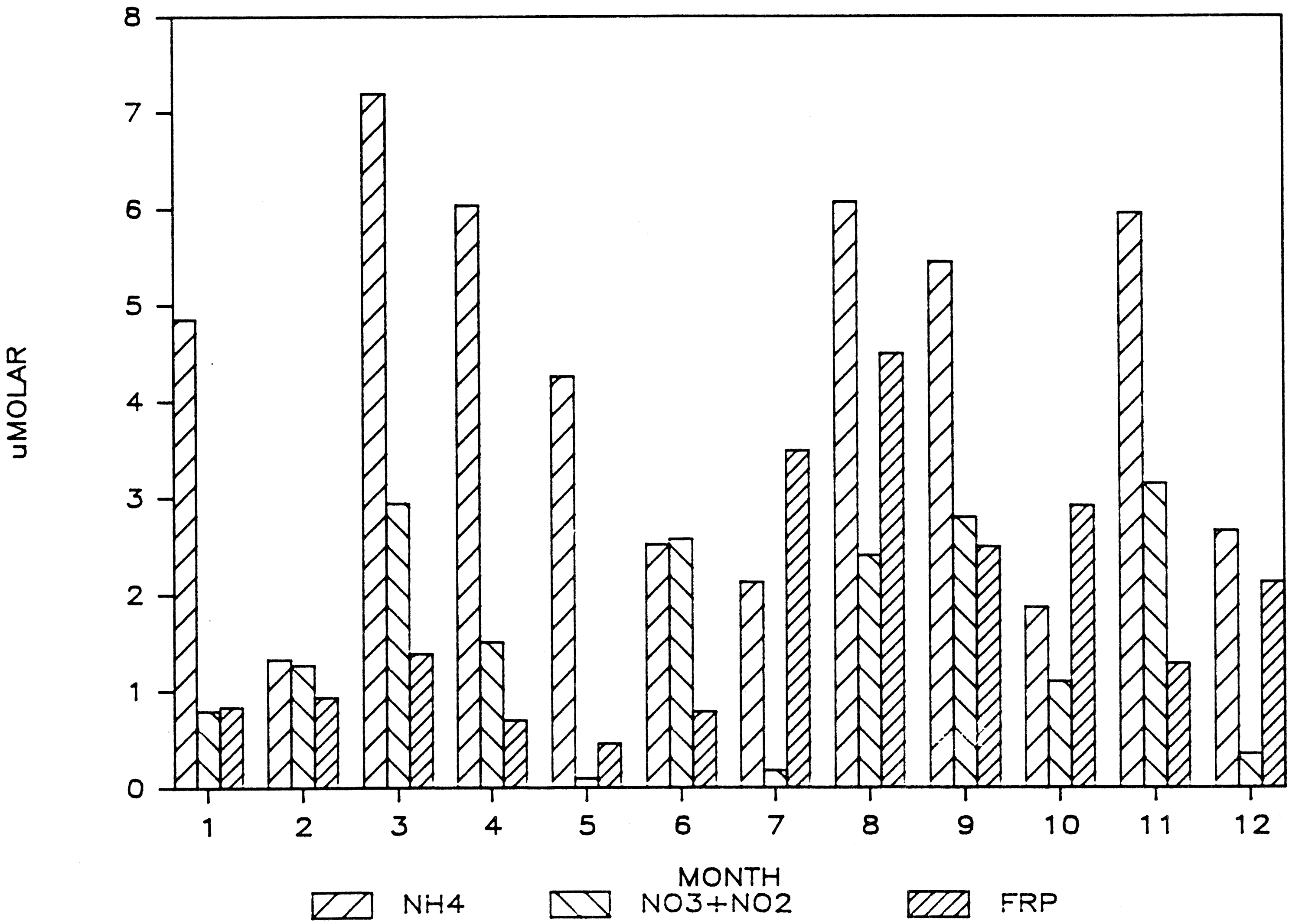


Figure 3. Composite, average monthly mean nutrient concentrations from station A at mouth of the Neuse River Estuary. Samples were from winter 1985 to spring 1987.

Table 1. Comparison of overall mean concentrations of inorganic nutrients between the head (station G) and mouth (station A) of the Neuse River Estuary

Location	Water Mass	NH_4	NO_3+NO_2 µM(x + SD)*	FRP	TIN:P µM:µM
Head	Total	7.6 ± 2.7	55.3 ± 16.7	5.7 ± 2.1	11.0
Mouth	Total	4.2 ± 2.0	<1.6 ± <1.1	1.8 ± 1.3	>3.2
Mouth	Estuarine**	3.6 ± 2.0	<1.4 ± <1.1	0.9 ± 1.0	>5.6
Difference	Total	3.4	>53.7	3.9	14.6

* Mean is of twelve composite monthly means for samples from 1985-1987.

** Concentrations were corrected for contribution from sound water.

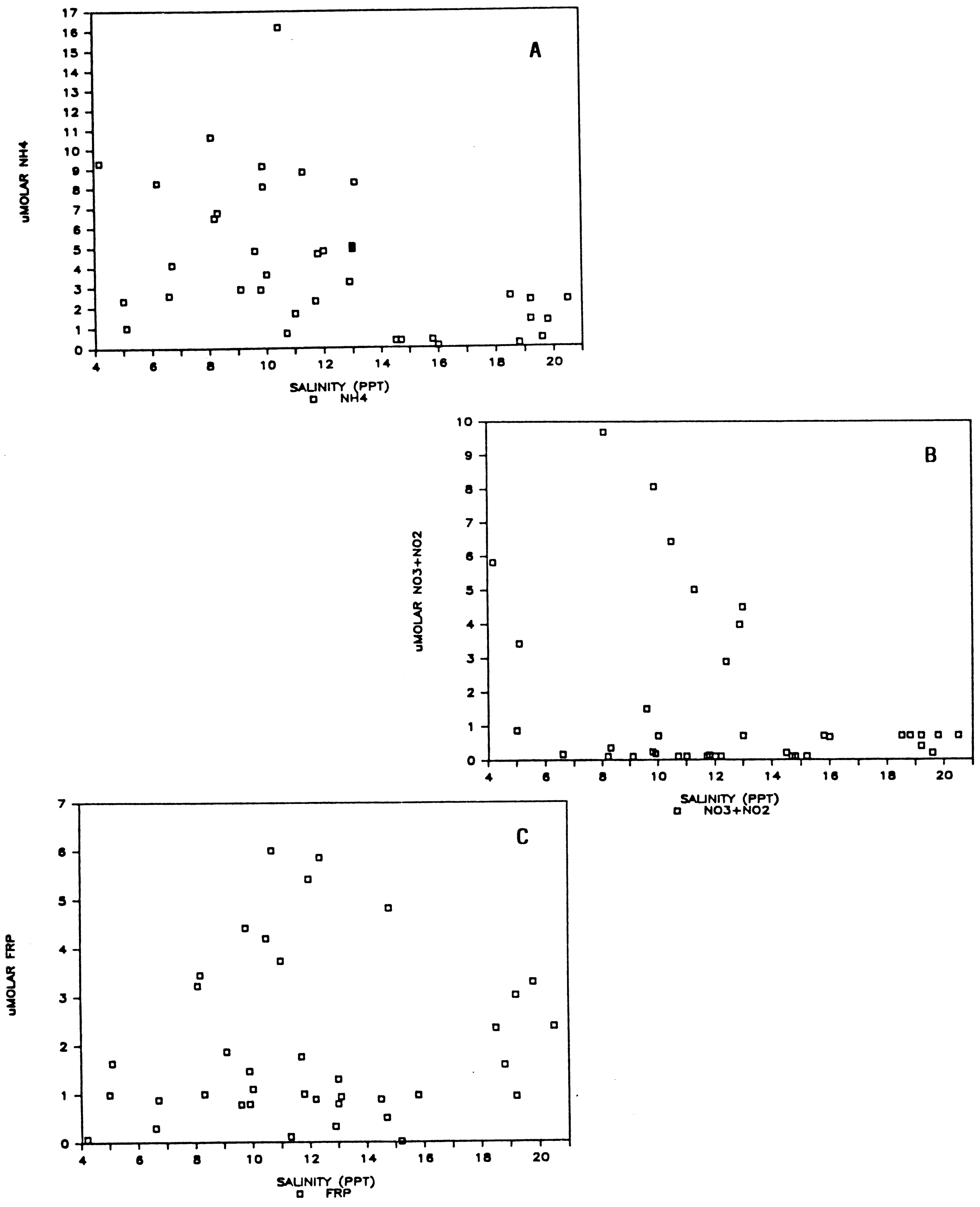


Figure 4. Concentrations of NH_4 (A), NO_3+NO_2 (B), and FRP (C) at station A, the mouth of the Neuse River Estuary, plotted against salinity.

SD) ppt for salinity, 1.1 ± 1.0 µM for NH_4, 0.5 ± 0.3 µM for NO_3 + NO_2, and 1.9 ± 1.4 µM for FRP. Then, for all samples from station A, the measured salinity was divided by 17.4 ppt to estimate the fraction of sound water in the sample. Values greater than 1 were considered 1. Finally, this fraction was multiplied by the average nutrient concentrations of sound water, and the product was subtracted from the measured concentrations for each sample to give the estuarine nutrient contribution. Negative values were considered as 0.0. Table 1 summarizes the results. The estimated estuarine contributions to the total concentration were 86, 88, and 50% for NH_4, NO_3 +NO_2, and FRP, respectively. Thus the relative contribution of Sound FRP is greater than that for the nitrogen species.

Salinity versus property plots are often used to normalize flow patterns and to indicate whether a substance acts conservatively or nonconservatively within an estuary (Sharp et al., 1984). For example, if, under steady state conditions, the decreases in concentrations between Neuse Estuary stations G and A were the result of Pamlico Sound water dilution alone, nutrient concentration would be linearly related to salinity across the estuary. The actual relationship between nutrients and salinity in the Neuse River Estuary is illustrated by the salinity property plots in Figure 5 for nutrient concentration data from two days in May having vastly different flow regimes. On the first of these two sampling dates (13 May 1986) salinity at station A was 14.7 ppt. On the second day (7 May 1987) it was only 2.0 ppt. Thus the curves from the latter date are compressed to the left. In all cases nutrient concentrations were not linearly related to salinity. NH_4 concentrations were variable at low salinities and in freshwater (Figure 5A). This variation probably reflects the influence of Weyerhaeuser pulp mill effluent which increased NH_4 concentrations downstream of station G, so that the concentrations peaked at station F on 13 May 1986 and at station E on 7 May 1987. Concentrations of NH_4 rose at the mouth of the estuary on both dates. NO_3 + NO_2 concentrations fell to the limits of detection by the time water reached station E on 13 May 1986, but remained above 1 µM through station B on 7 May 1987 (Figure 5B). Similarly, FRP remained above 2 µM through station C on May 1987, but was depleted to <1 µM by station E on 13 May 1986 (Figure 5C). In summary: 1) all nutrients declined considerably in estuarine water before it reached Pamlico Sound, 2) conservative mixing alone was not evident, 3) and river flow affected the nutrient concentration patterns.

Nutrient Loading at the Estuarine Head

A summary of annual nutrient loading for two twelve-month periods beginning on 1 March 1985, is shown in Table 2. NO_3 comprised almost 90% of the total dissolved inorganic nitrogen (DIN) input, far more than the NH_4 input. The Neuse River basin above station G is the largest source of nutrients to the

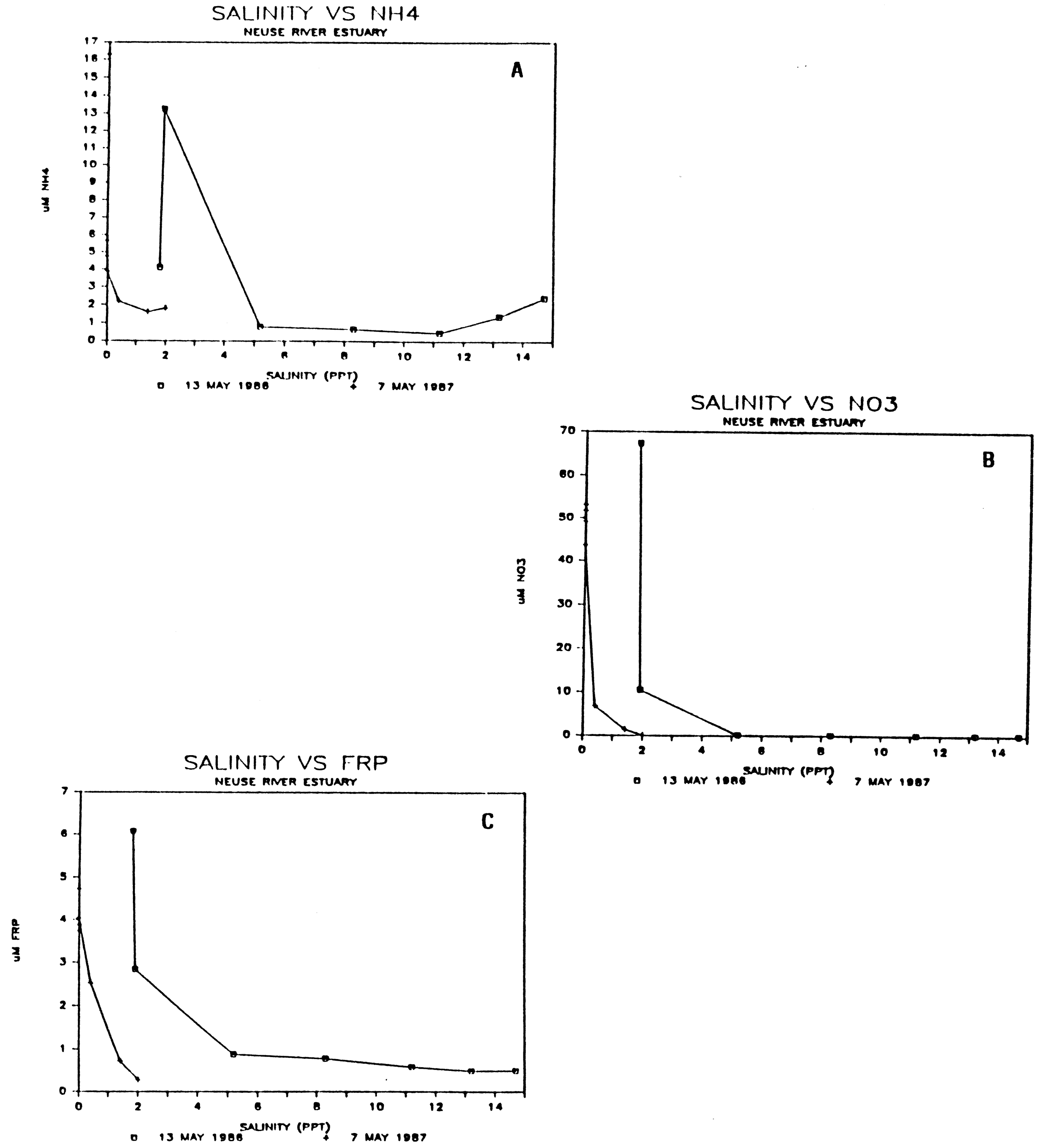


Figure 5. Concentrations of NH_4 (A), NO_3+NO_2 (B), and FRP (C) plotted against salinity for stations G through A along the Neuse River Estuary. ▭ represents 13 May 1986 samples, and + represents 7 May 1987 samples.

Table 2. Summary of loading to the Neuse River Estuary, March 1985-March 1987. Values are MMol/yr

March 1985-February 1986	NH_4	% Total	No3+NO2	% Total	FRP	% Total	Total DIN
Neuse River	11.8	57.8	82.6	90.9	7.0	79.6	94.4
Trent River	2.4	11.8	6.9	7.6	0.8	9.1	9.3
New Bern STP	2.4	11.8	0.5	0.6	0.7	8.0	2.9
Weyerhaeuser	3.8	18.6	0.9	1.0	0.3	3.4	4.7
Total	20.4		90.9		8.8		111.3
March 1986-February 1987							
Neuse River	16.7	63.5	144.7	85.4	9.2	80.0	161.4
Trent River	3.4	12.9	23.4	13.8	1.4	12.2	26.8
New Bern STP	2.8	10.7	0.6	0.4	0.6	5.2	3.4
Weyerhaeuser	3.4	12.9	0.8	0.5	0.3	2.6	4.2
Total	26.3		169.5		11.5		195.8

estuary, contributing 58-64% of the total NH_4 load, 85-91% of the total NO_3 + NO_2 load, and 80% of the total FRP input. Combined point source inputs of NO_3 + NO_2 below station G (Weyerhaeuser + New Bern STP) were <2% of the total NO_3 + NO_2 input, while FRP and NH_4 inputs from these point sources were about 8% and 22% of the total loading of these species to the estuary. The Trent River supplied between 7 and 14% of the total loads of the dissolved nutrients.

Figures 6A-B show the monthly nutrient loading to the Neuse River Estuary during the two year study period. The vast majority of the annual NO_3 + NO_2 load entered the estuary during the December-March period. For example, 60% of the annual NO_3 + NO_2 load (March 1986 - February 1987) from the upper Neuse basin came into the estuary during January and February. Seasonal variations in loading were not as dramatic for NH_4 and FRP as for NO_3 + NO_2, but inputs of both did peak during the winter (Figures 6A-B).

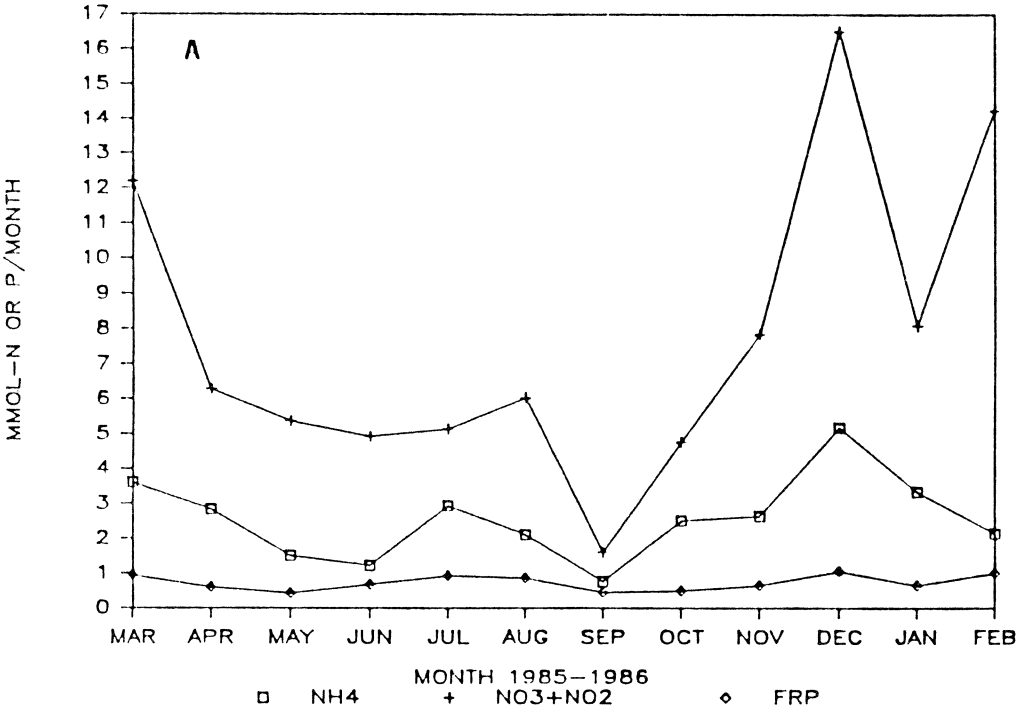
Figures 6A-B and Table 2 also reveal substantial interannual variation in dissolved inorganic N and P inputs to the estuary. For example, NO_3 + NO_2 loading from the upper Neuse basin increased nearly twofold in the second twelve-month period. NH_4 loading increased 1.4 times, and FRP loading increased slightly. About the same relative magnitude of interannual variation in nutrient input is also apparent for the Trent River; all nutrients inputs were higher in the second year. Point source nutrient inputs were essentially the same in each year (Table 2).

Loading rates from the Neuse and Trent Rivers are highly dependent on river flows (Figures 7A-B; Table 3). NO_3 + NO_2 loading is much more dependent on water discharge than NH_4 or FRP loading. Variation in river flow can account for 80-90% of the variation in NO_3 + NO_2 loading, compared to about 65% for NH_4 and FRP loading (Table 3).

DISCUSSION

Concentration Changes

Our data for dissolved inorganic nutrients at the head of the Neuse River Estuary are similar to those described by Paerl (1987) for nearby sites on the Neuse River, and they are similar to those at a comparable position on the Tar River, which enters the neighboring Pamlico River Estuary (Stanley, 1987). NH_4 and NO_3 + NO_2 concentrations for the Neuse head are similar to or lower than those at the heads of the Delaware and Chesapeake Bays, but FRP concentrations tend to be higher in the Neuse (Harding et al., 1986; Sharp et al., 1984).



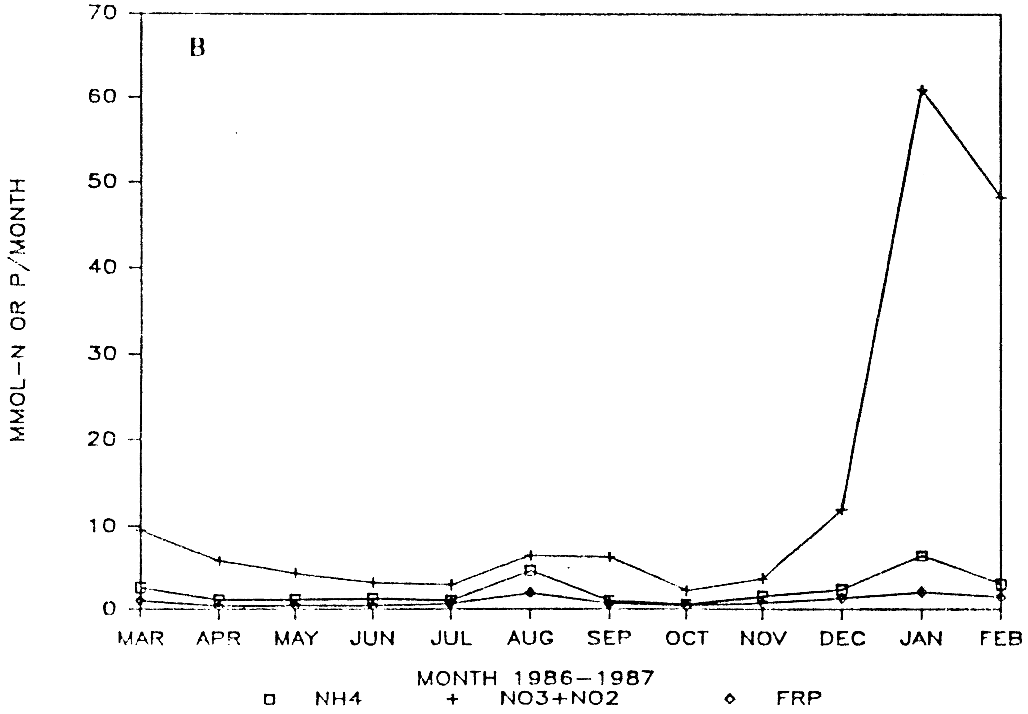


Figure 6. Monthly loading (Mmol N or P) of DIN and FRP to the Neuse River Estuary from all sources considered during the periods March 1985-February 1986 (A) and March 1986-February 1987 (B).

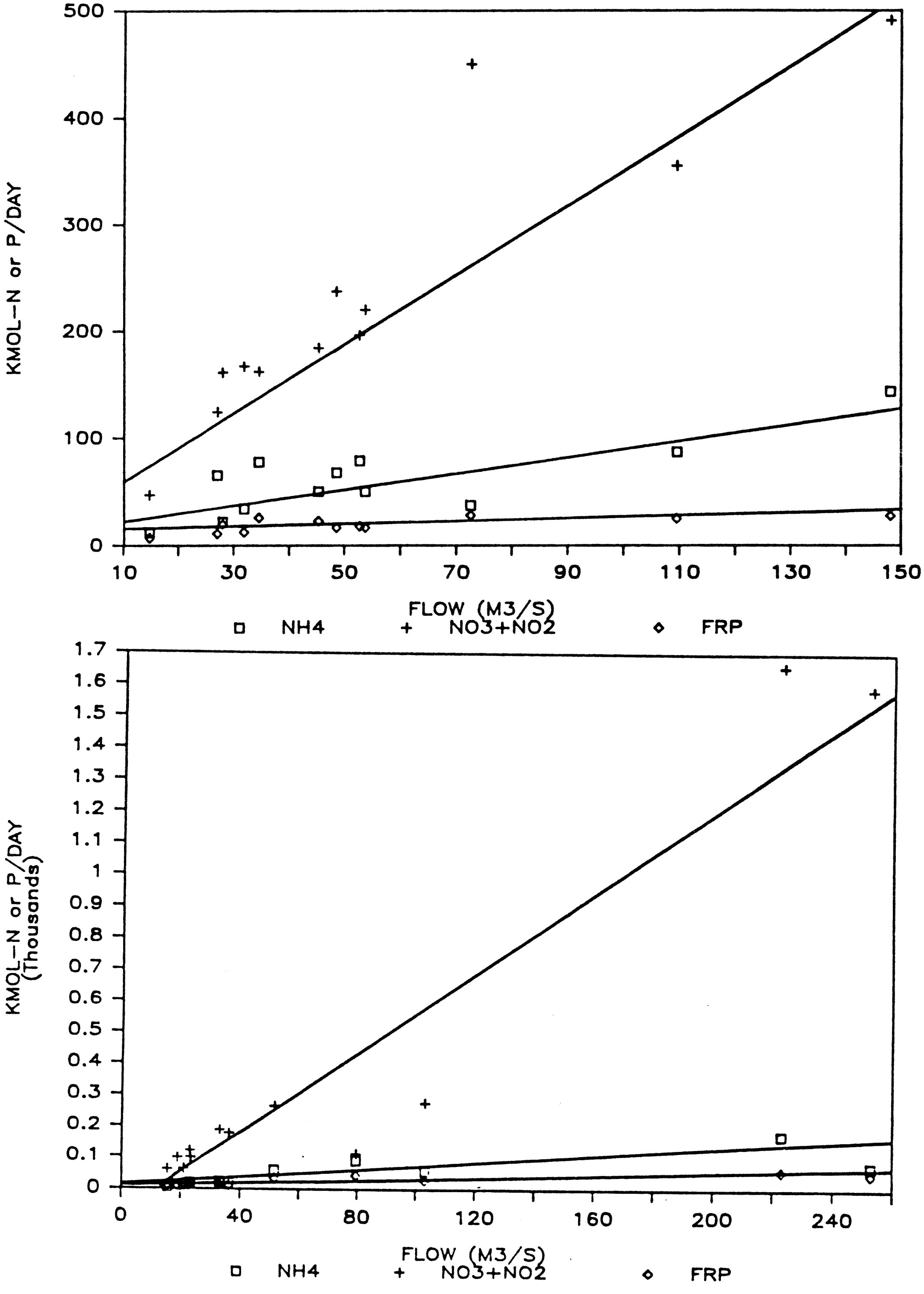


Figure 7. Daily loading (kmol N or P) from the upper Neuse River basin as a function of flow (m^3/s) at station G during the periods March 1985-February 1986 (A) and March 1986-February 1987 (B). The regression lines from Table 3 are also plotted.

Table 3. Summary of linear regreession analyses of nutrient loading vs. flow at station G (Cowpen)

	Nutrient Loading	Flow (m^3/s)	r^2	n
Mar. 85 - Feb. 86	NH_4 (kmol-N/day)	= .74 (Flow) + 20	0.65	12
Mar. 86 - Feb. 87	NH_4	= .47 (Flow) + 11	0.63	12
Mar. 85 - Feb. 86	NO_3	= 3.12 (Flow) + 60	0.81	12
Mar. 86 - Feb. 87	NO_3	= 6.82 (Flow) + 109	0.92	12
Mar. 85 - Feb. 86	FRP (kmol-P/day)	= .12 (Flow) + 12	0.46	12
Mar. 86 - Feb. 87	FRP	= .17 (Flow) + 13	0.75	12

Although larger than the Neuse, the Delaware and Chesapeake Bays are also drowned river valley estuaries. The Pamlico River Estuary watershed is similar to, but somewhat smaller than, the Neuse (Matson et al., 1983). All four estuaries show similar patterns of nutrient change from head to mouth (Harding et al., 1986; e.g. Stanley, 1986). $NO_3 + NO_2$ decreases greatly over the length of the estuaries. NH_4 and FRP concentrations also decline, but concentrations at the mouth often remain near or above 1 µM.

The depletion of riverborne nutrients in the estuary may result from a number of processes. One is simple dilution caused by the mixing of nutrient-rich river water with nutrient-poor seawater. But the property-salinity plots shown above, as well as other plots examined (data not shown), are indicative of nonconservative mixing; that is, other processes besides dilution are involved. Although there are a number of assumptions inherent in such plots (Loder and Reichard, 1981; Sharp et al., 1984; Sharp et al., 1986) that may obfuscate patterns of physical mixing, the observed patterns, plus other evidence, are indicative of biological and chemical processing of the nutrients. Chlorophyll a concentrations rise in the upper estuary as a result of phytoplankton primary productivity (Christian et al., 1984). This production consumes nutrients. It is interesting, although perhaps fortuitous, that the N:P ratio of the total differences between DIN and FRP concentrations of stations G and A is 14.6:1. This ratio is very close to the expected ratio for phytoplankton nutrient uptake (16:1, Redfield et al., 1963). We, as well as other researchers, have accumulated other data that supports the contention that both planktonic and benthic processing of nutrients is considerable within the estuary (Paerl, 1983; Matson et al., 1983; Fisher et al., 1982). It appears that the net result of this processing is that the estuary removes large quantities of dissolved inorganic nutrients from the water, which, along with seawater dilution, leads to greatly reduced nutrient concentrations for primary producers within Pamlico Sound.

As seen in Figures 4 and 5, Neuse flow affects how much of the riverine nutrients reach the lower estuary and Pamlico Sound. High river flow can sweep nutrients through the estuary so rapidly that there is not time for much chemical or biological processing. Woods (1969) estimated travel times in the Neuse River Estuary to be approximately 26 to 27 days during low flow, summer conditions. Unfortunately, the travel times under other flow conditions are unknown. As nutrient concentrations at station A are highly variable at low salinities, chemical and biological processing of nutrients may be substantial even at high flow conditions. We are currently evaluating process rate data on planktonic primary productivity, nitrogen cycling, and benthic/water column fluxes of nutrients which will provide this much-needed information.

Nutrient Loading to the Estuary

The estimates of daily FRP and $NO_3 + NO_2$ loading for the Neuse River shown in Figures 7A-B agree well with other recent loading estimates made at a station slightly downstream from station G (Paerl, 1987). Paerl reported maximum $NO_3 + NO_2$ and FRP loadings ranging between 580-2800 kmol N/day and 50-110 kmol-P/day respectively, for the period May 1981-April 1986. Maximum $NO_3 + NO_2$ and FRP loadings respectively in our study were 490-1658 kmol N/day and 28-56 kmol P/day. Paerl's results underscore the large interannual variability in loading shown in Figures 6A-B. The total $NO_3 + NO_2$ loading which occurred during January and February 1987 is the highest loading reported for the late winter and early spring period since 1983.

Interannual variation in point-source nutrient inputs was small, as were monthly variations. This variation might be expected since these discharges are largely independent of meteorological events. However, because of this relatively constant input, the impacts of point-source loading could be greatly enhanced during low flow periods. Loadings from direct precipitation and local land use were not considered here but are probably of minor importance.

Paerl (1987) also reported a strong, direct link between $NO_3 + NO_2$ loading and river flow. Surface and subsurface runoff to the Neuse River Estuary is maximal in winter when evapotranspiration is lowest (Harned, 1980). Since these flows carry dissolved nutrients, maximum nutrient loading tends to occur in winter. However, the relationship between river flow and $NO_3 + NO_2$ loading can also be spuriously influenced by anthropogenic factors. Fertilization of farmland generally occurs in late winter and early spring (Humenik et al., 1983). Consequently, more nitrate is available (both from direct application to fields, and through nitrification of ammonium fertilizers) for input to the river through stormwater runoff at this time than at other times of year. Greater winter availability of nitrate is evident in Figures 6A-B, where an anomalously high August 1986 river flow was equal to or greater than the river flows of the preceding winter/spring period. Although August flows were equivalent to those winter flows, August nutrient loadings were much less than winter loadings.

NH_4 and FRP loadings are less affected by river flow. Paerl (1987) also noted a relatively weak link between NH_4 or FRP loading and river flow and suggested that this weakness is due to the relatively smaller contribution of non-point sources to NH_4 and FRP loading. Greater point source contributions, unrelated to river flow, also would explain the smaller seasonal changes in loading of NH_4 and FRP than of $NO_3 + NO_2$.

High spring river discharges to their receiving estuaries are a common feature of temperate, drowned-river valley estuaries (Sharp et al., 1986; Schubel and Pritchard, 1986). Annual loading of the upper Chesapeake Bay by the Susquehanna River follows the same seasonally asymmetric pattern found for the Neuse (Schubel and Pritchard, 1986). Such loading patterns are probably typical of these estuaries. The timing and magnitude of the spring discharge may also determine the location, timing, and extent of spring phytoplankton blooms by determining patterns of water column stratification (Sharp et al., 1986).

Nutrient loading and other discharge related effects are determined by a complex interaction of man's activities, hydrology, geochemistry and biological processing. Loading studies represent one part of the picture. Our studies of the biological responses to these interactions will hopefully supply another part.

SUMMARY

The Neuse River Estuary serves as a filter for riverborne nutrients on their way to Pamlico Sound. Concentrations of NH_4, $NO_3 + NO_2$, and FRP consistently declined in water passing through the estuary. $NO_3 + NO_2$ concentrations decreased the most, such that they often were near or below the limits of detection upon reaching the estuarine mouth. These decreases were not merely due to physical mixing. Thus the estuary acts as a dynamic "sink" for dissolved inorganic nutrients.

Nutrient loading to the estuary is substantial with most dissolved inorganic nutrients coming from the Neuse River. Local point sources and the Trent River provide minor inputs. Both nutrient loading and concentration patterns within the estuary are dependent on river flows. However, even under high flow conditions nutrient concentrations at the mouth are less than at the head. Thus the Neuse River Estuary acts to preserve low nutrient concentrations within Pamlico Sound and perhaps prevent eutrophication there.

ACKNOWLEDGMENTS

For assistance with field sampling and laboratory and data analyses, we are grateful to Joe Boyer, Deborah Daniel, Loede Harper, Martha Jones, and Greg Lackey. Support for this work was provided by the National Oceanic and Atmospheric Administration Office of Sea Grant under grant NA85AA-D-SG022, and the State of North Carolina. The grant is administered by the University of North Carolina Sea Grant College Program. Also, support was provided by the U.S. Environmental Protection Agency under grant agreement R-812475-01-0.

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Chapter 2. Estuarine Pathogens

Chairperson - Dr. Jesse H. Meredith

PATHOGENIC VIBRIOS IN NORTH CAROLINA WATERS

James D. Oliver
Department of Biology
University of North Carolina at Charlotte
Charlotte, North Carolina

ABSTRACT

The bacterial genus, Vibrio, is generally the major taxonomic group of bacteria cultured from estuarine waters, and one of the most common in open ocean waters. Although of great significance as saprophytic agents (they are active chitin mineralizers) and the source of several economically important fish and shellfish diseases, a number of members of this genus are also the causative agents of a variety of important human infections. These range from superficial wound or gastrointestinal infections to severe and frequently fatal septicemias. This paper reviews the medically important Vibrio diseases of man, and notes their incidence in North Carolina waters.

INTRODUCTION

The genus Vibrio constitutes one of the most common genera of bacteria in estuarine and marine oceanic environments. In the 1974 edition of Bergey's Manual of Determinative Bacteriology, the taxonomic "bible" of bacteria, five species of the genus Vibrio were listed. Of these, only V. cholerae and V. parahaemolyticus were known human pathogens. V. cholerae, implicated in seven worldwide epidemics of cholera since its first isolation in 1884, continues to be a significant health hazard, with 79,000 cases of cholera reported from around the world during the last two years. V. parahaemolyticus is a major cause of food poisoning, especially in those countries where raw seafood is commonly consumed. It causes 70% of the food poisonings in Japan, where 13,000 cases were reported in 1972 alone. Now physicians and microbiologists are confronted not only with these two pathogenic marine vibrios, but with a number which has literally been increasing every year. As of 1986, there were 30 described species of the genus Vibrio, of which 11 have been associated with human disease (Table 1). The majority of these newly described species are gastrointestinal pathogens causing relatively mild food-poisoning symptoms with diarrhea (for recent reviews see Farmer et al., 1985; Morris and Black, 1985; Oliver, 1985; Tison and Kelly, 1984). A notable exception among these "newcomers", however, is Vibrio vulnificus, one of the most invasive and rapidly lethal human pathogens known today. This review summarizes the taxonomy, distribution, and diseases caused by the most important of these marine vibrios, with special reference to their presence in North Carolina waters.

Table 1. *Vibrio* spp. Associated with Human Disease

1974	1987
Vibrio cholerae	Vibrio cholerae
V. parahaemolyticus	V. parahaemolyticus
	V. alginolyticus
	V. vulnificus
	V. damsela
	V. hollisae
	V. fluvialis
	V. furnissi
	V. mimicus
	V. metcshnikovii
	V. cincinnatiensis

Vibrio cholerae

This bacterium, first isolated in 1884, has been the cause of seven world-wide epidemics. The current pandemic has involved some 34 countries and caused nearly 80,000 cases. The symptoms, which begin as little as six hours after infection, are typical of gastrointestinal disease, and include abdominal discomfort, vomiting, and diarrhea. Unlike other vibrios causing similar symptoms, however, intestinal ulceration is common, generally resulting in bloody diarrhea. The patient may suffer massive fluid loss, a result of 20 to 30 watery stools per day. The resultant dehydration causes collapse, coma, and often death (Morris and Black, 1985).

Taxonomically, *V. cholerae* isolates may be subdivided by their cell surface chemistry. Those strains which agglutinate in "01" antiserum have historically been considered the most important type, responsible for the epidemic, or Asian, form of cholera described above. Those isolates which do not agglutinate in 01 antiserum have been collectively referred to as NAG ("non-agglutinating") vibrios, NCV ("non-cholera") vibrios, or more properly, "non-01" *V. cholerae*. Although not considered to be of great importance as agents of epidemic cholera, it is becoming increasing apparent that some of the non-01 strains are, in fact, capable of producing the cholera toxin and of causing cholera-like symptoms. Further, and in contrast to the 01 strains which are capable of causing only intestinal disease, non-01 *V. cholerae* strains are significant in causing potentially serious wound infections. Non-01 strains of *V. cholerae* have been isolated from ear infections, blood and sputum samples, appendices, gallbladders, and cerebrospinal fluid, as well as wounds. Septicemias, some with fatal outcomes, have also been reported for non-01 strains. This indicates an ability to invade tissue, a trait not associated with the 01 type (Oliver, 1983).

Although an occasional case of cholerae appeared in the early 1970's, cholera was not considered a problem in this country until 1978 (Table 2). At that time, 11 cases were reported in Louisiana, all a result of consumption of contaminated crabs. In 1981, 17 more cases were reported in a single outbreak, with contaminated drinking water on an oil rig in the Intracoastal Waterway of Texas being implicated as the source of infection. In both outbreaks, _V. cholerae_ group 01 were isolated and shown to be identical to a strain isolated from a cholera case in Texas in 1973. More recently, 5 cases were reported in August of 1986. It has now been clearly established that these strains differ from those found in other countries, and represent a population indigenous to this country. Indeed, _V. cholerae_ group 01 bacteria have been isolated from oysters and waters from the East and Gulf coasts, and thus appear to be quite ubiquitous. Strains of non-01 cholera appear to be even more common in estuarine environments, being present in both water and shellfish (Oliver, 1983). One study (DePaola et al., 1981) carried out in the Gulf Coast reported 36%, 37%, and 84% of the 477 samples of shellfish, mud, and seawater studied to harbor _V. cholera_ isolates.

Table 2. Cases of _Vibrio cholerae_ in the United States[a]

Date	State	Cases	01	Vehicle
1973	TX	1	+	?
1976	AL	1		shrimp gumbo
1977	AL	1	+	oysters
1978	LA	11	+	crab
	AL	2		oysters
1979	FL	6		oysters
	TX	2		"seafood"
	LA	6		"seafood"
1980	FL	1	+	oysters
1981	TX	2	+	?
	TX Gulf	17	+	drinking water
	NH	1		clams
1984	MD	1	+	crabs
1985	CA	1	+	oysters
1986	FL	2	+	oysters
	AL	14		oysters
	LA	4	+	crab, shrimp
	GA	1	+	oysters

[a] No cases had occurred in the United States Between 1911-1972

It is now evident that both 01 and non-01 strains of V. cholerae are capable of causing epidemic cholera, and that the non-01 strains may also produce potentially fatal wound infections. Further, V. cholera, generally regarded in the United States as being a problem only in eastern and mid-eastern countries, is in fact a part of the normal estuarine microflora in this country, having been isolated from the Chesapeake Bay of Maryland to the Gulf of Mexico. Despite the ubiquity of this species in southeastern waters, we have been most fortunate in that no cases of cholera have occurred in N.C.

Vibrio vulnificus

The wound infections and septicemias occasionally caused by non-01 strains of V. cholerae are similar to those caused by V. vulnificus. This marine pathogen is one of the most invasive bacterial species ever described and has been the subject of intense investigation since its first description in 1976 (for a review, see Oliver, 1989). V. vulnificus can cause infection by two routes: ingestion of contaminated raw seafood, particularly oysters, or introduction of seawater containing the bacterium into a wound injury. Of the two routes, ingestion is the more serious. The organism appears able to penetrate the intestinal tract and produce a massive infection with a 40-60% fatality rate. In almost all of these cases, the infected individual has some underlying disease. These include hepatitis, thalassemia major, hemochromatosis, or most commonly liver cirrhosis as a result of alcoholism. Such diseases typically result in elevated levels of serum iron, a situation apparently essential to the overwhelming infections this bacterium is capable of producing. Symptoms of V. vulnificus septicemia generally include fever, chills, and decreased blood pressure leading to shock (Table 3). The time to death is often quite rapid, with patients frequently dying within hours after hospital admission (Oliver, 1987). It is essential that persons with diseases such as those mentioned above refrain from eating raw seafood, as this combination has potentially disastrous consequences.

Wound infections involving V. vulnificus often occur while fishing, crabbing, or shucking oysters, and are always seawater associated. Although the fatality rate is lower (ca. 20%) as compared to the septicemias, the wounds are characterized by swelling, redness, edema, and a rapidly developing subcutaneous tissue destruction often resulting in limb amputation. Unlike most septicemia cases, these wound infections often occur in otherwise healthy individuals.

Vibrio vulnificus has been shown to occur on the East, West, and Gulf coasts of the United States. Our studies of east coast waters have shown this organism to be present in oysters, water, sediment, and plankton. While we have found the numbers of V. vulnificus in seawater to be relatively low (ca. 5-10/ml), filter-feeding oysters and clams concentrate this bacterium to over 10^4/gram (Oliver et al., 1982; Oliver et al., 1983).

Table 3. Summary of Primary Septicemic and Wound Infections produced by *Vibrio vulnificus*

	Primary Septicemias (n=57)	Wound Infections (n=54)
Symptoms		
Fever	94%	85%
Chills	86	68
Hypotension[a]	43	19
Nausea	60	37.5
Vomiting	35	30
Diarrhea	30	7
Abdominal pain	44	0
Secondary lesions	69	6
Edema		91
Cellulitis		94
Chronic disease	94%	57%
Liver disease	76	21
Diabetes	9	15
Cancer	3	13
Raw oyster consumption	85%	11%
Seawater/shellfish exposure	19	89
Median incubation time (h.)	26	16
Amputation/debridement/grafting	38%	58%
Fatal	56	22

[a] Systolic pressure less than 85 mm

We have isolated *V. vulnificus* from samples taken from Cape Hatteras and Fort Fisher in North Carolina, and from Myrtle Beach in South Carolina. In N.C. during 1985, three cases were reported, but the number of cases involving this vibrio appear to be increasing in southeastern waters. Nine fatal cases have already been reported in Florida during 1987 (personal communication, Richard Howard, University of Florida School of Medicine).

Vibrio parahaemolyticus

Another disease-causing marine vibrio, *V. parahaemolyticus*, has long been known as a serious pathogen occurring in fish and shellfish. Nearly three-fourths of all food poisonings in Japan, where significant amounts of raw or slightly cooked seafood is consumed, are caused by this bacterium. From 1971 through 1978, at least 16 outbreaks of *V. parahaemolyticus* gastroenteritis have been reported in the United States (Beauchat, 1982). In the largest, 1133 people who had consumed contaminated crabmeat and shrimp in Louisiana became infected. Although no large outbreaks have occurred in North Carolina, two cases were reported here in 1985. It should be emphasized here that, of all the pathogenic vibrios, only *V. cholerae* is "reportable", i.e., it is the only one which physicians must report to the State Health laboratory in Raleigh, Thus, we suspect that the actual number of infections with this microorganism is far greater than the numbers reported here.

Unlike *V. vulnificus*, the disease caused by *V. parahaemolyticus* involves watery diarrhea (98%), acute abdominal pain (82%), nausea (71%), vomiting (52%), headache and fever (27%), and chills (24%) (Beuchat, 1982). The diarrheal stools are occasionally bloody. The incubation period between consumption of the contaminated seafood and onset of symptoms is from 4 to 96 hours, and the disease typically lasts three days. Interestingly, pathogenicity of this vibrio species is not associated with all isolates. Only those strains which produce a hemolytic toxin (the "Kanagawa" hemolysin) have been found to be virulent.

V. parahaemolyticus is a ubiquitous microorganism that has been isolated throughout the world from nearly every estuarine environment which has been examined. It occurs in seawater, sediments, and shellfish, and a strong association with zooplankton and water temperature has been demonstrated.

The most comprehensive study carried out on the incidence of *V. parahaemolyticus* present in seafood taken from North Carolina waters was reported by Hackney et al., in 1980. They analyzed 716 seafood samples over a three year period and found *V. parahaemolyticus* to be present in 46% of them. Of the various seafoods examined, *V. parahaemolyticus* was found most commonly in unshucked oysters (79%) and clams (83%), and in live crabs (100%). As is generally the case with bacteria such as *V. parahaemolyticus* which are part of the normal flora in estuarine environments, no correlation was found between the presence of *V. parahaemolyticus* in these samples and the occurrence of such pollution indicators as fecal coliforms or enterococci. The occurrence of *V. parahaemolyticus*, which has been shown in several studies to prefer warm waters, was also found by Hackney et al. to demonstrate a seasonal variation in the seafood examined. Samples examined during the cold water months of

January and February were generally free of *V. parahaemolyticus*. Significant numbers of *V. parahaemolyticus* in the water column were only found in the months of May through November, when water temperatures were about 20°C, and were maximum between June and September, when temperatures were around 30°C. As is the case with non spore-forming bacteria such as the vibrios, adequate heat processing reduces or eliminates *V. parahaemolytics*, although recontamination through contact of cooked seafood with seawater or utensils harboring the bacterium remains a major problem in the epidemiology of these infections. Further, it has been found that steaming of crabs for more than eight minutes is required to remove the vibrio hazard.

Other Pathogenic Marine Vibrios

A number of other vibrios known to be pathogenic for man also exist in estuarine waters of the United States (Oliver, 1985). *V. alginolyticus* has been isolated around the world from seawater and seafood, and has been implicated as a cause of usually superficial wound infections of the eyes, ears, or skin. These infections, which generally occur following swimming in the marine environment, tend to remain localized and involve swelling, mild tissue destruction, and pussey exudates. Occasionally, cholera-like symptoms have been reported, but such infections appear to be restricted to immunosupressed patients. In 1985, two cases attributed to this vibrio were reported in N.C.

V. mimicus is closely related to *V. cholerae*, both phenotypically and clinically. Like cholera, symptoms of infection with this bacterium generally involve diarrhea, nausea, vomiting, and abdominal pain. This *Vibrio* occurs in seawater and shellfish, and the consumption of raw oysters has again been correlated with infection.

The next two species, *V. fluvialis* and *V. furnissii*, are closely related and both cause symptoms similar to cholera, including diarrhea, vomiting, and cramps. At least one death, apparently due to severe dehydration, has been documented as a result of *V. fluvialis* in the United States. Infections with *V. furnissii* do not involve dehydration, and appear to be milder than those involving *V. fluvialis*. Both bacteria are ubiquitous in estuarine environments, and two cases involving *V. fluvialis* were reported in N.C. during 1985.

V. damsela is unusual in being both a major pathogen of the damselfish, but also able to cause seawater-associated wound infections in man. Recent studies suggest it produces one of the more potent extracellular cytotoxins known. Unfortunately, the distribution of this potentially important human pathogen in the marine environment is virtually unknown.

V. hollisae, first described in 1982, has been implicated in human diarrheal infection, and has also been isolated from a blood culture. As is typical of those vibrios causing gastrointestinal infection, the disease produced by this bacterium has been associated with the consumption of raw seafood. Unfortunately, due primarily to its inability to grow on TCBS, the bacterial medium generally employed to isolate marine and estuarine vibrios, little is known regarding the ecology of this pathogen. There was one case involving this bacterium reported in N.C. during 1985, however.

Taxonomy

A recurring problem regarding the study of all of these pathogenic marine vibrios has been the lack of adequate isolation methods and considerable difficulty in our ability to rapidly and accurately identify the bacteria once they are isolated. Most researchers have employed thiosulfate-citrate-bile salts-sucrose (TCBS) agar, a medium originally developed for the isolation of *V. cholerae* from fecal specimens. Unfortunately, some estuarine vibrios (e.g. *V. hollisae*) are unable to grow on this medium, some non-vibrios are able to grow (hence limiting its selectivity value), and TCBS has very little differential capability. Thus, one must resort to tedious and time-consuming phenotypic testing to determine the identity of those organisms isolated from marine environments. Even then, many of the marine vibrios differ in only a few commonly examined phenotypic traits, and rapid identification methods, such as the API-20E system commonly employed in clinical laboratories, frequently misidentify these pathogens. Thus, in many cases, genetic analysis (such as DNA/DNA hybridization methods) must be resorted in order to provide an absolute identification of the isolated vibrio. The situation is further complicated by the abundance of marine vibrios that have yet to be described or identified taxonomically.

One avenue which offers hope in avoiding some of the above problems is the development of novel media for the isolation of these vibrios. The recently described "CPC" agar, a medium designed to be highly selective for *V. cholerae* and *V. vulnificus* is an example of one such medium (Massad and Oliver, 1987). Unlike other media typically employed for the isolation of marine vibrios, CPC does not depend on a limited ability to differentiate between species. Instead, this medium employs a number of selective characteristics such that only *V. vulnificus* and *V. cholerae* are able to grow (Table 4). Although field studies are only now being initiated, such a medium holds promise for adding to our knowledge regarding the distribution and ecology of at least these two human pathogens.

Another advance which holds even greater promise for the rapid and accurate identification of marine vibrios is the recent development of both gene probes and monoclonal antibody reagents designed to react specifically with target vibrios.

Table 4. Comparison of Vibrio-selective media[a]

Species (No. of Strains)	Growth on TCBS (sucrose rxn)	 SPS[b] (halo)	 CPC (cellobiose rxn)
Vibrio vulnificus			
Clinical (23)	+ (-)	+ (+)	+ (+)
Environmental (34)	+ (-)	+ (32/34+)	+ (+)
V. cholerae 01 (7)	+ (+)	+ (2/7+)	+ (-)
non-01 (8)	+ (+)	+ (3/8+)	+ (-)
V. aestuarianus (2)	+ (+)	+ (-)	NG[c]
V. alginolyticus (9)	+ (+)	+ (-)	NG
V. anguillarum (1)	+ (+)	+ (-)	NG
V. campbelli (3)	+ (-)	+ (-)	NG
V. damsela (1)	+ (-)	+ (-)	NG
V. fischeri (2)	+ (-)	+ (-)	NG
V. fluvialis (6)	+ (+)	+ (-)	NG
V. furnissii (5)	+ (+)	+ (-)	NG
V. harveyi (10)	+ (V)	+ (-)	NG
V. hollisae (4)	+ (-)	+ (-)	NG
V. mimicus (7)	+ (-)	+ (-)	NG
V. natriegens (1)	+ (+)	+ (+)	NG
V. nigripulchritudo (1)	+ (-)	+ (-)	NG
V. parahaemolyticus (9)	+ (-)	+ (-)	NG (1/9+)
V. pelagius (1)	+ (-)	+ (-)	NG
V. proteolyticus (1)	+ (-)	+ (-)	NG
V. splendidus (1)	+ (-)	+ (-)	NG
Photobacterium leiognathi	+ (-)	+ (-)	NG
Pseudomonas spp. (10)	1/10+ (-)	8/10+ (-)	NG
Flavobacterium spp. (5)	NG	2/5+ (-)	NG

[a] Oliver, J.D. and G. Massad, 1987. Appl. Environ. Microbiol. 53: 2262-2264.

[b] Media of Kitaura et al., 1983. FEMS Microbiol. Let. 17: 205-209.

[c] No growth

Table 5. Hybridization of Reference Strains with a DNA Probe for the *Vibrio vulnificus* Cytotoxin-hemolysin Gene

Reference strain	No. of strains hybridizing with probe/no. tested
V. vulnificus	103/103
V. parahaemolyticus	0/25
V. cholerae 01	0/4
V. cholerae non-01	0/6
V. hollisae	0/3
V. mimicus	0/5
V. alginolyticus	0/3
V. harveyi	0/16
V. ordalii	0/2
V. aestuarianus	0/3
V. campbellii	0/5
V. damsela	0/1
V. fluvialis	0/2
V. furnissii	0/1
V. metschnikovii	0/1
V. natriegens	0/1
V. pelagius	0/1
V. proteolyticus	0/1
V. splendidus	0/1
V. anguillarum	0/1
V. fischeri	0/1
Aeromonas hydrophila	0/1
Photobacterium leiognathi	0/1
Pseudomonas aeruginosa	0/5
Providencia stuartii	0/3
Proteus mirabilis	0/6
Serratia marcescens	0/3
Escherichia coli	0/13
Morganella morganii	0/3
Acinetobacter calcoaceticus	0/1
Klebsiella pneumoniae	0/1
Klebsiella oxytoca	0/1
Enterobacter cloacae	0/1
Citrobacter diversus	0/4
Salmonella spp.	0/4
Yersinia enterocolitica	0/1

Data taken from Wright et al., 1985. Infect. Immun. 50: 922-924 and Morris et al., 1987. Appl. Environ. Microbiol. 53: 193-195.

Cases in point are the recently described probe for the V. vulnificus hemolysin. This hemolysin gene has been found to be unique to V. vulnificus, and thus the probe can be employed to determine the presence of this vibrio even in the presence of great numbers of other vibrio and non-vibrio species (Table 5). Similarly, antibodies produced against the flagella of the various pathogenic marine vibrios have been shown to be extremely specific, and potentially of great value for the rapid identification of these bacteria. Tassin et al. (1983) reported the seven Vibrio species they studied to be correctly identified using this method, with accuracies of 93-100%. In a later study, Simonson and Siebeling (1986) found 99.3% of the V. vulnificus isolates examined to agglutinate within two minutes after the addition of the antibody preparation. Further, excellent specificity has been demonstrated in that 18 other vibrios examined did not agglutinate with the anti-V. vulnificus reagent.

CONCLUSIONS

The number of vibrio species recognized by public health officials has increased dramatically in the last 10 years. This awareness and recognition is likely linked to the greatly increased number of vibrio infections occurring in the United States. The cause of this increase is not known, but the potential for debilitating illness, amputation, and occasionally death, is significant, especially in coastal states. These bacteria are common in North Carolina waters and shellfish, and are known to have caused several serious infections in North Carolina. It is essential that awareness of physicians and clinicians be heightened as to the potential seriousness of these infections, and to improve our understanding of the ecology, pathogenesis, and treatment of these diseases. It is also critical that persons with elevated serum iron levels be made aware of the significant danger they face with the marine vibrios if they consume raw seafood.

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NATURAL TOLERANCE OF BACTEREMIA IN THE BLUE CRAB, CALLINECTES SAPIDUS

Ronald K. Sizemore
Department of Biological Sciences
University of North Carolina at Wilmington
Wilmington, North Carolina 28403-3297

ABSTRACT

The blue crab, *Callinectes sapidus*, has been found to harbor as part of its normal body flora several species of bacteria belonging to the genus *Vibrio*. Members of this genus are common inhabitants of temperate estuarine waters worldwide. Some *Vibrio* species such as *Vibrio parahaemolyticus* are known pathogens of man and marine organisms. These bacteria are common in and on healthy blue crabs. Furthermore, blue crabs seem to be able to tolerate these bacteria in their hemolymph, a condition which is usually associated with the diseased state in man. The public health implications and the role of these infections in crab mortalities is discussed.

INTRODUCTION

The blue crab, *Callinectes sapidus*, is an important commercial species along the Atlantic and Gulf Coasts of the United States with an annual commercial catch ranging from 9-36 million kg, plus an indeterminate quantity taken non-commercially (Gosner, 1979). The bacterial flora associated with this species has been the subject of several studies (e.g. Welsh and Sizemore, 1985). Reports in the literature regarding the bacterial burden of *C. sapidus* have shown that potential human pathogens can be isolated not only from processed crabmeat but also from apparently healthy and, therefore, marketable crabs (Fishbein, et al., 1970; Phillips and Peeler, 1972; Sizemore, et al., 1975; Tubiash, et al., 1975). Furthermore, the levels of infection which can occur in this species are such that ingestion of one crab could conceivably constitute an infective dose (the quantity of bacteria which must be ingested to cause disease) for humans.

The obvious public health implications have provided the rationale for much of the work with *C. sapidus*. While the medical profession may be satisfied with knowing what pathogens are present in the blue crab and how the consumer can best be protected, there are many additional questions related to the bacterial load of this species which are of interest to other scientific disciplines. In particular, the source of crab infections and the bacterial mode of entry into crabs are of concern to microbial ecologists, invertebrate pathologists and mariculturists.

Bacterial Flora of Crab Hemolymph

The exterior surface of crabs contains a rich variety of bacteria including species in the genus Vibrio (e.g. Sindermann, 1971; Sizemore et al., 1975). Vibrio species are also predominate in the abundant crab gut flora (Davis and Sizemore, 1982). The hemolymph of healthy blue crabs like other organisms was assumed to be sterile, however, several reports have documented the bacterial flora of crab hemolymph. Table 1 shows the relative bacterial load of blue crabs in several of these studies. Although sampling techniques and sites were different in these studies, it can be concluded that blue crabs do routinely harbor bacteria in their hemolymph.

The source of bacteria in crab hemolymph remains undetermined. Davis and Sizemore (1982) speculated that hemolymph bacteria could originate in the crab gut. This speculation contradicts earlier studies by Tubiash and co-workers (1975), who concluded that bacteria probably entered the hemolymph as a result of injury. A subsequent study by Sizemore and Davis (1985) showed a similarity in species composition between the hemolymph bacteria and the bacteria on the exterior of the crabs. This similarity made them reconsider their earlier hypothesis and conclude that bacteria from the crab's exterior, perhaps through the gills, are constantly penetrating into the crab's hemolymph.

Vibrio species are the predominate bacteria in all studies of healthy blue crab hemolymph (e.g. Colwell et al., 1975; Sizemore et al., 1975). Other portions of the crab anatomy also harbor Vibrio species and in some cases contain higher percentages of Vibrio species than in the hemolymph. For example, Sizemore and Davis (1985) report that 96% of the bacteria in crab feces are members of the genus Vibrio. Table 2 shows a breakdown of the Vibrio species associated with a variety of tissues in a typical crab. Despite the abundance of Vibrio in other parts of the crab, the emphasis of many studies has been on the hemolymph. The rationale for this bias is that hemolymph bacteria are more likely to cause disease in man because the normal cleaning and cooking processes are more likely to remove or kill bacteria on other sites of the crab. Furthermore, latent or chronic crab disease may also be related to prevalent crab hemolymph infections.

The most extensive study of the Vibrio species composition of crab hemolymph was probably the study of Davis and Sizemore (1982). They found that there was a large variation in the percentage of Vibrio ssp. (0 - 100%) found in different crabs. However, Vibrio was generally predominate and in 40% of the crabs studied, Vibrio spp. made up 75% of the bacteria in the hemolymph. Of particular significance was the occurrence of several pathogenic Vibrio species. For example, Vibrio parahaemolyticus, an organism which causes gastroenteritis in

Table 1. Summary of available data on the incidence of bacterial infections in the hemolymph of blue crabs.

	Tubiash et al. (1975)	Colwell et al. (1975)	Davis and Sizemore (1982)	Welsh and Sizemore (1985)
Study Site	Chinoteague Bay, Va.	Chesapeake Bay, Md.	Galveston Bay, Tx.	Wrightsville Beach, N.C.
Collection Method	Crab pots & dredge	Commercial sources & "collections"	Crab traps & trawls	Crab traps, pots & commercial sources
Enumeration Technique	MPN	Spread plate	Spread plate	Spread plate
Sampling Dates	8/68 - 11/69	Summer 1970	11/79 - 11/80	8/82 - 11/83
No. of Crabs	289	48	81	649
% Infected	82	100	88	75
Mean Level of Infection	1.9×10^{3}#	2.6×10^{5}*	6.5×10^{5}*	14@
Range	$0 - 6.6 \times 10^{3}$#	$100 - 3.0 \times 10^{5}$*	$0 - 3.0 \times 10^{7}$*	$0 - 9.5 \times 10^{4}$@
Summer Counts Higher than Winter Counts	YES	NR	NO	YES
Bacterial Levels Higher in Males	YES	NR	YES	NO
Bacterial Levels Higher in Injured Crabs	YES	NR	NO	YES

\# MPN per ml of hemolymph
@ Geometric mean

* Colony forming unit per ml of hemolymph
NR Not reported

Table 2. The relative abundance of Vibrio spp. in tissue of the blue crab, Callinectes sapidus.

Tissue	Bacterial Counts*	Percentage Vibrio
Eggs	10^6	50
Hepatopancreas	10^6	32
Stomach	10^8	50
Claw Meat	10^5	42
Mouth Parts	10^8	12
Shell	10^4	22

* Bacterial counts given as colony forming units per gram wet weight of tissue

humans, was the most common (found in 23% of the crabs) species isolated. A couple of more virulent species: V. cholerae, the causal agent of epidemic cholera and V. vulnificus, a bacterium which can cause fatal septicemia, were also commonly found in healthy crabs (2 and 7% respectively). When pooled hemolymph samples from several crabs were exposed to latex beads coated with antibodies against V. cholerae (generously provided by R. Siebeling, Louisiana State University), these beads routinely precipitated bacterial strains, which by clinical standards, are identical to V. cholerae.

The significance of this infection can be appreciated if one considers that the infective dose of these bacteria is usually high and casual contact with low number of the bacteria does not result in illness. A few crabs were found in their study which contained a high number and a pure culture of a Vibrio species. Ingestion of a single, poorly cooked crab with this level of infection could provide a logical route for the spread of this infection. Thus, crabs should be cooked carefully before consumption.

Crab Shedding Tank Mortality

Shedding soft shelled crabs from premolt hard crabs is a profitable business which is growing in North Carolina. Success of the shedding operation often depends on the availability of premolt crabs and the ability to prevent crab mortality before marketing. Since most shedding tank mortalities have been assumed to be due to microbial infection, studies have been conducted to determine the role of hemolymph infections in crab shedding tank mortalities.

Documenting mortality rates in shedding tanks is difficult and variations are extensive between individual shedders and facilities. Published reports have, however, reported mortality rates as high as 50-80% (Krantz et al., 1969; Haefner and Garten, 1974). Usually, these infections are believed to be the result of microorganisms introduced and encouraged in their growth by poor handling procedures and/or poor water quality. However, the documentation of chronic hemolymph infections in healthy blue crabs (Welsh and Sizemore, 1985) suggests a different route for shedding mortalities. To test this hypothesis, wooden shedding tanks were built similar to those used locally for commercial shedding. Premolt hard crabs were then placed into these tanks and monitored as they molted to soft crabs. These carefully controlled conditions allowed for continuous bacteriological sampling and analysis.

Approximately 450 crabs were shed in our experimental tanks with the majority of the crabs dying during the experiment. Crab mortalities varied between 8-80%, with an average mortality rate of 75%. This rate was presumed to be high due to the experimental conditions to which the crabs were subjected (i.e. periodic hemolymph sampling). A survey of local shedders suggested that their mortality rates generally were in the range of 10-30%. This study was terminated before conclusion but some preliminary results were obtained. Most premolt crabs (91%) contained bacteria in their hemolymph and most (85%) contained *Vibrio* species. No correlation was found between a particular bacterial species and increased mortality, but several human and crab pathogens were isolated. The most common of which was *V. parahaemolyticus*. Crab mortality was highest (43%) in the first few days of shedding and generally affected crabs which were not close to shedding more than those which were just about to shed. Crabs which died generally had higher bacterial counts in their hemolymph suggesting that bacteria caused their deaths, but 3% of the dead crabs had very low bacterial levels in their hemolymph suggesting another etiology. The preliminary recommendations of the study were that shedders should attempt to molt only those crabs which show signs of being very near molting so that time in the shedding tank is minimized. Preliminary results also suggested that shedding crabs in low salinity water may reduce mortality since *Vibrio* species require salt for growth and generally cannot grow in fresh water.

Crab Immunology

Despite the prevalence of bacteria in the crab hemolymph reported above, invertebrates similar to the crab are known to have immune systems. Decapod crustaceans exhibit immune responses including encapsulation, phagocytosis with or without the aid of serum factors, bactericidins, hemagglutins, agglutinins, and precipitins (Schapiro, 1975). Some success has been reported in immunizing blue crabs (Pauley, 1973), and blue crabs are known to produce phagocytic cells which should be effective in removing bacteria from the interior of the crab's body (Rabin, 1970). In light of these reports, the frequency of blue crab bacteremia is perplexing. Several investigators have postulated that crab hemolymph infections may be temporary with frequent re-entry of the bacteria resulting in the observed bacterial infections (Sizemore and Davis, 1985). This hypothesis assumes that the crabs have effective immune systems which can remove bacteria. An alternate hypothesis is that the crab has no effective immune system or that Vibrio spp. have found a way to avoid detection and/or destruction by the crab's immune system.

To test this hypothesis, experiments were conducted to determine if the blue crab's hemolymph could kill a Vibrio isolate. Fresh crab hemolymph was collected from healthy uninjured crabs which were maintained in a flowing seawater tank in this laboratory. The hemolymph was collected with a sterile syringe and then split into 3 fractions. One portion of the hemolymph was used whole, while the other 2 portions were treated to remove the cellular portion of the hemolymph to yield serum. This process involved centrifugation either with or without filtration through membrane filters (0.22 µm). Each fraction of the hemolymph was challenged with an equal aliquot of a Vibrio isolate and incubated for various time intervals. At the end of the exposure, bacterial numbers were determined and compared with the numbers before exposure to the hemolymph. Decreasing bacterial levels are assumed to be due to an immune response. To avoid hemolymph clotting, strontium chloride was added to most of the hemolymph fractions; however, controls were also performed without strontium chloride or with strontium chloride alone to determine the effect of this anticlotting agent.

Preliminary results from these experiments are inconclusive with little if any "immune response" observed. Whole unclotted hemolymph seemed to have the most bactericidal effect and it appeared that a cellular immune response which could be removed by centrifugation and/or filtration was present. This bactericidal response was very weak in our experimental conditions. This data could be artifactual and the immune response may be stronger in situ, or the blue crab may simply lack an active immune system.

SUMMARY

Blue crabs routinely harbor bacteria, mainly of the genus Vibrio, in their hemolymph. If the crab is stressed these bacteria may increase in number and could be responsible for the initial mortality seen in crab holding tanks. Attempts to quantitate a crab immune response using fractionated crab hemolymph were unsuccessful.

ACKNOWLEDGMENTS

The technical help of Ms. Lilli Wolf, Dr. John Davis and Mr. James Jones is gratefully acknowledged. Portions of this work were supported by a mini-grant R/MG-8406 from the UNC Sea Grant College Program.

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Chapter 3. Marine Biotechnology Aquaculture

Chairperson - Dr. Dirk Frankenberg

KARYOLOGICAL INVESTIGATIONS OF CHROMOSOME VARIATION PATTERNS ASSOCIATED WITH SPECIATION IN SOME RHODOPHYTA

Donald F. Kapraun
Department of Biological Sciences
University of North Carolina at Wilmington
Wilmington, North Carolina 28403

ABSTRACT

Cytogenetic details other than chromosome numbers are unavailable for most marine red algae because of the small size of nuclei, difficulty in obtaining adequate nuclear staining, and rarity of nuclear divisions in collected material. Recently, improved cytogenetic techniques and use of periodically fixed material have made karyological studies more rewarding. Published data suggest that both polyploidy and aneuploidy have accompanied speciation in red algal taxa. The present communication documents the occurrence of these phenomena in species of Rhodymeniales and Ceramiales. In addition, an attempt is made to determine the role processes such as centric fission and fusion, reciprocal translocations, and pericentric inversions may have played in algal speciation.

INTRODUCTION

Although speciation can occur without detectable chromosomal changes, in both plant and animal groups phenotypic variations are typically accompanied by karyotype modifications (Swanson et al., 1981). Variation in chromosome number and size as well as symmetry (relative size difference between the smallest and largest chromosomes) are among the modifications most commonly encountered (Stebbins, 1971; Jackson, 1976).

Polyploidy is considered to be much more important and widespread than aneuploidy in producing chromosome number variations in vascular plants (Grant, 1971; Stebbins, 1971) and has been demonstrated as well in the red algae Plumaria elegans (Bonnem.) Schmitz and Spermothamnion repens (Dillw.) Rosenv. (Drew, 1934, 1939, 1943). However, evidence suggesting that aneuploidy may have been a significant feature of evolution at both the species and population levels in red algae is now emerging (Kapraun, 1977, 1978; Kapraun and Freshwater, 1987).

The present cytogenetic investigation was initiated to identify patterns of karyotype transformations in additional taxa of Rhodophyta and to suggest karyological processes which may have produced them.

MATERIALS AND METHODS

Specimens for this study were collected in the vicinity of Wrightsville Beach, North Carolina (see Kapraun, 1980 for location map and habitat descriptions). Field collected tetrasporophytic specimens were fixed in 3:1 absolute ethanol-glacial acetic acid (Austin, 1959) and left overnight. Fixed material was stored in 70% ethanol, hydrolyzed in 1 N HCl for 10 min at room temperature to soften tissue, rinsed in distilled water, and stained in 2% aceto-orcein for 2-3 h prior to squash preparation. Chromosome numbers for all species are based on meiotic prophase nuclei in tetraspore mother cells. Representative karyotypes were made from various stages of prophase contraction. Documentation was made by microphotographs using an Olympus BH2-RFK microscope. Karyotypes were prepared by viewing 35 mm Kodak Plus-X film with a 48 X microfiche reader and tracing the chromosomes projected on the screen (Kapraun and Freshwater, 1987).

RESULTS AND DISCUSSION

Cytogenetic investigations of red algae are hampered by technical problems including the small size of their chromosomes, persistence of chromatin droplets until late prophase, failure of the nuclear envelope to disappear and allow chromosomes to spread, and synchrony of meiotic divisions which makes a determination of the exact time of cell divisions essential (Kapraun, 1977, 1978; Kapraun and Freshwater, 1987).

In the present study, fixation time of 23:00 - 24:00 for field collected specimens provided adequate numbers of nuclear division stages for all species. Use of a procedure to trace chromosome images of 35 mm film projected and magnified by a microfiche reader greatly increased the accuracy of karyotype analysis (Kapraun and Freshwater, 1987; Kapraun and Martin, 1987).

Rhodymeniales

Results of the present (Figure 1) and previously published cytogenetic investigations (Magne, 1964; Yabu, 1976) indicate that members of the Rhodymeniales have symmetric karyotypes with no relative size differences apparent among the small (0.4 - 0.8 µm) dot-like chromosomes. In contrast, with the closely related Palmariales, e.g. Palmaria palmata (L.) O. Kuntze (as Rhodymenia palmata (L.) Greville, Yabu, 1972, 1976) and P. mollis (Setchell et Gardner) van der Meer et Bird (van der Meer and Bird, 1985), are reported to have strongly asymmetric karyotypes.

In both Rhodymenia pseudopalmata (Lamour.) Silva (Figure 2) and Lomentaria baileyana (Harv.) Farl. (Figure 6), 10 bivalents are visible in a plate during diakinesis in tetraspore mother cells. Karyotypes for both species are characterized by a distinct ring of five equal-sized chromosomes which are separated from the other five randomly placed metaphase I chromosomes (Figure 1). Anaphase and telophase stages of the first meiotic division do not exhibit any special features, with

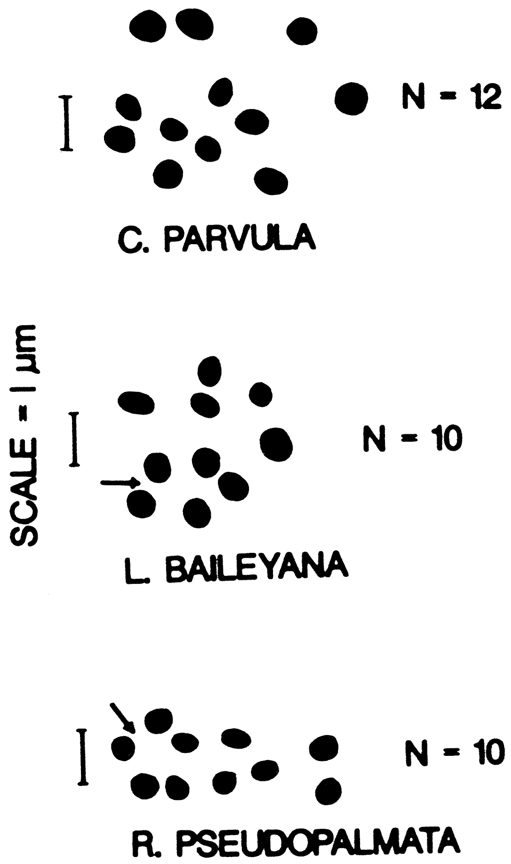
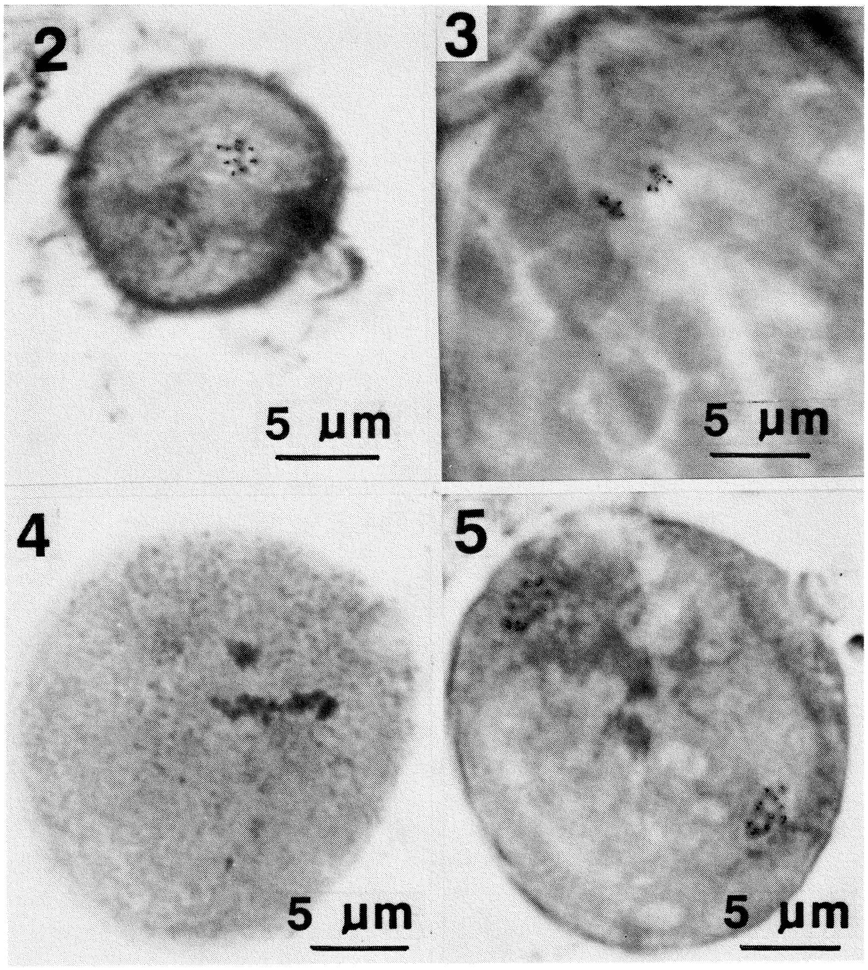
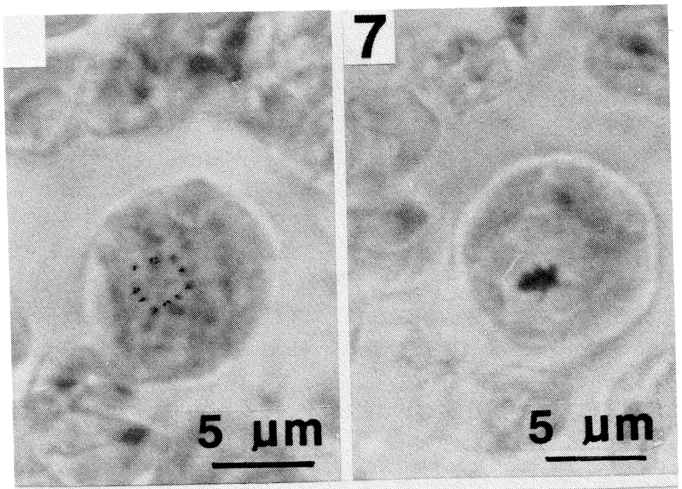
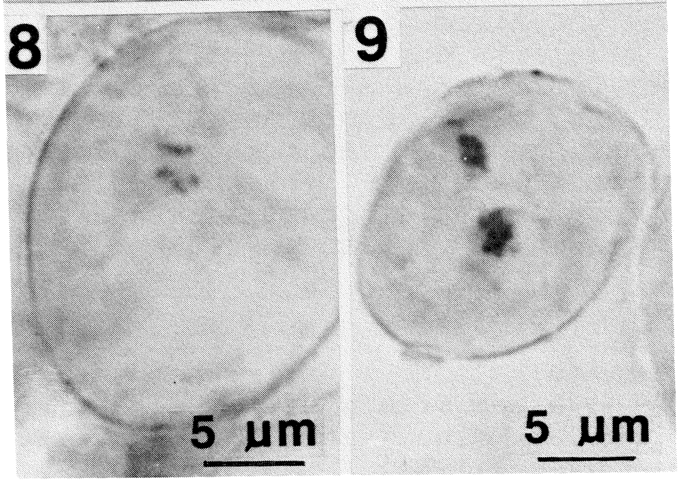


Figure 1. Typical karyotypes of <u>Champia parvula</u>, <u>Lomentaria baileyana</u> and <u>Rhodymenia pseudopalmata</u> representing average late prophase preparations.



Figures 2-5. Tetraspore mother cell meiotic chromosomes in *Rhodymenia pseudopalmata*. (2) Early meiotic metaphase showing equatorial aggregation, (3) Side view of metaphase, (4) Anaphase, (5) Late prophase in the second nuclear division.





Figures 6-7. Tetrasporee mother cell meiotic chromosomes in Lomentaria baileyana. (6) Early meiotic metaphase, (7) Late Anaphase.

Figures 8-9. Tetraspore mother cell meiotic chromosomes in Champia parvula. (8) Side view of metaphase, (9) Late prophase in the second nuclear division.

the two chromosome complements separating as a mass toward the poles (Figures 3-5, 7).

In *Champia parvula* (C. Ag.) Harv., 12 bivalents were seen during diakinesis (Figure 1). In early anaphase (Figure 8) of the first division and early prophase of the second division (Figure 9), the two groups of 12 chromosomes appeared smaller, but remained distinct. The conspicuous ring of five chromosomes described for *Lomentaria baileyana* above was not observed in *Champia*.

Chromosome numbers for eight species of Rhodymeniales in the present and previously published investigations are given in Table 1. The basic haploid number appears to be 10. Aneuploidy, which involves an increase or decrease in chromosome number by less than a complete genome (Jackson, 1971), is indicated for *Champia parvula* with N = 12. Haploid counts of N = 22-23 for *Lomentaria clavellosa* (Turn.) Gaill. and N = 28 for *Rhodymenia pertusa* (Post. et Rupr.) J. Ag. suggest a more complex sequence of karyotype modifications involving both aneuploidy and polyploidy. For example, the karyotype of *L. clavellosa* appears to consist of a 2X polyploid supplemented by two-three additional chromosomes while that of *R. pertusa* could have evolved from a 3X polyploid which lost two chromosomes. Since normal diploids cannot generally tolerate the loss of genetic information (Jackson, 1971), the success of these aneuploid species further supports the assumption of their polyploid origin. Centric fusion, centric fission and non-disjunction of bivalents during meiosis are known to result in chromosome number variations similar to those observed in the Rhodymeniales (Grant, 1971; Stebbins, 1971). However, lack of data in the present study for the relative size of each species' chromosome complement and its behavior during meiosis preclude any attempt to confirm the significance of these karyotype repatterning processes in the Rhodymeniales.

Ceramiales

The Ceramiales, one of the largest and most phylogenetically advanced orders of red algae, is characterized by a wide range of highly specialized, structurally diverse species (Bold and Wynne, 1985). The family Ceramiaceae, which includes the genera *Antithamnion*, *Antithamnionella* and *Callithamnion*, is usually considered to retain many features assumed to be primitive or ancestral in the order (Hommersand, 1963).

Despite the large number of *Antithamnion*, *Antithamnionella* and *Callithamnion* species for which chromosome data have been published (Tables 2 and 3), it is remarkable that photographic documentation is available only for species of *Antithamnion*: *A. heterocladum* Funk (Athanasiadis, 1983), *A. tenuissimum* (Hauck) Schiffner (Rueness and Rueness, 1973), and *A. cruciatum* (C. Ag.)

Table 1. Chromosome numbers for four genera of rhodymeniales

Species	Reference	1 N	2 N
Champia parvula (C. Ag.) Harv.	Present Study	12	
Chylocladia verticillata (Lightf.) Blid. (as *C. kaliformis* (Good. et Wood.) Hook.	Kylin 1923	c.20	
Lomentaria articulata (Huds.) Lyngb.	Magne 1964	10	20
Lomentaria baileyana (Harv.) Farl.	Present Study	10	20
Lomentaria clavellosa (Turn.) Gaill.	Svedelius 1937	10	20
" "	Magne 1964	22-23	44-46
Lomentaria orcadensis (Harv.) Coll. ex Tayl. (as *L. rosea* (Harv.) Thur.)	Svedelius 1935		c.20*
Rhodymenia pseudopalmata (Lamour.) Silva	Present Study	10	20
Rhodymenia pertusa (Post. et Rupr.) J. Ag.	Yabu 1976	28	

* Reported as unconfirmed diploid counts

Table 2. Chromosome numbers for some *Callithamnion* specis

Species	Reference	1 N	2 N
Callithamnion arbuscula (Dillw.) Lyngb.	Harris 1962	28-33	
C. byssoides Arnott ex Harv. in Hook.	Harris 1962	28-33	
" "	Present Study	c.30	
C. corymbosum (Sm.) Lyngb.	Hassinger-Huizinga 1952	30	60
" "	Harris 1962	28-33	
C. hookeri (Dillw.) S.F. Gray	Harris 1962	28-33	
C. roseum (Roth) Lyngb.	Harris 1962	39	
C. tetragonum (With) S.F. Gray	Harris 1962	28-33	
C. tetricum (Dillw.) S.F. Gray	Harris 1962		90-100*

* Reported as unconfirmed diploid counts

Table 3. Chromosome numbers for some species of *Antithamnion* and *Antithamnionella*

Species	Reference	1 N	2 N
Antithamnion cruciatum (C. Ag.) Naeg.	Whittick & Hooper 1976		85-110*
" "	Present Study	c.24	
Antithamnion heterocladum Funk	Athanasiadis 1983	46±4	86±8
Antithamnion plumula (Ellis) Thur. in LeJol.	Magne 1964	23	46
Antithamnion tenuissimum (Hauck) Schiffner	Rueness & Rueness 1973	c.32	c.64
Antithamnionella sarniensis Lyle	Magne 1986	c.34	c.60
Antithamnionella spirographidis (Schiffner) Wollaston (as *Antithamnion spirographidis* Schiffner)	Rao 1959	32-34	

* Reported as unconfirmed diploid counts

Naeg. (Whittick and Hooper, 1977). All published reports agree that in these genera, chromosomes are minute, dot-like, ranging from about 0.3 - 1.5 µm in length. In contrast, our observations on Callithamnion byssoides Arnott ex Harv. in Hook. (Figure 10) and Antithamnion cruciatum (Figure 11) from coastal North Carolina indicate that for both species, late prophase chromosomes are heteromorphic, resulting in an asymmetric karyotype with a combination of spherical and distinctly rod-shaped chromosomes. We speculate that such karyotypes are highly evolved and could have resulted from karyological phenomena such as reciprocal translocations.

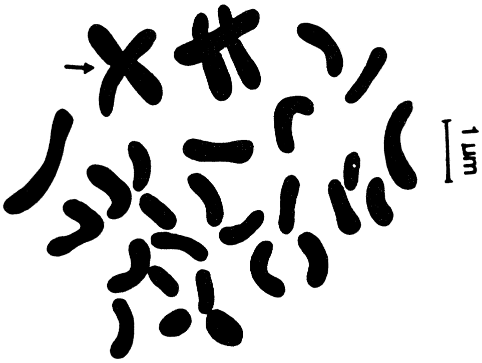
In the present study, approximately 30 bivalents were observed in late prophase and diakinesis in tetraspore mother cells of C. byssoides (Figures 12-15). These results are consistent with previously published reports which give a haploid number of N = 30 for most species (Table 2). The report by Harris (1962) of N = 90-100 for C. tetricum (Dillw.) S.F. Gray undoubtedly represents a triploid complement.

Approximately 24 bivalents were observed in late prophase and diakinesis in Antithamnion cruciatum tetraspore mother cells (Figures 16 and 17). These results are in agreement with previously published investigations which indicate a basic chromosome number of N = c.24 in Antithamnion species (Magne, 1964), with N = 46 reported in A. heterocladum (Athanasiadis, 1983) representing a diploid derivative.

Antithamnioid algae have recently undergone extensive taxonomic revision with the result that several genera, including Antithamnionella, have been segregated from Antithamnion (Wollaston, 1971, 1972; Abbott, 1979). Data from cytogenetic investigations appear to confirm the genetic distinctness of these two groups as Antithamnionella species having a different basic chromosome number of N = c.32 (Table 3), with higher numbers reported for A. cruciatum (Whittick and Hooper, 1976) and A. heterocladum (Athanasiadis, 1983) representing polyploid derivatives. Consequently, the chromosome complement of N = 32 reported for A. tenuissimum (Rueness and Rueness, 1973) appears anomalous, suggesting that transfer of this species to Antithamnionella should be given serious consideration.

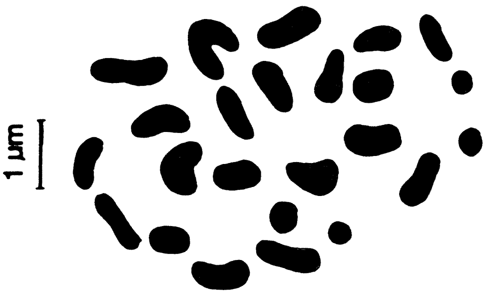
CONCLUSION

In summary, cytogenetic investigations indicate that both aneuploidy and polyploidy have accompanied speciation processes in the red algal orders Rhodymeniales and Ceramiales. In addition, patterns of karyotype asymmetry strongly suggest that transformation processes common in higher plants such as centric fission and fusion, reciprocal translocations, and pericentric inversions have occurred in these red algae.



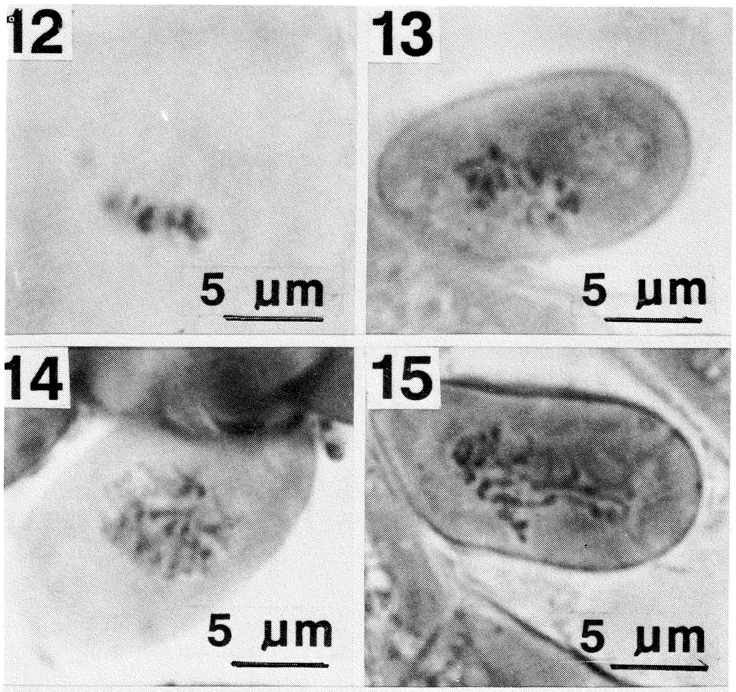
CALLITHAMNION BYSSOIDES
N - c.30

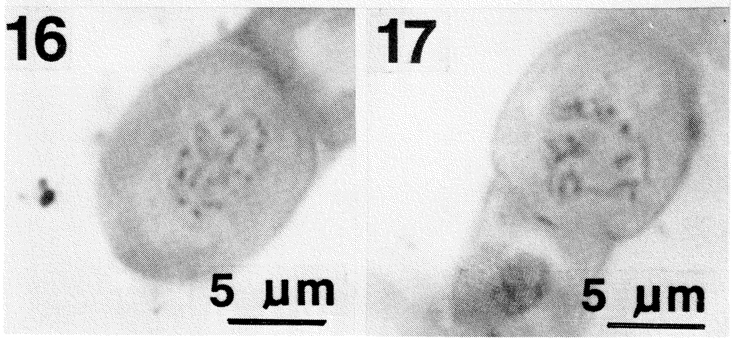
Figure 10. Typical karyotypes representing average late prophase preparations - <u>Callithamnion byssoides</u>



ANTITHAMNION CRUCIATUM
N - c.24

Figure 11. Typical karyotypes representing average late prophase preparations - <u>Antithamnion cruciatum</u>





Figures 12-15. Tetraspore mother cell meiotic chromosomes in *Callithamnion byssoides*, (12) Side view of equatorial aggregation at metaphase, (13) Metaphase, (14-15) Late prophase showing combination of dot-like and rod shaped chromosomes.

Figures 16-17. Tetraspore mother cell meiotic chromosomes in metaphase nuclei of *Antithamnion cruciatum*.

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THE USE OF AGRICULTURAL SLASH WASTE TO SUPPORT THE GROWTH OF MARINE NITROGEN FIXING MICROORGANISMS: POTENTIAL APPLICATIONS IN AQUACULTURE

Brad M. Bebout and Hans W. Paerl
Institute of Marine Sciences
University of North Carolina at Chapel Hill,
Morehead City, North Carolina 28557

ABSTRACT

The addition of an agricultural waste product, small particles of corn slash, to seawater resulted in stimulation of nitrogen fixation (nitrogenase activity) by the naturally-occurring microbial community. Specific concentrations of corn particles appeared to be most effective in eliciting this response. The microbial community in the seawater was able to respond very quickly to the addition of corn; maximum rates of nitrogenase activity were often reached within six days and considerable activity was present within 48 hours. Agitation of the corn-seawater mixture had a negative effect on the magnitude of nitrogenase activity observed. The addition of corn slash lowered dissolved oxygen concentrations in the seawater markedly, often resulting in anoxic conditions even in containers open to the atmosphere. Oxygen microelectrode profiles near the corn particles revealed strong gradients in oxygen concentration, with oxygen concentrations much lower than ambient at the particle surface. Application of tetrazolium salt (TTC = 2,3,5-Triphenyl 3-tetrazolium chloride) confirmed the presence of reduced microzones on, and within the particles. The proposed application of corn slash as a means of generating nitrogen-enriched seawater for the mass culture of algae and nitrogen-enriched corn particles as a food source for aquaculture is discussed.

INTRODUCTION

Primary production, and resultant marine fertility, is frequently limited by the availability of biologically utilizable nitrogen (Dugdale, 1967). It follows that organisms which are able to make use of nitrogen in any chemical form would have a competitive advantage in such systems. One microbial strategy to alleviate nitrogen limitation is nitrogen (N_2) fixation, in which atmospheric nitrogen, abundant in seawater, is "fixed", at the expense of an energy source by the enzyme nitrogenase into the biologically utilizable from ammonia. Certain marine eubacteria and cyanobactgeria present in seawater are known to have this ability (Jensen, 1981; Guerinot and Colwell, 1985), yet rates of nitrogen fixation measured in seawater are usually very low or undetectable. Various explanations for this apparent paradox have been proposed, including oxygen inhibition of the enzyme nitrogenase (Paerl and Prufert, 1987), molybdenum limitation (Howarth and

Cole, 1985), and organic matter availability (Paerl et al., 1987). It appears from the latter that there are relatively large populations of nitrogen fixing microorganisms present in seawater which can be readily (within 24 h) stimulated with the addition of a limiting nutrient or through the creation of environmental conditions favorable for the process to proceed.

The addition of plant material, such as that found in naturally occurring detritus, has been found to result in greatly enhanced rates of nitrogen fixation in the coastal waters of North Carolina (Paerl et al., 1987). In an analogous fashion, straw has been used in some terrestrial agricultural systems to increase nitrogen fixation by naturally-occurring soil microorganisms (Jensen and Swaby, 1941; Halsall and Goodchild, 1986). The present work is an attempt to determine the feasibility of using a local, readily available agricultural waste product having a high carbon/nitrogen (C/N) ratio to enhance nitrogen fixation in seawater. Ideally, this waste product should provide a readily-utilizable organic carbon, and hence energy source, for supporting heterotraphic (and possibly autotrophic) N_2 fixation. Post-harvest corn slash (leaves and stalks) satisfies both requirements. Here, we intend to examine the possibility of inducing naturally occurring populations of nitrogen fixing microorganisms in seawater to enrich corn slash waste with biologically available nitrogen. Potential applications for this material include its use as a fertilizer for the mass culture of algae and cyanobacteria and as an "internally produced" food material (protein, carbohydrate) for aquaculture.

MATERIALS AND METHODS

A series of experiments were performed in which nitrogen fixation, as determined by a modified acetylene reduction method (Stewart et al., 1967; Paerl and Kellar, 1978), was measured in seawater to which corn slash had been added. These experiments were initially conducted in the laboratory and later scaled up to larger containers which were incubated outdoors.

Laboratory experiments were conducted as follows: Stalks and leaves of corn grown locally without the use of pesticides were collected in the post-senescence state (standing-dead). Some of the corn material was mulched at the field using a garden shredder-mulcher, and some was transported back to the laboratory whole and later shredded with hand tools. The corn slash was then air dried and/or freeze dried and stored in a freezer until use. Prior to experiments, the slash was further fragmented using either a Wiley mill (#20 mesh) or an electric household coffee/spice mill having a stainless steel rotating blade. Final particle sizes ranged from <0.1 mm to >1.0 cm in length. Varying amounts (0.05-2.0 g, depending on the individual experiments) of corn slash were then placed in Pyrex or polycarbonate 125 ml flasks. The flasks and corn were then sterilized by autoclaving and allowed to cool. Subsequently, 60 ml of freshly collected seawater was added to each flask. The flasks were then stoppered with foam rubber stoppers which permitted gas exchange between the aqueous phase and the atmosphere. The flasks were incubated for varying lengths of time (5-12 days, again depending on the experiment) in darkness at 25°C. At 1-3 day intervals the incubation flasks were assayed for acetylene reduction (nitrogenase activity) as follows: Flasks were swirled to obtain a homogeneous distribution of corn particles and seawater. A 10 ml sample was withdrawn asceptically from each incubation flask with a sterile large bore pipette and placed into a 25 ml Erlenmeyer flask. The 25 ml flasks were then stoppered with rubber serum stoppers, resulting in a 10 ml acetylene phase and a 20 ml vapor phase in each flask. Purified acetylene (6 ml) was injected into the aqueous phase of inverted flasks using a 10 ml syringe having a 25 ga. needle. After a 3 h incubation with acetylene, the flasks were shaken vigorously for 10 s to release ethylene and a 0.3 ml sample of the vapor phase was taken with a 1 ml syringe having a 25 ga. needle for gas chromatography. Samples were analyzed using a Shimadzu GC-9A gas chromatograph (FID) having a 2 m Poropak-T column held at 80°C. The gas chromatograph was coupled with a Shimadzu Chromatopac C-R3A integrator. Ultra high purity nitrogen served as the carrier gas.

Outdoor incubations were conducted in a similar fashion. containers constructed of both PVC and polycarbonate were used to incubate 3 1 quantities of corn-amended seawater. The containers were floated in a large seawater pond to maintain _in situ_ temperatures. containers both open and closed to the atmosphere have been used for these experiments. All outdoor incubations were assayed for acetylene reduction activity as described previously for the laboratory experiments.

Dissolved oxygen concentrations in outdoor incubation containers were measured in some of the experiments using a YSI dissolved oxygen meter (model 54) having a model 5750 BOD probe. In addition, we examined gradients in dissolved oxygen concentrations near the surface of corn particles using oxygen microelectrodes. The construction and use of these microelectrodes has been described elsewhere (Revsbech and Jorgensen, 1986). We used a glass cathode type electrode with a sensing tip about 8 um across. Polarization voltage was supplied by, and electrode output was recorded with, a chemical microsensor (Diamond Electrotech model 1021). The electrode was calibrated using air and nitrogen-bubbled seawater standards. Corn particles used for oxygen microelectrode profiles were supported on a grid constructed of Nitex screen in well oxygenated seawater (see Paerl and Prufert, 1987). The microelectrode was positioned using a micromanipulator and oxygen measurements were taken at 100 um intervals.

The tetrazolium salt 2,3,5-Triphenyl 3-tetrazolium chloride (TTC), which requires highly reduced conditions (-0.4 V) for reduction, was applied to corn particles to help visualize the distribution of redox conditions within the particles. Tetrazolium salts are soluble in their oxidized form and are deposited as colored (red in the case of TTC) formazan crystals under reduced conditions. Localized oxygen consumption associated with the microbial oxidation of organic matter could thus be examined in parallel with N_2 fixation potentials associated with particles.

RESULTS

Corn slash particles were effective in stimulating nitrogenase activity in seawater at every concentration tested (Figure 1). The nitrogenase activity of seawater alone during the same incubation period was not detectable, being no greater than heat-killed seawater (abiotic controls). Some concentrations of corn particles appeared more effective in developing and stimulating nitrogenase activity than others. The period of time necessary for development and stimulation of nitrogenase activity varied from 1-7 days. Distinct peaks and declines in activity were observed during the incubation period.

Physical disturbance of incubation flasks had a pronounced negative effect on measured rates of nitrogenase activity (Figure 2). Flasks subjected to even gentle agitation (a laboratory orbital shaker at < 50 rpm) had much lower rates of acetylene reduction than undisturbed flasks.

The addition of corn slash to seawater ($1.67\ g \cdot l^{-1}$) had a dramatic effect on the dissolved oxygen content of the seawater (Figure 3). Anoxic conditions resulted, even in flasks open to the atmosphere, within 24 h of addition of corn particles. These anoxic conditions were maintained thorughout incubation periods lasting up to 14 days.

Oxygen microelectrode profiles near corn particles suspended in oxygenated seawater revealed marked consumption of oxygen by these particles (Figure 4). Oxygen tensions at the surfaces of the particles were much lower than ambient oxygen levels soon after being placed into oxygenated seawater.

The presence of these oxygen poor regions was confirmed with the application of TTC (Figure 5). Highly reduced regions were visible within, and on the particles.

DISCUSSION

There are a number of possible mechanisms which could be responsible for the observed stimulation of nitrogenase activity in seawater receiving corn slash. The corn slash almost certainly released organic carbon compounds into the seawater

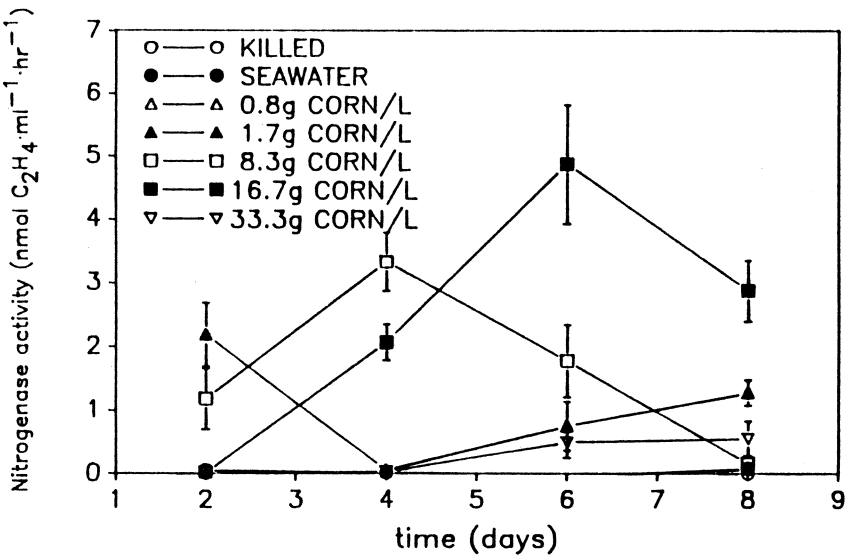

Figure 1. Nitrogen fixation (nitrogenase activity) over time in corn-amended seawater. Results are shown for a number of different concentrations of corn particles in seawater. "Killed treatment denotes heat-killed seawater sample used as a control for abiotic acetylene reduction. Error bars represent one standard error above and below the mean of five replicates.

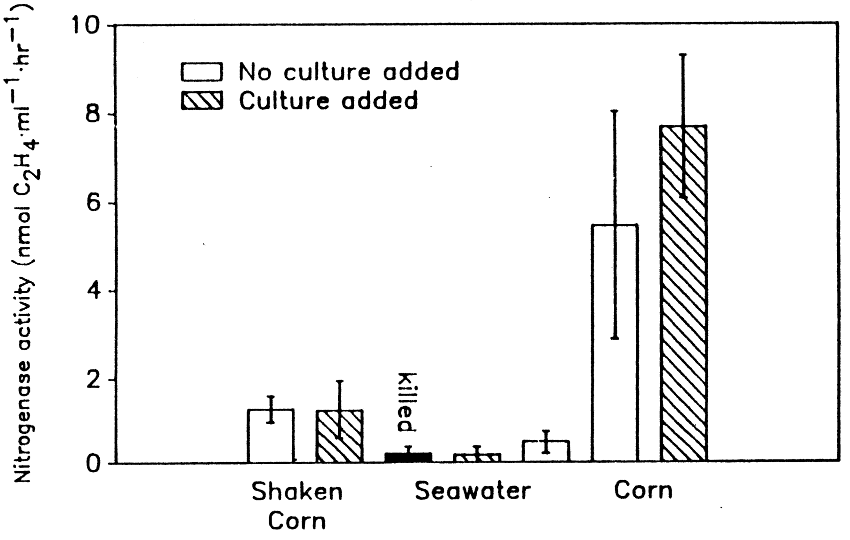

Figure 2. Impacts of physical disturbance (shaking) on nitrogenase activity of corn-amended seawater. A culture of nitrogen fixing bacteria was added to some of the treatments. Error bars represent one standard error above and below the mean of five replicates.

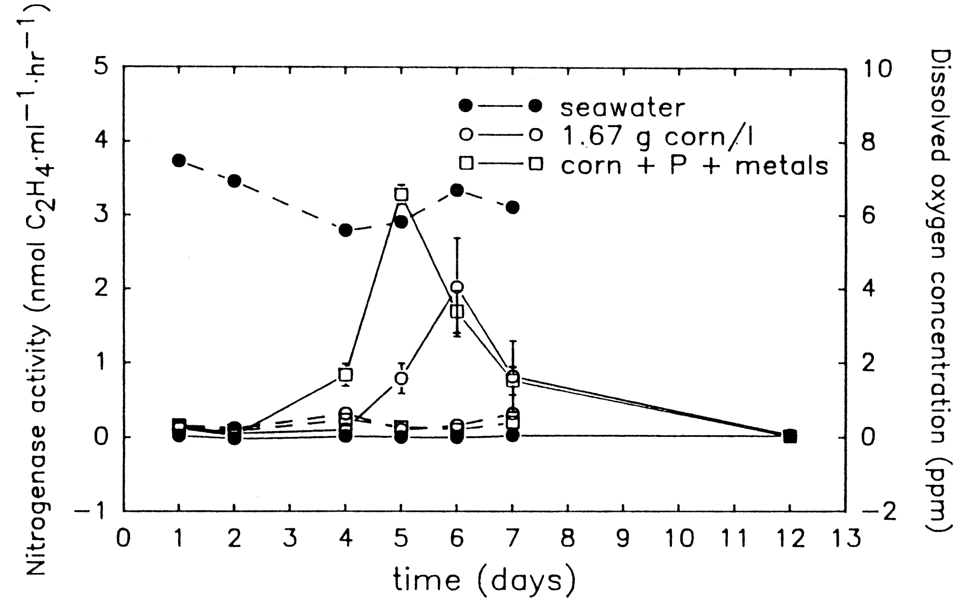

Figure 3. Nitrogenase activity and bulk-phase dissolved oxygen concentrations over time in corn-amended seawater. The dashed lines represent dissolved oxygen concentrations, and solid lines nitrogenase activity, in seawater (closed circles) and in corn-amended seawater (open circles). Trace metals and inorganic phosphorus were added to one of the treatments (open squares). Error bars represent one standard error above and below the mean of three replicates.

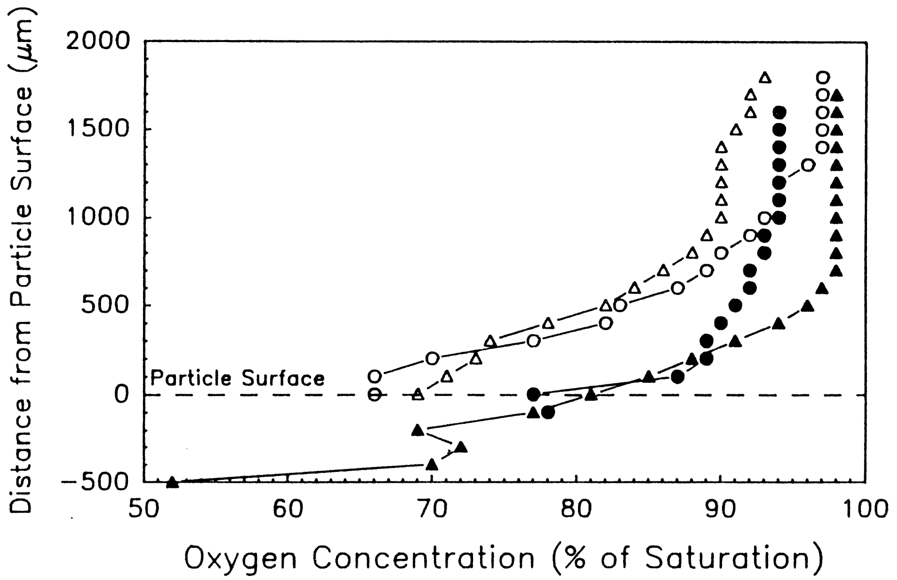

Figure 4. Dissolved oxygen concentration gradients associated with corn particles suspended in seawater. Oxygen microelectrodes were used to obtain profiles near the corn particles. Four replicate profiles are shown.

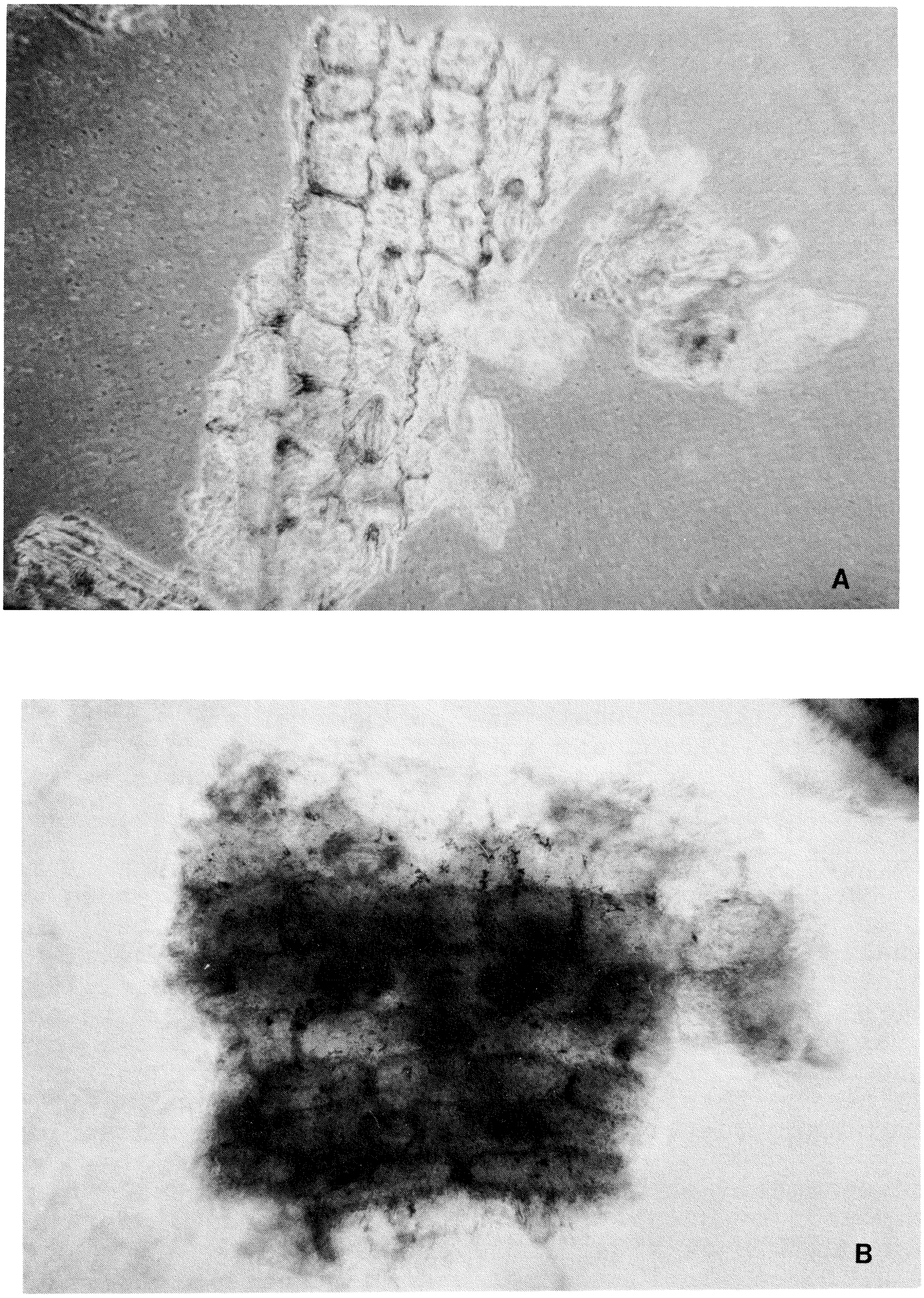

Figure 5. Photomicrographs of corn particles to which the tetrazolium salt TTC has been added. Figure 5a shows the appearance of a particle prior to incubation in seawater and Figure 5b shows the appearance of a particle after a several day incubation period. Localized regions where oxygen is absent (reduced microzones) appear darker. The corn particles are ca. 0.5 mm long.

which would be available to support microbial heterotrophic metabolism and nitrogen fixation. There is evidence from a number of natural systems, including coastal North Carolina waters, that organic carbon availability controls the development and proliferation of nitrogen fixation (Jensen, 1981; Paerl et al., 1987). In addition to acting as an energy (reductant) source, corn particles serve as a substrate to which nitrogen fixing microorganisms may attach. The addition of inorganic and organic particulate matter has been shown to stimulate rates of nitrogenase activity in seawater (Paerl et al., 1987). These authors found locally depleted oxygen concentrations near the particle surfaces, similar to those found near corn particles. These oxygen poor microzones offer some protection to the oxygen sensitive enzyme nitrogenase, which is essential for catalyzing N_2 fixation among resident microorganisms. When enough organic matter is present, as in the case of corn-amended seawater, high rates of respiration may lower oxygen tension throughout the incubation container, conferring protection from atmospheric oxygen concentrations to planktonic microorganisms as well as those attached to the particle surfaces.

SUMMARY

It is likely, whatever the mechanism for the observed stimulation of nitrogenase activity may be, that the input of "new" (fixed) nitrogen into the corn-seawater system is substantial. It seems possible that this new nitrogen (as protein in microbial biomass) may be harvested for commercial applications at a relatively low cost. High rates of bacterial growth and anoxic conditions in seawater amended with corn result in high levels of ammonium which could be used as an (internally-generated) fertilizer for mass culture of algae and cyanobacteria (blue green algae). Another possibility is that the corn particles, enriched with nitrogen due to associated microbial growth and attachment, could be used as a food source for aquaculture. We are presently engaged in research designed to examine the feasibility of such applications. Some of the more important questions currently being addressed include:

1) Can seawater enriched with microbially produced nitrogenous compounds be used as an inexpensive source of fertilizer for mass culture of algae and cyanobacteria?
2) Is nitrogen enrichment of corn particles significant enough to constitute a protein source?
3) Can corn particles enriched with microbial biomass be used as a chief or supplementary food source for commercially important aquaculture organisms?

ACKNOWLEDGMENTS

This work was supported by the North Carolina Biotechnology Center (project 86-G-01013) and the National Science Foundation (grants OCE 8500740 and BSR 8614951).

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PART II. STUDIES ON NORTH CAROLINA CONTINENTAL MARGIN

Chapter 4. Continental Shelf - Slope Dynamics

Chairperson - Dr. Larry Atkinson

THE GULF STREAM AND WIND EVENTS ON THE CAROLINA CAPES SHELF

Leonard J. Pietrafesa
Marine, Earth and Atmospheric Sciences
North Carolina State University
Raleigh, North Carolina 27695-8208

ABSTRACT

The subdiurnal frequency motions and thermohaline distributions on the Carolina Capes continental shelf are controlled by navifacial momentum and buoyancy flux exchanges and offshore Gulf Stream frontal events. Atmospheric forcing dominates current fluctuations and thermohaline variability in inner to midshelf waters in which gulf Stream frontal meanders and filaments become increasingly more important from middle to outer continental shelf waters. Gulf Stream frontal events are created as a result of the interaction of the Gulf Stream and the Charleston bump, a topographic feature at 32°N, 79°W, and propagate north into North Carolina waters. The alongshore component of the wind provides the principal forcing of inner to mid-shelf waters. Wind effects are manifested directly and mechanically via Ekman dynamics, but also occur indirectly through the setup of coastal pressure gradients. The mid to inner shelf current field consists of a wind driven surface component and slope currents which extend throughout the water column and are geostrophically coupled to both surface and mass field slopes. The bottom boundary layer consists of geostrophic and bottom stress induced current components. Water masses are derived principally from the Gulf Stream via frontal event processes, which not only advect warm, saline surface layer stream waters onto and along the mid to outer shelf, but also create an upwelling ridge along the outer shelf, during the passage, within which offshore waters are advected up and onto the shelf. Georgian shelf waters are advected into the CC region during periods of persistent southwesterly winds while Virginian coastal waters cross Diamond and even Lookout shoals, from the north, during periods of persistent northerly winds. In the offshore direction the thermohaline structure is essentially formed by the Gulf Stream front. Finally, the Red Tide, a dinoflagelate, can be carried from Florida coastal waters by the Gulf Stream to North Carolina where the presence of warm frontal filaments may allow the plant to be carried into shelf outer waters. Thereafter the plants can be carried towards the coast by wind induced currents.

INTRODUCTION

The coupled influence of the marine atmosphere and of the western boundary current, the Gulf Stream, are considerable in terms of the physical, chemical and biological aspects of the oceanography of the Carolina Capes, the region between Cape Romain, S.C., and Cape Hatteras, N.C., (cf. Figure 1). It is of use to present the setting and briefly review some of our understanding of the Gulf Stream influence, which provides the offshore boundary, and then to proceed with a presentation of concepts and data which serve to lend insights into the dynamics and effects of Gulf Stream frontal, wind and buoyancy flux events on the outer shelf of the Carolina Capes including: Capes Romain, Fear, Lookout and Hatteras.

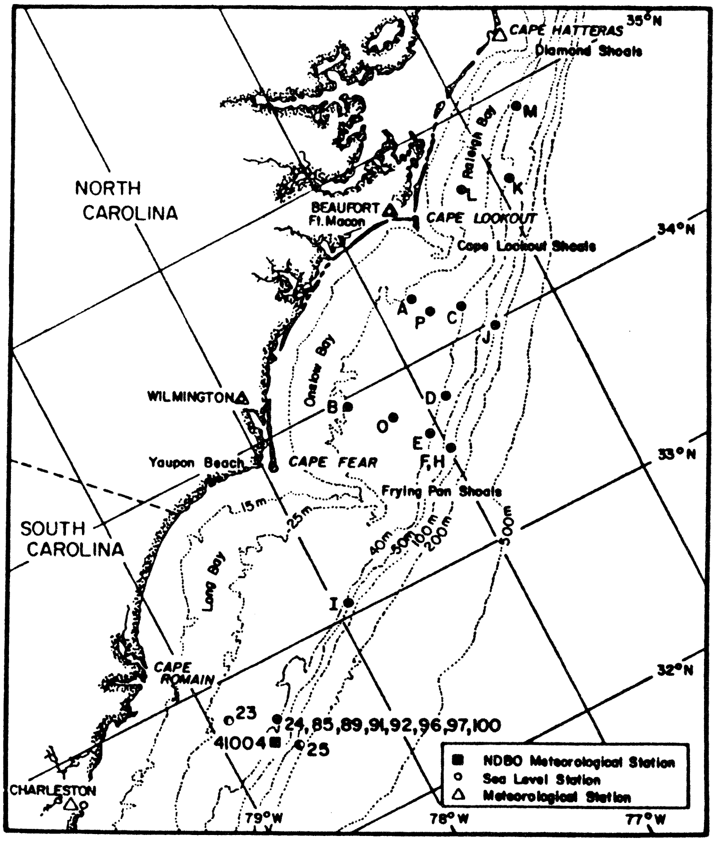

Figure 1. Mooring (large black dot), meteorological buoy, sea level station, and meteorological station locations, the data from which was available for this study.

The bathymetry of the shelf from Cape Romain to Cape Hatteras includes three shoals extending to the shelf break, forming a series of cuspate shaped semi-enclosed bays, as shown in Figure 1. The shelf width, which is approximately 100 km off Charleston and 120 km at Onslow Bay, narrows to 30 km off Hatteras. Water depth at the shelf break varies from 50 to 75 m. A more complete description of the geographic setting of the entire SAB can be found in a document entitled "Oceanography of the Southeastern U.S. Continental Shelf" (AGU, 1985).

Very High Resolution Radiometer (VHRR) satellite imagery suggests that south of 32°N the GSF follows the 100 m isobath and onshore-offshore displacements of the GSF seldom exceed 25 km. At 32°N, 79°W, a topographic feature on the upper slope, known as the "Charleston bump", causes the Gulf Stream to deflect to the east causing a quasi-permanent excursion of the GSF in the near downstream vicinity of this point (cf. Figure 2). This feature was first noted by U.S. Navy Commander J.R. Bartlett in 1880 as he conducted a series of "soundings and hauls of the trawl" from the Florida Straits to Cape Fear aboard the U.S. Streamer Blake. Commander Bartlett (1883) dutifully noted the offshore departure of the axis of the Gulf Stream from the 100 m due east of Savannah in what may be the first recorded reference to this feature. More recently, Pratt (1963), Pashinski and Maul (1973), Legeckis (1979), Pietrafesa (1977), Pietrafesa, Blanton and Atkinson (1978), and Brooks and Bane (1978) have presented testimony derived variously from VHRR, satellite altimeter and ocean station data, which provided further corroboration to Bartlett's contention. Pietrafesa, et al. (1978) estimated that the GSF was deflected 60-100 km offshore of the shelf break 70% of the time.

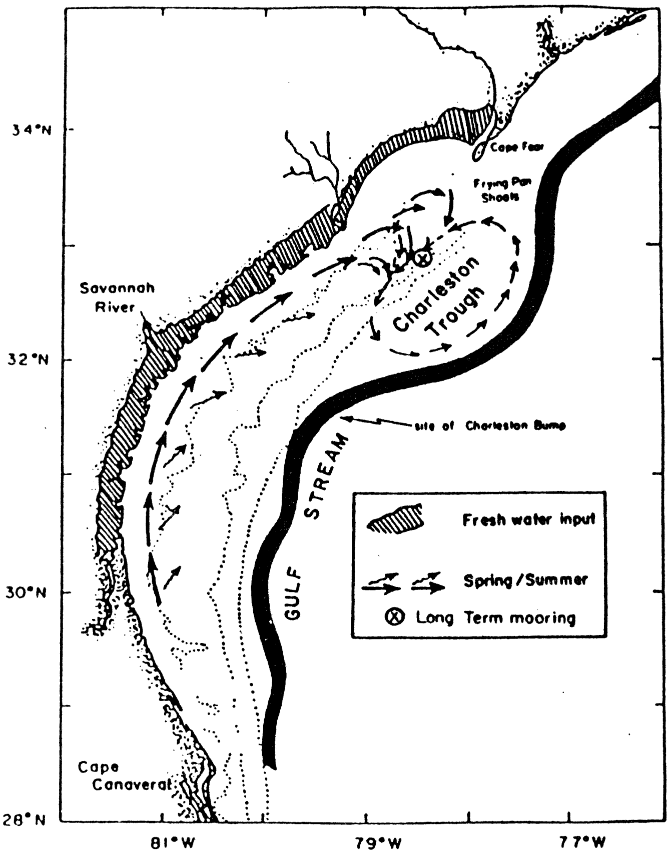

Figure 2. Conceptual shematic of continental margin transport features related to the Charleston Trough. (See text for details).

According to Rooney, Janowitz and Pietrafesa (1978) and Chao and Janowitz (1979), the interaction of the Gulf Stream with the topographic irregularity, the bump, would affect the generation of a quasi-stationary Topographic Rossby Wave with wavelength the order of one to three hundred kilometers. In the lee, i.e. to the north and west of the point of deflection, the trough of the wave would exist. The easterly half of the trough is defined by the Gulf Stream front as observed in VHRR satellite imagery, but the western part of the trough is not easily discerned by IR techniques. We are aided here by current meter data and satellite altimeter data.

Monthly averaged currents on the outer shelf at the forty m isobath offshore of Cape Romain (east of Charleston, S.C.) display a net southerly motion except during the spring when an easterly motion is suggested (Figure 3). Additionally, a sea surface topography map (Figure 4) constructed from Seasat satellite altimeter data suggested that the trough is a large blow like depression about which there might be a cyclonic circulation. The circulation resulting from such a cyclonic cell, not necessarily closed, could entrain low salinity water from off the shelf and there could also be persistent upwelling within the trough itself as first suggested by Pietrafesa (1979). Hydrographic observations (Figure 5) support this notion.

Imagery from NOAA's Coastal Zone Color Scanner (CZCS image compliments of C. McClain, NASA Goddard) shows a large pool of high chlorophyll-a situated near the shelf break at 33°N (Figure 6). Pietrafesa (1983) hypothesized that such pools could form in the trough of the TRW to the north of 32° as a consequence of the sudden turning of the Gulf Stream eastward at 32° and return of the Gulf Stream to the shelf break at 33.5°N Pietrafesa (1987) finds relatively high concentrations of organic carbon and nitrogen in the surface sediments on the north-northwest tip of the Charleston bump. This find is clearly suggestive of a mesoscale, isolated, persistent upwelling process.

The aforementioned pioneering works of Rooney, Janowitz and Pietrafesa (1978) and Chao and Janowitz (1979) established the theoretical bases for long wave generation at the "bump" and provide speculation that the lee waves generated are the "meanders" discussed by Webster (1961a,b) (Figure 7a). It is of note here that Hansen (1970) tracked the position of the GSF off North Carolina for a year and determined that these meanders left a signature of a wave pattern.

Other features frequently observed along the GSF are warm-core folded back filaments or "shingles" (Von Arx, Bumpus and Richardson, 1955). These shingles are manifested as warm, southward oriented tongue-like extrusions of GSF surface waters onto the shelf (cf. Figures 7a,b). While these features have been described from VHRR imagery by DeRycke and Rao (1973),

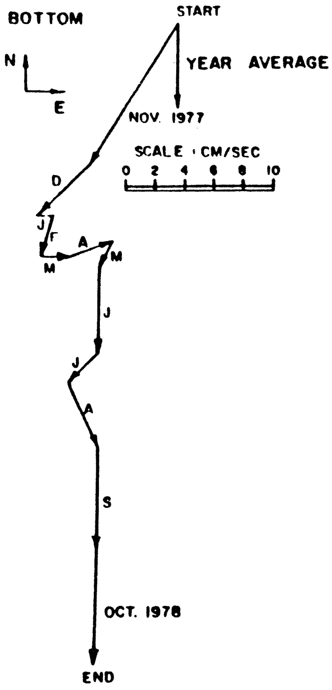

Figure 3. Monthly averaged currents at 40 meter isobath mooring location off Charleston; Nov. 1977 - Oct. 1978. Indicated is the net southerly flow dominated by Charleston Trough dynamics at the "Long Term Mooring" shown in Figure 2.

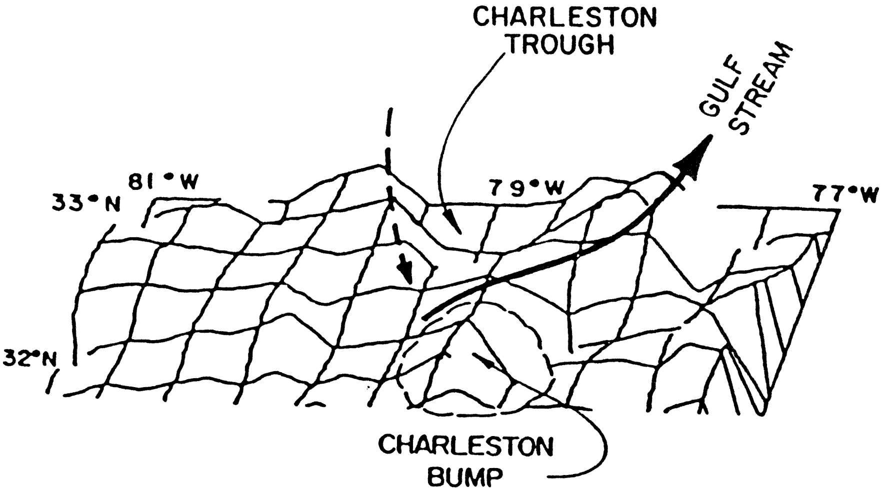

Figure 4. Sea surface map constructed from Seasat Satellite altimeter data which indicates the deflection of Gulf Stream at 32N, 79W by Charleston "Bump", and a bowl shaped depression in center of Charleston Trough.

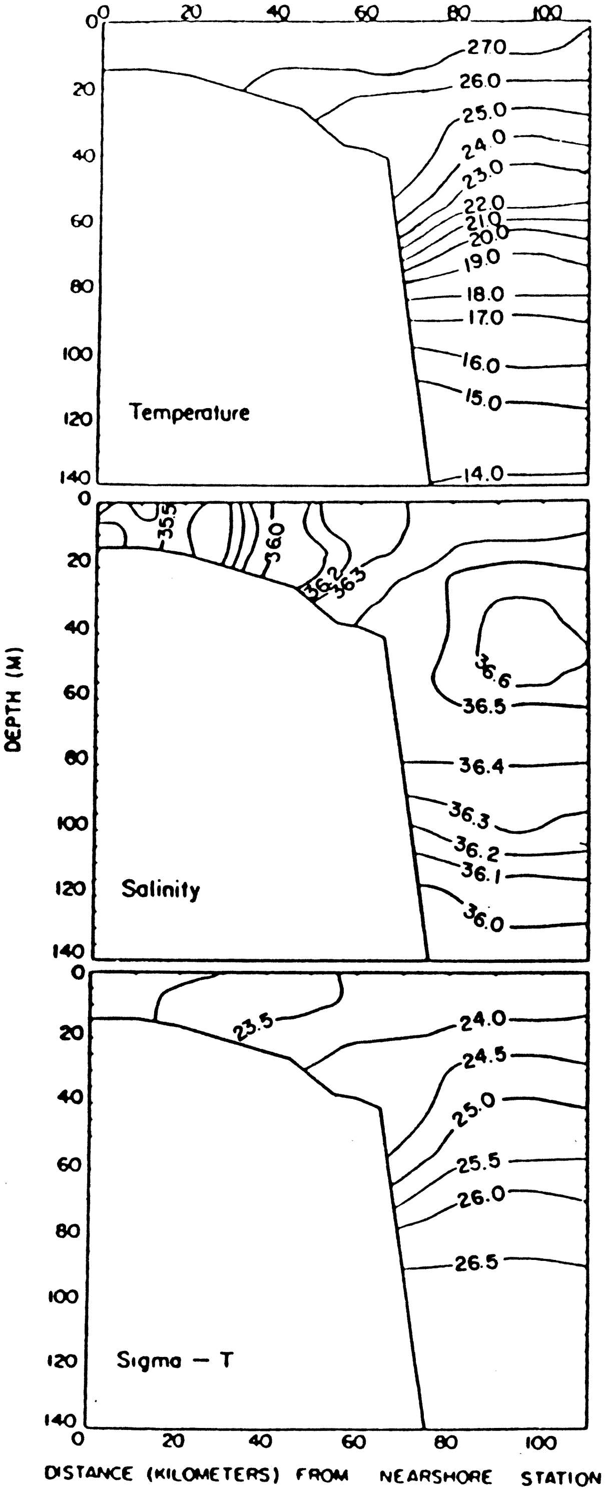

Figure 5. T, S, σT dome of upwelled water in a cross-continental margin transect across the Charleston Trough. (cf. Figure 2 for "Trough" location).

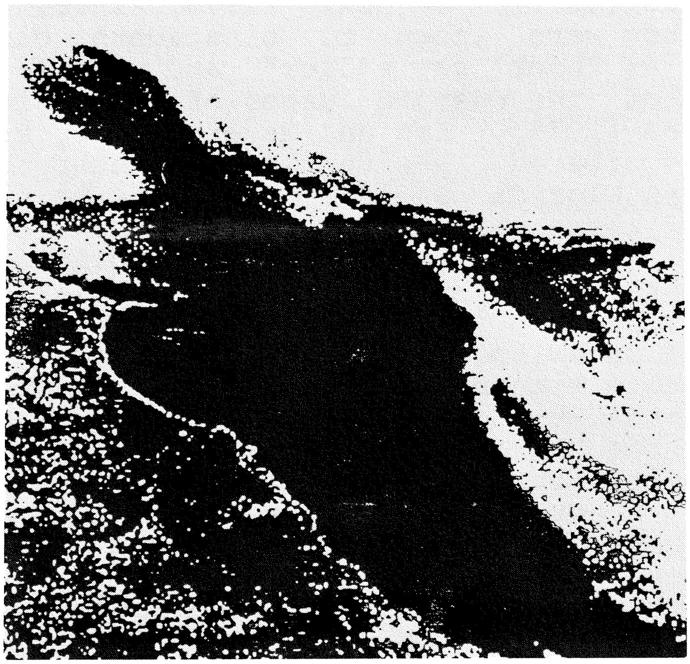

Figure 6. CZCS image showing high chlorophyl concentrations found in Charleston "Trough". (From C. McClain, NASA Goddard).

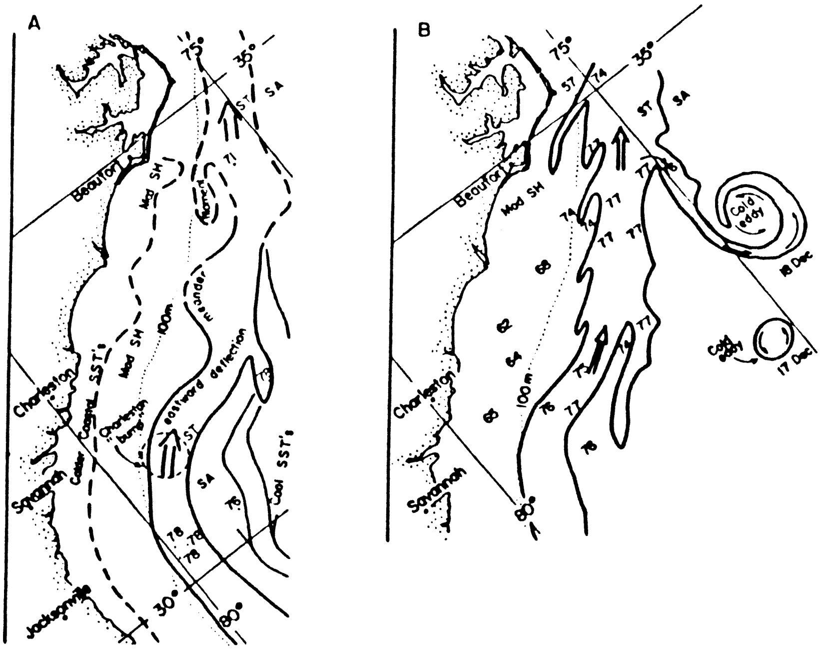

Figure 7. (a) Sea surface temperature as observed by satellite VHRR sensor, December 21, 1977. (b) EOFA chart for December 22, 1976.

Stumpf and Rao (1975), Legeckis (1975, 1979) and Vukovich, et al. (1979), they were known to nineteenth century scientists (Abbe, 1895) as "back set eddies" and were deemed responsible for the shape of the cuspate capes of the Carolina coastline. Studies by Lee (1975), Lee and Mayer (1977), and Duing, Mooers and Lee (1977) offered in-situ current meter observations made on the eastern Florida Shelf as evidence to the frequency and persistence of these shingles, which were called "cyclonic cold cores eddies", because these authors identified the appearance of these events as a cyclonic rotation of current vectors accompanied by a drop in temperature. However, it was shown by Pietrafesa and Janowitz (1979) that these so called "eddies" can appear to rotate either cyclonically or anti-cyclonically in an Eulerian representation relative to the location of a current meter within the Lagrangian event and consequently, looking for a single sense of rotation, can lead to an underestimate of frequency of events as well as a misunderstanding of the Lagrangian makeup of the event itself.

There have been a number of theoretical attempts to explain the nature of the GSF meandering and filament (shingle, cold core eddy) formation. Of note are the following: Orlanski (1969) considered the effects of bottom topography in inducing growing wavelike instabilities of baroclinic jets, such as the Gulf Stream; Niiler and Mysak (1971) investigated subinertial waves in a barotropic, horizontally sheared jet over variable topography; deSzoeke (1975) investigated the interaction between a topographically trapped baroclinic wave and a thermal baroclinic wave; Saltzman and Tang (1975) described the consequences of baroclinic instabilities in a two layer jet; Rooney, Janowitz and Pietrafesa (1978) and Chao and Janowitz (1979) separately considered the generation of long waves as a left-bounded jet passed over a topographic rise, and finally, Brooks and Mooers (1977), Grimshaw (1977), McKee (1977) and Helbig (1980), all studied different aspects of the character of continental shelf waves in the presence of variously sheared jets. Sun (1982) added a moving bottom layer to Orlanski's model while Luther and Bane 1985 reconsidered Orlanski's model on an inverse eigenvalue problem. It is clear that the problem of modeling the stability characteristics of a baroclinic, time-dependent sheared jet flowing over variable topography in both the downstream and cross-stream directions and modified from the surface by varying atmospheric sources is not an easily formulated, let along mathematically tractable problem.

Blanton and Pietrafesa (1978) concluded that filament features provide a mechanism for rapid shelf water mass exchange in Onslow Bay, N.C. This flushing frequency is thought to be directly related to the frequency with which meanders and filament events occur. Pietrafesa (1977) indicates that the frequencies of the events themselves are between 0.08 and 0.4 cycles per day (cpd) on the North Carolina shelf, but the frequency of occurrence of these events is not known because

VHRR imagery cannot provide definitive detection of the features given the shielding of cloud cover. However, Pietrafesa (1978) was able to detect 70 filament and large amplitude meander events in the CC region during the 24 month period, May, 1976-April, 1978. This estimate was derived from a culling of weekly Environmental Ocean Frontal Analysis Gulf Stream maps (produced by Mr. R. Pershall of the Naval Oceanographic Office) and from actual images obtained from the Environmental Space Service. It indicates that at a minimum, one well defined frontal event is evident in the CC region every 10.4 days. From the many data sets collected the past decade, it is obvious that large amplitude current fluctuations with periods ranging from several days to several weeks are common features on the continental shelf off North Carolina. These data indicate that cycles in diabathic flow rarely are correlated with local wind events which occur more or less simultaneously at Cape Hatteras and Wilmington at either end of the CC region (Weisberg and Pietrafesa, 1983). Perturbations in the GSF represent a mechanism that causes those mid-shelf flow cycles that seem poorly or only weakly correlated with local winds. These cycles also represent processes that either flood water into, or alternatively, flush water from the embayment. They may also pump the shelf with an essential fraction of the nutrients and larvae necessary to maintain the productivity of the shelf. This conclusion was in fact reached by Hofmann, Pietrafesa and Atkinson (1981) and Atkinson, Pietrafesa and Hofmann (1982), for the North Carolina shelf. These events may also be the supply agents of the "red tide".

In this manuscript, the importance and characterization of Gulf Stream spawned frontal events and marine atmosphere effects on the shelf will be assessed using current and temperature data collected in the Carolina Capes.

Data Sets

Studies supported by the U.S. Dept. of Energy (DOE) and the U.S. Dept. of the Interior (DOI) have produced a dramatic increase in the amount of physical oceanographic data available for the area. A composite of the moorings deployed in the area between 1975 and 1979, the years encompassing data referred to in the text, is presented in Figure 1, with mooring designations noted for later reference. Each DOE mooring was nominally equipped with 2 Aanderaa RCM-4s, one positioned 17 m below the surface and one 3 m above the bottom as shown in Figure 8.

Routine processing of the data includes the production of 40-hour low pass (40 HLP) filtered time series, which represent the smoothed original data retaining the "low-frequency" (subtidal) time series. All velocity vectors are rotated into a "normal" coordinate system where the off diagonal element of the Reynolds' stress is zero (Fofonoff, 1969). In the text, the alongshore (or parabathic) component is positive 55° east of

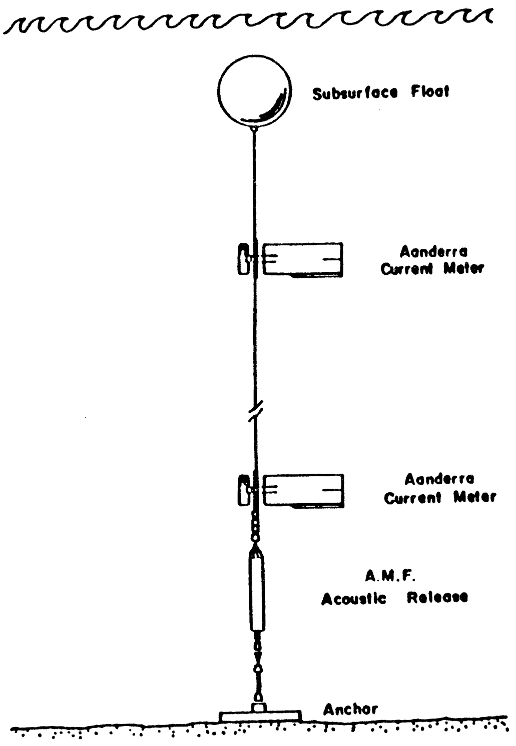

Figure 8. Mooring Configuration.

north and the offshore longshore (or diabathic) component is positive offshore, or 146° east of north. The alongshore component of the rotated vectors tends to be aligned with the local isobath orientation and is positive toward the northeast. The cross-shelf component (u) is positive offshore toward the southeast. Coastal meteorological and sea level data, collected at Charleston, Wilmington, Beaufort and Cape Hatteras (cf. Figure 1) are treated in a manner consistent with the current meter data. Coastal meteorological data were obtained from the National Climatic Center in Asheville, N.C., and coastal sea level data were supplied by the National Ocean Survey in Rockville, Md.

Observations of Wind Driven Currents and Gulf Stream Frontal Events

Current meter data collected on the Carolina Capes shelf reveal the variability of the shelf. In the frequency domain, it is clear from the kinetic energy density spectra (KEDS) of representative currents at the shelf break (HTOP), mid-shelf (ETOP) and inner-shelf (OTOP) (refer to Figure 1 for instrument locations and Figure 9 for KEDS) that 2 to 13 day period stochastic processes dominate the sub-inertial frequency end of the spectrum throughout the water column. The only deterministic features evident are the semi-diurnal and diurnal tidal constituents.

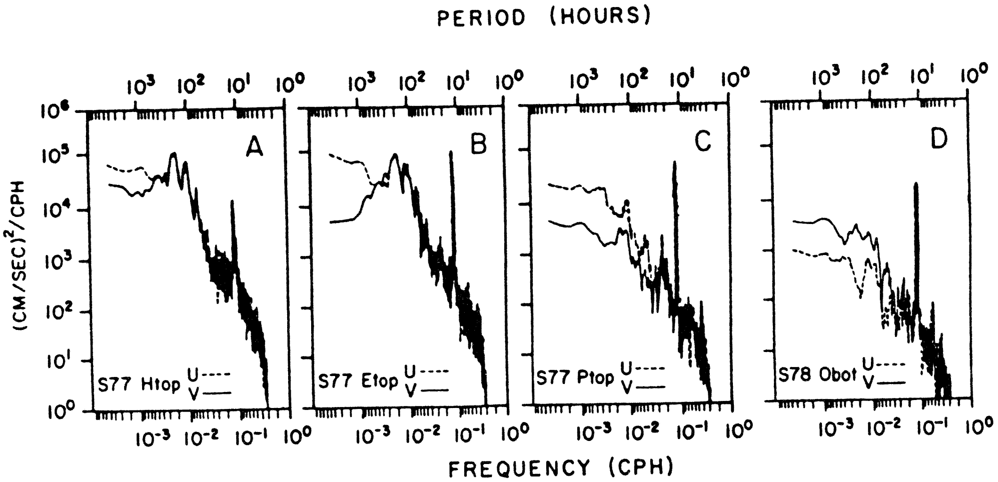

Figure 9. Kinetic energy density spectra for u and v components for (a) HTOP, summer 1977, (b) ETOP, summer 1977, (c) P TOP, summer 1977 and (d) O BOT, summer 1978.

A closer examination of the sub-inertial end of the KEDS reveals that both cross-shelf and alongshore current variances contain broad (±2 days) spectral peaks centered about 4, 8, 12 and 16 day periods at sites H and E. The low frequency drop-off in the alongshore current spectra contrast rather sharply with the monotonic rise in the cross-shelf spectra, suggestive of either the absence of lower frequency external forcing or a limitation in the low frequency response of mid to outer shelf alongshore currents to external forcing. This is not the case for site P. where there is a prominent, monotonic rise at the low frequency end of both the u and v spectra. Thus, inner shelf alongshore currents are not response limited to external forcing of periods between one and three months as are outershelf alongshore currents. The prominent peaks in both the u, v KEDS at these inner shelf sites (only site O is shown) are centered at 3, 5 and 12 days.

Presumably, one could accept these spectral peaks in the current component variance as conclusive indicators of the importance of two day to two week events in the dynamics budget of the outer shelf, but is useful to consider an alternative way of showing these data. One could take another view of the current fluctuations by considering their kinetic energy distributions as shown in Figure 10. These diagrams depictment the velocity fluctuations in terms of spectral density functions that have been integrated over the frequency variable and then normalized relative to their individual total variance. The result is a partition of the fluctuation kinetic energy, in terms of percent of normalized variance, into the dominant modes of flow. These partitions are quantified in Table 1. Table 1 also includes energy fractions of additional current sites and seasons to establish a more representative feel for the nature of current variability on the Carolina Capes shelf.

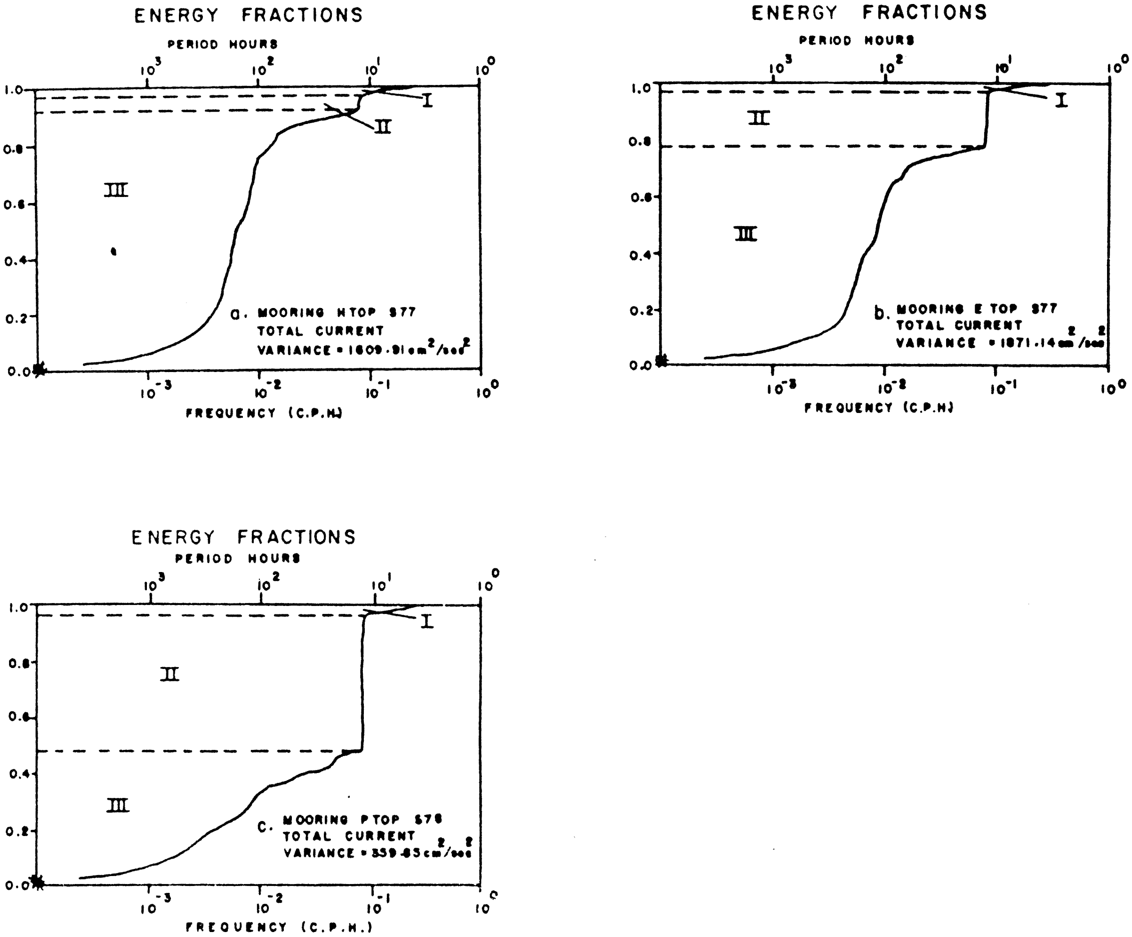

Figure 10. Energy Fraction diagrams for moorings (a) H TOP, summer 1977, (b) E TOP, summer 1977 and (c) P TOP, summer 1978.

Table 1. Velocity variances in total and in percent of total by location (Figure 1) and season (s = summer, w = winter) as a function frequency bands for motions with periods: equal to 12.42 hours; within the semi-diurnal tidal to inertial range; and greater than inertial.

Site	Level	Component	Season	cm^2/sec^2	%M2	%(M2+IP)	%<IP
E,O*,(K)	Top	Total	76S	1821.5			
			77S	1871.1	2*	21.5*	76.5*
			77W*	235.9*	4*	45.5*	50.5*
			(77S)	(1119.5)	(3.5)	(9)	(87.5)
E,O*	Bot	Total	77S	415.8	8.3	24.7	67
			77W*	225.3*	4.5*	45*	50.5*
			78S*	109.2*	4*	58.5*	37.5*
C,P*	Top	Total	77S	2348.2	2	12	86
			77W*	511.3*	3*	38*	59*
			78S*	359.9*	3.5*	60*	35*
P,*(K)	Bot	Total	(77S)	(197.5)	(5.5)	(4)	(90.5)
			77W*	275.2*	5*	38.5*	56.5*
			78S*	83.8*	3.5*	52.5*	44*
H	Top	Total	77S	1609.9	2.5	6	91.5
			77W	1149.4	6	10.5	83.5
			78S	1255.3	3.5	8	91.5
H	Bot	Total	77S	442.4	17.5	19.5	63
			77W	606.3	8	7	85
			778S	292.6	17	17.5	65.5
J	Top	Total	77S	3087.1	1.5	5.5	93
			77W				
			78S	2048	5.5	7.5	87
J	Bot	Total	77S	453.7	15.5	12	72.5
			77W				
			78S	425.5	16	12.5	71.5

From Figure 14 several conclusions can be drawn: the random forcing of the atmosphere and Gulf Stream dominate the mid to outer shelf, and at specific mid to outer shelf mooring locations, both the total variance and the partition of fluctuation kinetic energy (in terms of percent of total) of subinertial frequency motions are relatively constant from season to season and year to year (egs: ETOP-S76, S77; HTOP-S77, W77, S78). There is in general, a decrease in low frequency variance from top to bottom at a particular site and the upper current elements decrease slightly in the winter, while those near bottom increase in the winter, relative to summer values. Also, values at shelf-break sites H and J are higher in Summer 1977 than during other summer periods. The 1977 summer was a period of persistent and dramatic Gulf Stream frontal events (Pietrafesa and Janowitz, 1980). Finally, there is a half decade decrease in the level of low frequency variance at mid to inner shelf sites (O, L, P, A, B) as compared to mid to outer shelf sites (C, D, E, F, H, M, I, J, K). The four near coastal sites are located at the 29 and 33 m isobaths, while the deeper sites are in 40, 45 and 75 m of water. If one assumes that the atmospheric contribution to upper water column current variability is relatively constant across the shelf, then the other source of current forcing, the Gulf Stream, must comprise the other fraction of the total variance observed at mid and outer shelf sites and not observed at inner shelf sites. We first consider several prototypical Gulf stream Frontal events.

Since these frontal features dominate the outer shelf physics, several of these events can be considered using actual current meter data. As can be clearly seen in the Heat Capacity Mapping Mission (HCMM) infrared image (Figure 11), the wavetrain was well manifested on 27 March 1979. This was also true in the TIROS-N VHRR image and for 27 March shown in Figure 12. (The HCMM data was obtained from Mr. R. Crissman of the Research Triangle Institute.) The meanders are displayed quite clearly in the velocity vector time series shown in Figure 13 from upper water column instruments at sites H and J. The two wave "crests" (Pietrafesa and Janowitz, 1980) noted in the HCMM and TIROS-N thermal images are clearly evident in the in situ data.

The two waves (meanders), which are shown in Figures 11 and 12, and the leading edge of their crests strike the upper instrument at mooring H at:

.0000 hours, GMT on 23 march
and .0800 hours, GMT on 28 March, respectively.

The leading edge of the crest of the two-waves were initially sensed at site J, by the upper instrument, at:

.1800 hours, GMT on 24 March
and .2200 hours, GMT on 29 March, respectively.

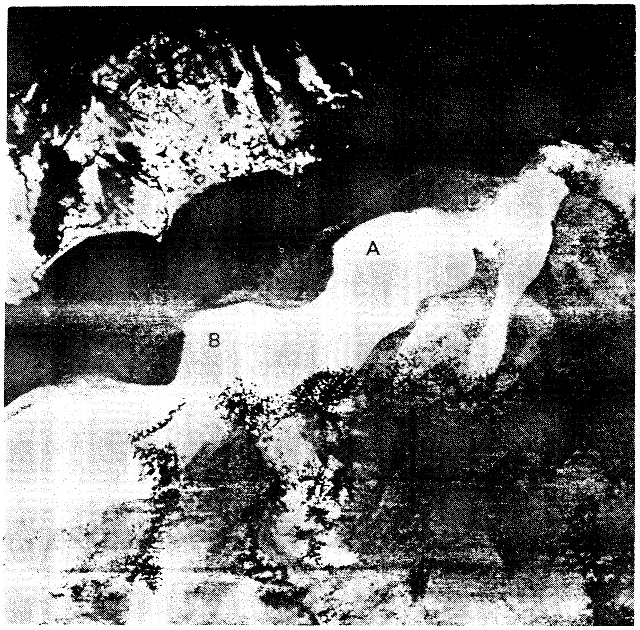

Figure 11. HCMM infrared image for 27 March 1979 (courtesy Mr. R. Crissman, Research Triangle Institute, RTP, NC).

Figure 12. TIROS-N infrared image from 27 March, 1979 indicating wavelike meanders along Gulf Stream front. Original image was enhanced to eliminate lightest shade of gray.

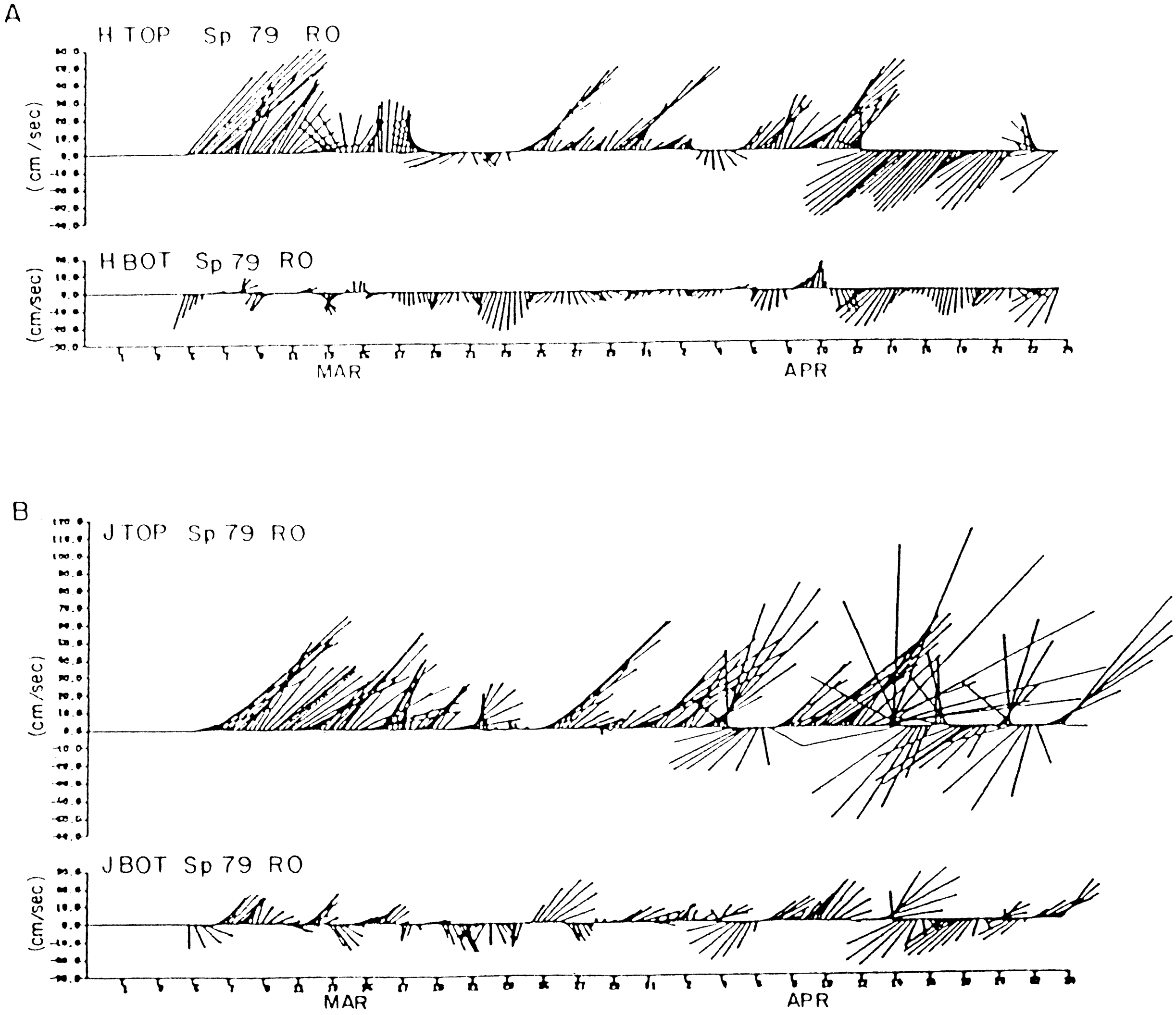

Figure 13. (A) Currents (cm/sec.) at 17 m from the surface (HTOP) and at 3 m from the bottom (HBOT) at mooring site H. (B) Currents (cm/sec.) at 17 m from the surface (JTOP) and at 3 m from the bottom (JBOT) at mooring site J. Currents are for 1 March to 24 April 1979.

Two wave crests, "A" and "B", (see Figure 11) will be studied. At approximately 0000 GMT on 23 March, 1979, the crest of wave A was observed at site H and caused the currents to set towards the northeast with speed of 7 cm/sec. and temperature of 19.0°C (Figure 16). Thirty-six hours later, the current achieves a maximum Eulerian speed of 72 cm/sec. and by 0000 GMT on the 25th, realized peak temperature of 21.8°C. The same wave was manifested at site JTOP with maximum Eulerian speed of 90 cm/sec. and temperature of 21.4°C. Thus, the propagation of phase of wave A was about 45 cm/sec. and that of wave B was 49 cm/sec. Calculations using satellite data indicated an average phase speed of about 42 cm/sec. for both waves which is essentially the same as that obtained from the current meter data.

The HCMM data (Figure 11) shows that these meanders were well offshore of the shallow moorings O and P. A discussion of wind induced currents in a paragraph below will show that currents at sites O and P were wind driven during this period. At this point, the crests of the waves A and B are both clearly discernable at sites H and J.

The regions upstream and downstream of the wave crests are wave "troughs" (Pietrafesa and Janowitz, 1980). From the HCMM imagery, it appears that the circulation is cyclonic in both of the troughs. In the center of the elliptically shaped trough is a relatively dark patch, indicative of waters cooler than those surrounding the patch. Given the orientation of the path of apparent propagation of phase of both waves A and B, it is seen from the thermal satellite imagery that the trough which is downstream of Wave A on 27 March, the western most part of trough 1 (Figure 11), reached site H with a total current directed toward the north at 20 cm/sec. The velocity vector sticks (Figure 13) then rotated slowly, counterclockwise, and by 1600 GMT on the 18th were westward at 12 cm/sec. By 0000 GMT on the 20th, the flow was to the southwest at 11 cm/sec. and finally by the 23rd at 0800 GMT, the flow was southeasterly at about 4 cm/sec.

The wind can effect currents in two ways on the middle to inner CC shelf. The actual surface current is the sum of both effects. First, due to the direct input of momentum, surface currents are driven, in part, to the right of the wind, possibly up to 25 degrees, with a magnitude of 0.035 V_W (Huang, 1979), where V_W is the wind speed. We call this component of the current V_{DW}. The thickness of the upper layer, δ, (an e-folding length) is on the order of $[2Av/f]^{1/2}$ (Pedlosky, 1979), where A_V is the vertical eddy viscosity and f is the local Coriolis parameter. Using

$$A_V = \overset{*}{U}_W/200\ f \text{ (Csanady, 1982)}$$

and

$$U_w^{*2} = p_a C_D V_W{}^2/p_w,$$

we find that

$$\delta \stackrel{\approx}{=} 1.4 \times 10^{-4} V_w/f;$$

where p_a is the density of air, $\overset{*}{U_w}$ is the friction velocity, C_D is the drag coefficient, and p_w is the density of water. At the base of this layer,

$$V_{DW} \stackrel{\approx}{=} 0.37 V_{DW}(\text{surface}).$$

Secondly, the presence of lateral coastal boundaries cause variations in the height of the sea surface due to the wind forcing off or onshore flow of water in the top layer. This sea-surface variation produces a pressure gradient throughout the water column and hence currents, which are manifested throughout the water column and which we call V_s. These slope currents are estimated as

$$V_s = 0(\tau_a/\delta_B f p_w),$$

where τ_a is the alongshore wind stress and δ_B is the thickness of the bottom layer (Janowitz and Pietrafesa, 1980). In that paper,

$$\delta_B = \overset{*}{U_w}/40f \stackrel{\approx}{=} 3.5 \times 10^{-5} V_w/f$$

and

$$V_s \stackrel{\approx}{=} .06 V_w$$

Thus, the order of the currents associated with wind induced sea-level fluctuations are of the order of V_{DW}. However, V_s depends on depth as well as the orientation of the wind vector with respect to the shoreline and on the past history of the atmospheric wind stress component. In waters of depths greater than δ, an alongshore wind will drive surface waters offshore and cause a set-down in coastal sea level, a cross-shelf pressure gradient, and, consequently, an alongshore current on the order estimated previously. In the CC region, an offshore wind is not as effective in producing pressure gradients. In fact, Chao and Pietrafesa (1980) showed the offshore winds are only one-tenth as effective as alongshore winds in producing coastal sealevel pressure gradients on the CC shelf. Thus, V_s cannot be as easily computed as V_{DW}, but is as important as the latter, since the actual surface currents are the sum of the two terms with comparable magnitudes. As mentioned earlier, V_s incorporates the past history of the wind as well as density stratification and has a spin-up time (in seconds) of approximately $3 \times 10^4\ D/V_w$, where D is the local depth (Janowitz and Pietrafesa 1980).

From March 15 - March 23, the winds were predominately from the north, northeast or northwest. For the remainder of the period, the winds were from the southern sector (Figure 14). The persistent southward wind during the first half of this period was probably the cause of an intrusion of Virginia Coastal Waters southwards of Cape Hatteras. The effects of this intrusion will be discussed later in the text.

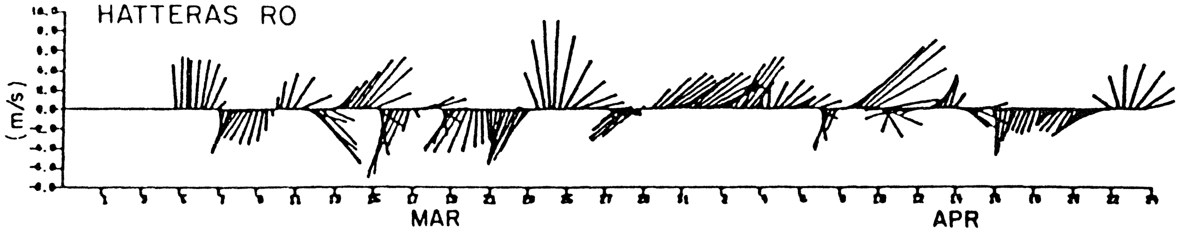

Figure 14. (A) Winds at Cape Hatteras meteorological stations. Wind speeds are in meters per second. The period is 1 March to 24 April 1979.

The current meter observations at moorings O and P, which are in 33 m of water with the upper sensors 17 m from the surface, will be the primary data source in this discussion. During this period, the wind speeds averaged 8 m/sec. This leads to an estimation of the upper Ekman layer thickness (δ) of approximately 13 m. Thus, measurements of 17 m below the surface reflect primarily V_S rather than V_{DW}. The observed currents are shown in Figure 15.

During this period, the currents at site O (Figure 15A) are north-northeasterly and then south-southwesterly at about 20 cm/sec. in both cases. The currents at site O are wind-driven during this period. The wind vectors are shown in Figure 8a. Comparison of wind and current vectors indicates nearly a perfect match of alongshore current to alongshore wind component. The relationship between current and wind is approximately $V \sim 40\sqrt{\tau_a/p_W}$ where τ_a is the alongshore component of the wind stress vector, p_W is the density of the water mass and V is the alongshore velocity. So, if we take the value of τ_a at 1200 GMT on the 19th, we find that V has a value of 25 cm/sec. The observed alongshore current associated with this wind is 22 cm/sec. This demonstrates that the currents are wind driven. In any case, the current at OTOP is 22 cm/sec. at 1200 GMT on the 19th, north-northeastward at 13 cm/sec. at 1800 GMT on the 17th, north-northeastward at 9 cm/sec. at 1600 GMT on the 18th, southerly at 6 cm/sec. at 0000 GMT on the 20th, and northeasterly at 5 cm/sec. at 0800 GMT on the 23rd.

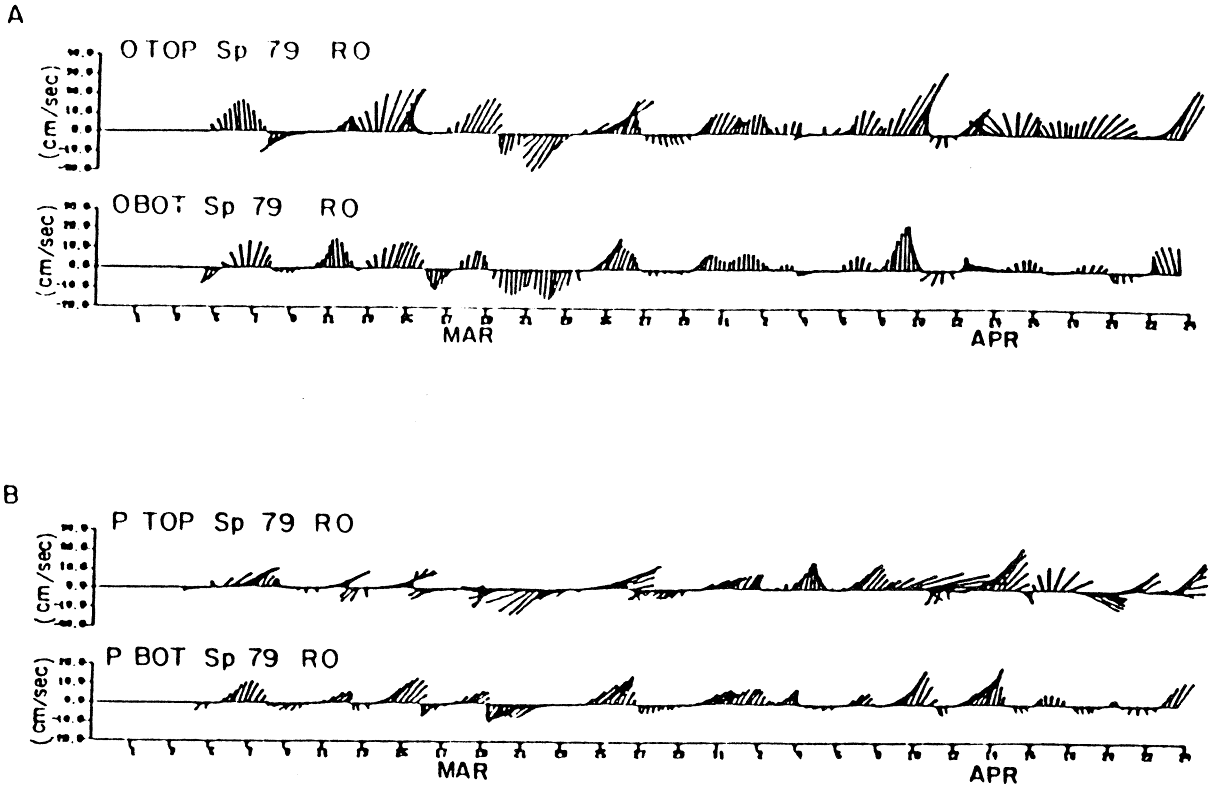

Figure 15. (A) Currents (cm/sec.) at 17 m from the surface (OTOP) and at 3 m from the bottom (OBOT) at mooring site O. (B) Currents (cm/sec.) at 17 m from the surface (PTOP) and at 3 m from the bottom (PBOT) at mooring site P. Currents are for the period 1 March to 24 April 1979.

Given the apparent superposition of currents, wind, and wave relationships that one must make at sites H and J, and along the entire mid to outer shelf of the Carolina Capes, it is concluded that the wave-trough related flow was to the SSW at 27 cm/sec. at 1800 GMT on the 17th, to the SW at 25 cm/sec. at 1600 GMT on the 18th, to the SSW at 5 cm/sec. at 0000 GMT on the 20th as trough 1 passed by site H. As trough 2 passed by site H, the total velocity field realized was to the NE at 7 cm/sec. at 0600 GMT on the 26th, to the NE at 20 cm/sec. at 1800 GMT on the 26th, to the NE at 8 cm/sec. at 1200 GMT on the 27th, and to the NE at 13 cm/sec. at 0600 GMT on the 28th.

The winds were consistently from the south to west quadrant during the period 23-24 March with stress values of the order of 1.5 dynes/cm^2. These winds indirectly drove slope currents to the northeast at 43 cm/sec. on the 26th and 27th of March, and at 25 cm/sec. on the 28th. Thus, it can be concluded that wave-trough related flow speeds were in excess of 50 cm/sec. on the 26th and early the 27th and about 40 cm/sec. during the latter part of the 27th and early on the 28th. The flow in all cases was to the southwest.

The temperature at HTOP associated with trough 1 was about 19.0°C followed by a peak of 21.7°C in crest A, then 19.4°C water in trough 2, and finally by 22.8°C water in crest B. The flow fields at site J were similar to those at site H with some variation and a phase lag of some 38-42 hours as discussed previously. This variation is shown in the u,v,T scenario depicted in Figure 16.

The TIROS-N, AVHRR frontal boundary analysis (Figure 17) shows a hugh filament extending southwestward from Raleigh Bay, across Onslow and into Long Bays. This feature was visually manifested in the thermal IR on 6 April and lasted until 4 May. The filament is 260-320 km long and up to 50 km wide. The event is evident throughout the entire current meter mooring array, most specifically at sites H, J, O and P. The frontal feature will be referred to as (filament) "F".

Frontal wave, F, a baroclinic frontal instability with many degrees of freedom is manifested in a discernable pattern in current meter data. Filament F is definitely sensed at site H by 0800 GMT on 10 April and at site J (Figure 16) by 0000 GMT on 12 April. At site HTOP, there is a net rise of 5.8°C, from an initial temperature of 18.8°C to a peak of 24.1°C. At site J, the rise is from 20.3 to 25.9°C. The rise in temperature was also evident at the bottom shelf break mooring sites with measured rises of 6.9°C at site JBOT, at 72 m from the surface in 75 m of water. This rise at JBOT occurred between 0000 GMT on April and 1200 GMT on the 14th, and was then followed by an immediate 5.1°C, drop in temperature. Upper water column temperatures are generally sustained at sites H and J. A very deep warm water mass, is suggested at sites H and J, extending to at least 72 m inshore of a colder water mass. The warm water mass originates at the top while the cold water mass has its origins at the bottom.

The filament is initially manifested at site HTOP as flow to the north-northeast at 55 cm/sec. at 0800 GMT on 10 April. By 0800 GMT on the 12th, the flow has swung counterclockwise ~ 150° to the southwest where it remains relatively fixed until 1600 GMT on the 23rd. There is a brief 20 hr. clockwise rotation at 1200 GMT on the 20th. The scenario at JTOP is very dramatic. Six hours before the event strikes, the flow is toward the NE at 60 cm/sec. At the onset of the event at 0000 GMT on 12 April, the flow is easterly at 121 cm/sec. and then begins to rotate counterclockwise to be NNE with speed of 133 cm/sec. at 0000 GMT on 13 April, to the N at 108 cm/sec. at noon (GMT) on the 13th, to the SW at 66 cm/sec. and 0000 GMT on the

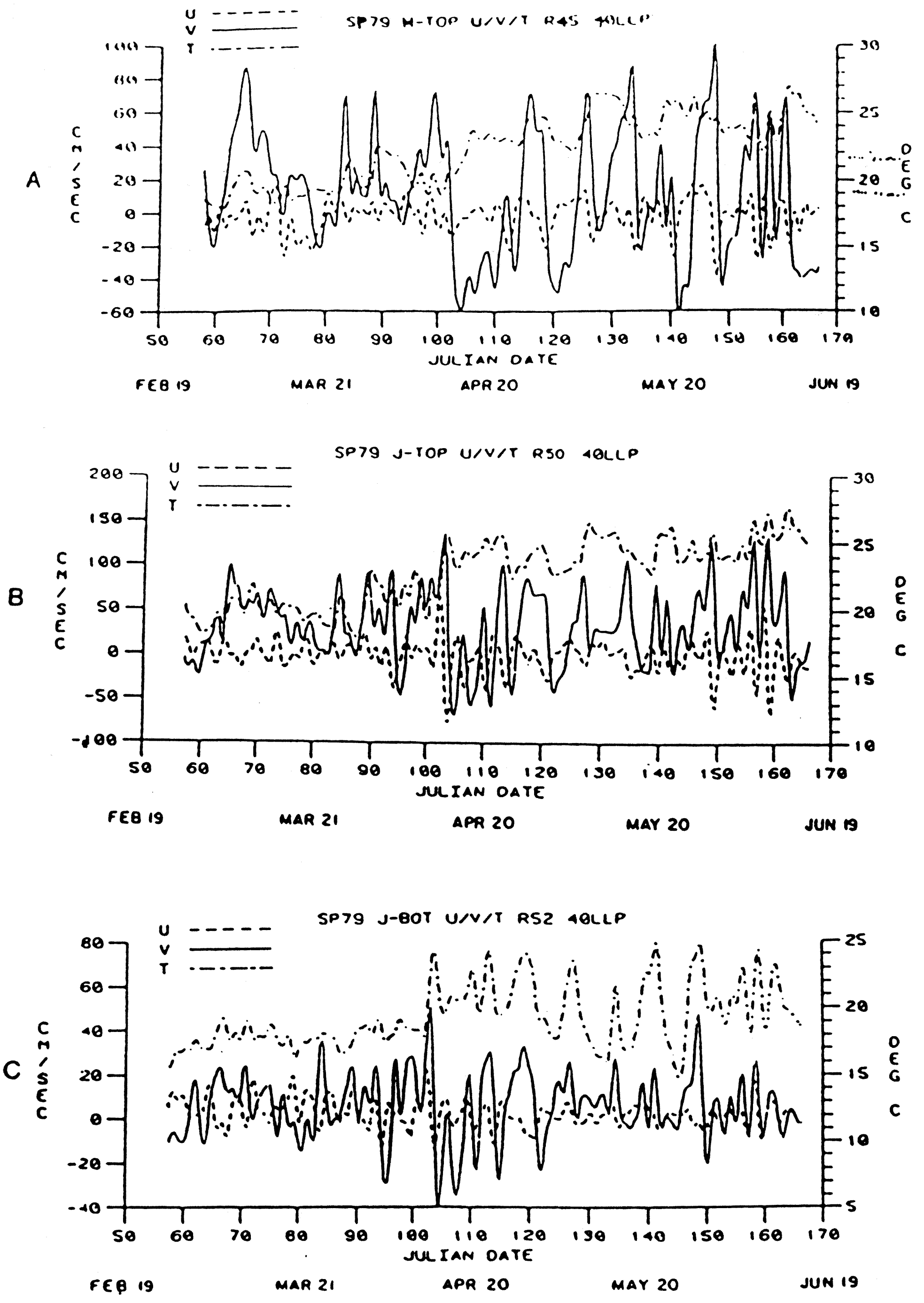

Figure 16. Variation of the u and v components of the currents and of temperature at HTOP, JTOP, and JBOT with time.

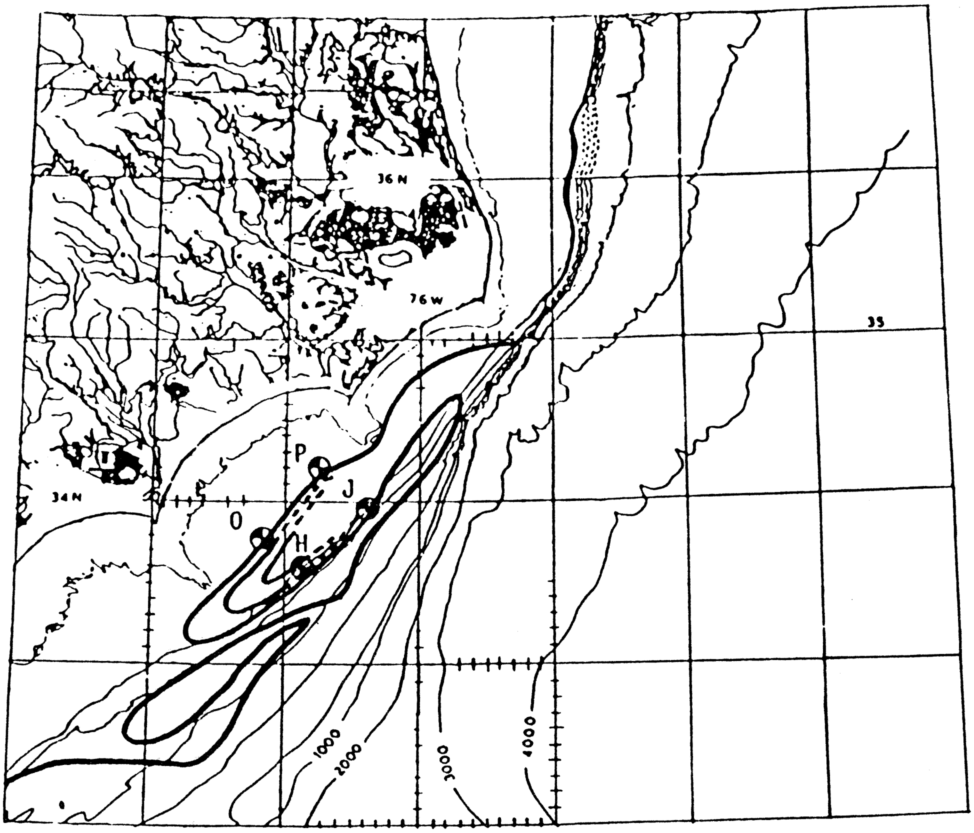

Figure 17. Gulf Stream frontal analysis for 15 April 1979 constructed using TIROS-N AVHRR data.

15th. The flow swings both clockwise and counterclockwise thereafter with clockwise swings accompanied by rises in temperature and counterclockwise swings accompanied by drops in temperature.

The jet, the 133 cm/sec. current, sensed at 0000 GMT on 13 April at site JTOP was accompanied by 5°C rise in temperature and, contemporaneously at site PTOP the flow rotates clockwise to become more easterly. This change at P is also accompanied by a rise in temperature of about 2.0°C. It is suggested that the entire feature has moved onshore and that now mooring P is closer to the center of the filament, in a regime of warmer Gulf Stream based water, while mooring J is in the Gulf Stream front proper, on the offshore side of the cold core.

The propagation of phase of the event from site H to J occurred with a speed of 47 cm/sec. from the 12th to the 14th April. Thereafter, the event appeared to lock in and become fixed spatially in the alongshore direction. In fact, in Figures 18 and 19 which are GOES imagery derived schematics of the event by (Dr. Steven Baig of NOAA/NWS) show the event still present with an apparent clockwise circulation pattern about the warm tongue. If the Baig rendering were correct, it could well be manifested by flow patterns at sties 0 and P which were positioned such to have been located within the event.

Mooring 0 is directly inshore, some 37.0 km, of site H and as such should have sensed the presence of filament F after it was noted at H but prior to it being felt at either site J or site P which is 40.2 km onshore of J. The event was first sensed at site 0 at 1600 GMT on 11 April and at site P at 0800 GMT on the 12th (see Figure 15). The curious point though is that the flow at site 0 becomes northeasterly to northerly for the next three weeks. At site P, the flow is northeasterly to east-northeasterly for four complete weeks save for the 15th of April, when P was out of the filament for a brief period and the currents followed the wind for a day. Site 0 stayed within the event as shown in Figure 19. Flows at both sites have magnitudes ranging from 10 to 60 cm/sec. generally about 25 cm/sec. at 0 and 40 cm/sec. at site P. It is noted that these currents persisted in opposition to the wind which was generally directed towards the southwest at Cape Hatteras throughout the entire period (see Figure 14).

Filament F had an apparently strong, intense hydrographic front with 26.6°C water registered at site JTOP and 15.9°C water sensed at JBOT. This feature likely blocked inshore water from penetrating offshore virtually throughout the entire length of Onslow, Raleigh and Long Bays. In fact, with the southward and southwestward winds which were present, it is likely that Virginia coastal waters were transported south around Cape Hatteras across Diamond Shoals and thereafter around Cape Lookout across its shoals and into Onslow Bay to be pinned against the coast. The picture created by frontal event F is shown schematically in Figure 20, in agreement with the previous results found by Pietrafesa (1983) and McClain, Pietrafesa and Yoder (1984) in studies of filaments off the coasts of Florida and Georgia.

In summary, a time domain comparison of cross-shelf (u) and alongshore (v) current components and contemporaneous temperature (T), suggests that at shelf break and mid-shelf locations, on the CC shelf, a north-easterly alongshore current (v) associated with the nonperturbed flow in the GSF will occasionally become diminished in magnitude or possibly reverse in concert with a decrease in temperature. Typically, this v and T scenario is followed several days hence by a return of the current of a northeasterly set and an increase in temperature. The rise in T usually peaks at values characteristic of those associated with the Gulf Stream front. The cross-shelf component of current (u) will have gone from being positive

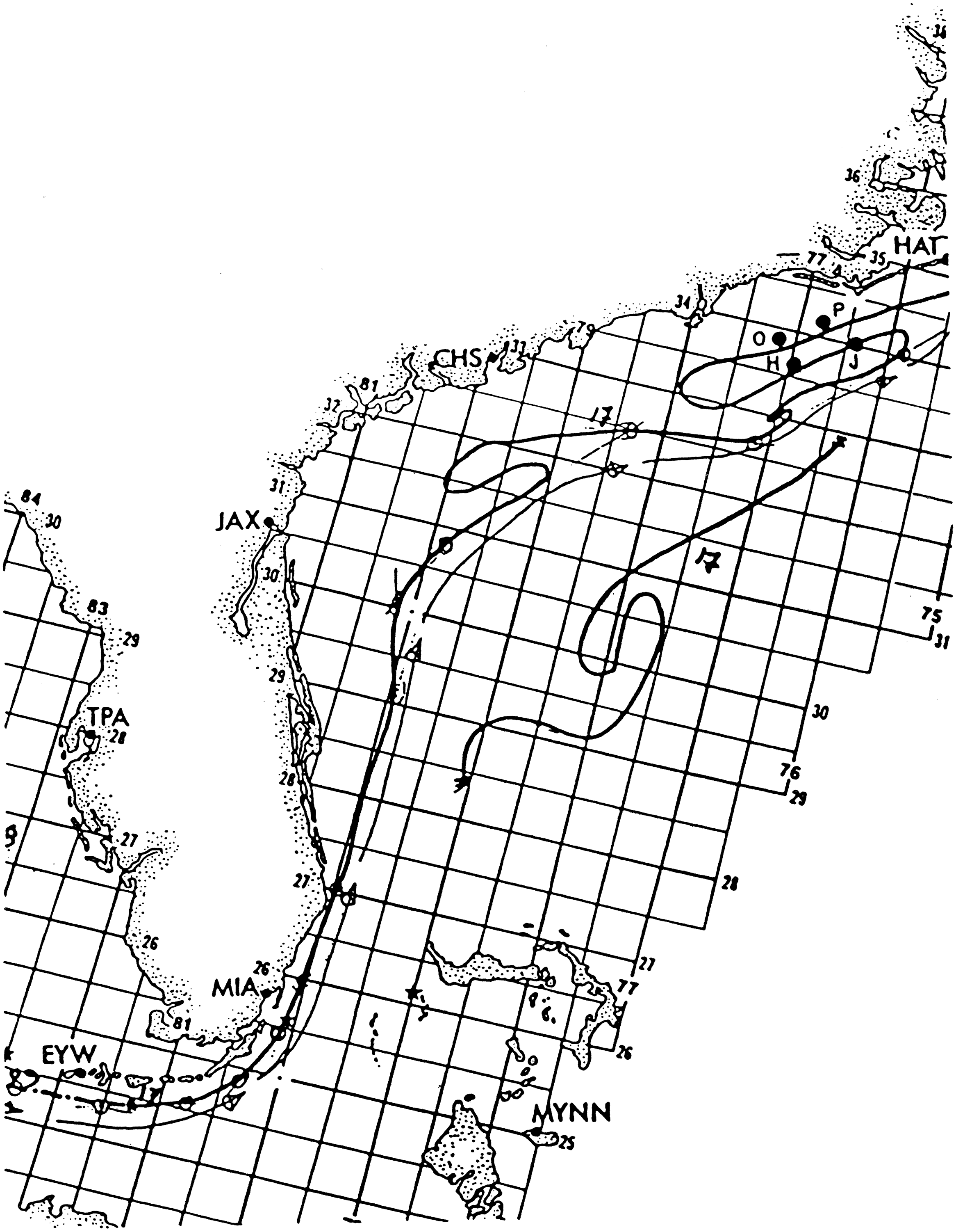

Figure 18. Analysis of Gulf Stream frontal boundaries using GOES satellite data for 18 April 1979 (after S. Baig, NOAA/AOMC) Mooring locations are indicated.

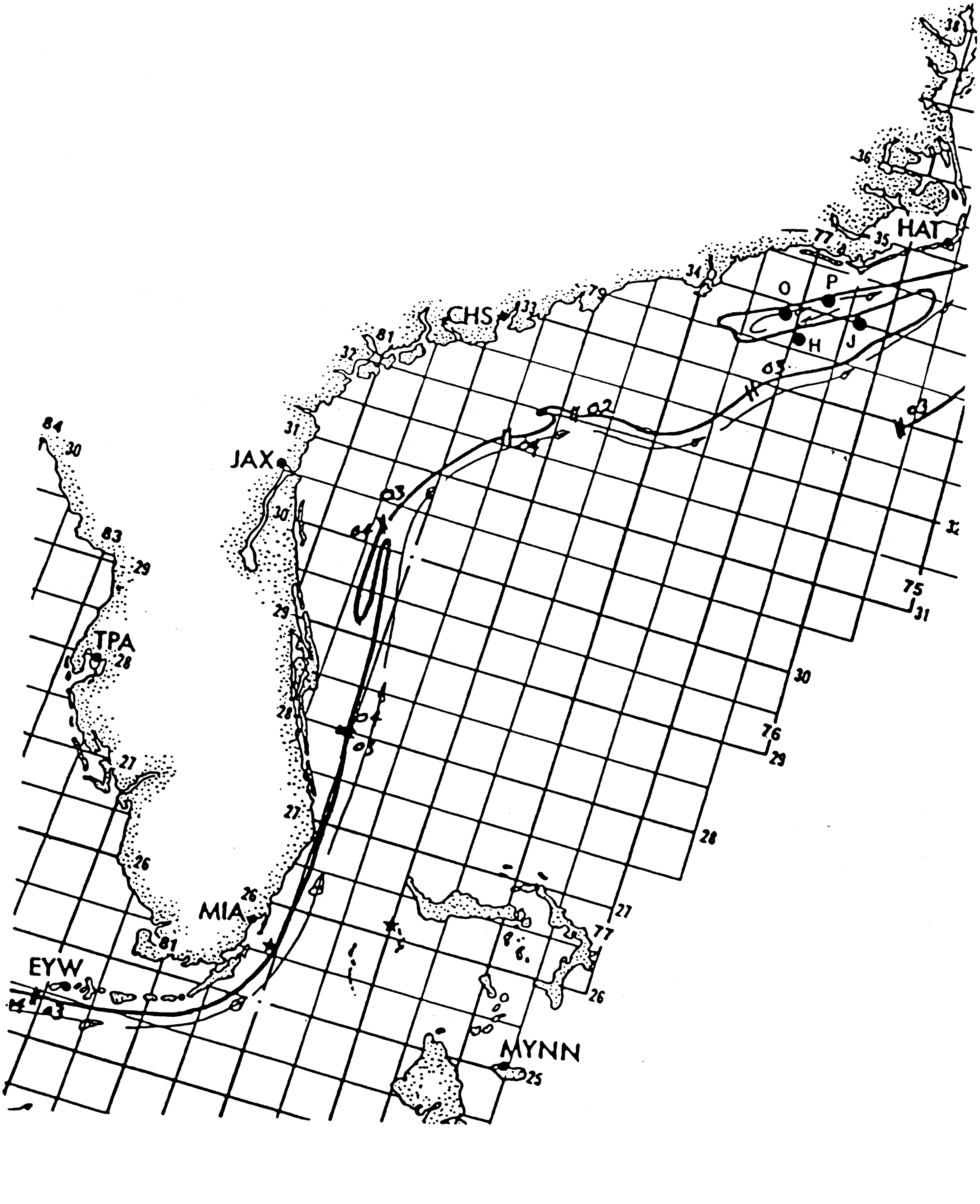

Figure 19. Analysis of Gulf Stream frontal boundaries using GOES satellite data for 4 May 1979 (after S. Baig. NOAA/AOML) Mooring locations are indicated.

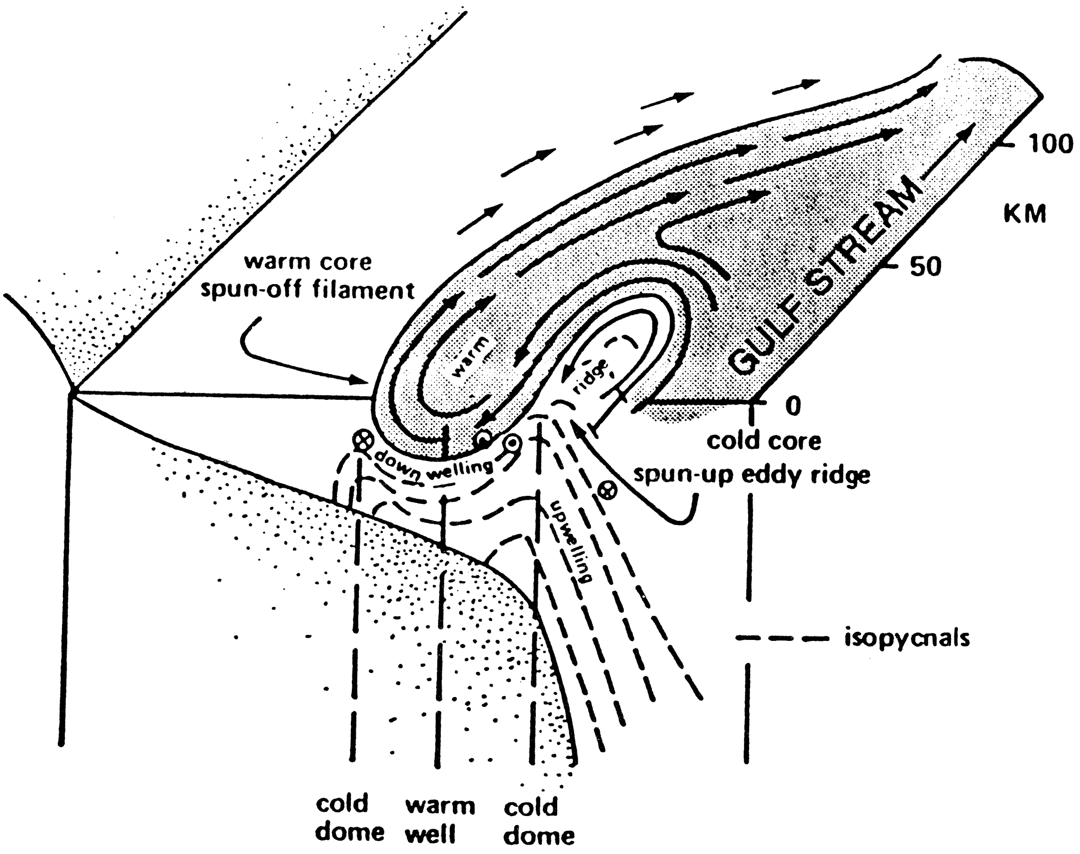

Figure 20. Conceptual schematic of frontal filament (Pietrafesa, 1983).

(offshore) to negative (onshore) to positive again during this period and precedes the changes in v. The drop in temperature related to the decrease in positive v could result from the fact that the warm frontal waters have moved offshore, making way for either a horizontal advection of cooler shelf/slope waters, both in response to or from an upwelling of cool, deep shelf/slope waters as a vertical consequence of a one-sided horizontal divergence. (Conductivity data collected at these sites indicates that the converging water masses are of Gulf Stream origin).

Gulf Stream frontal meanders and, more likely, Gulf Stream frontal filaments, frequently account for much of the coherent in-phase velocity and temperature fluctuations seen in u, v, T data. The observational evidence provided by the moored meter data suggests that meanders of the front are a form of long waves trapped over the steep bottom slope (a "waveguide") seaward of the shelf break in the SAB. These results are consistent with satellite observations (Legeckis, 1979), which suggest that the meander is a long wave with a length the order of 100 to 300 km centered about the Gulf Stream front and moving with the Gulf Stream so that the manifestation of sense of propagation is to the north(east). Within the wave crest, which is in the Gulf Stream proper, the streamlines of flow in the water column follow the shape of the crest and thus have a net anticyclonic sense of turning. In the wave trough, there is a closed, cyclonically rotating cell, a "cool pool".

Examples of the signatures of the passage of filaments at the Charleston "Long Term Mooring Site" (45 m isobath) are shown in Figure 21. These meanders are waves which grow in amplitude in the horizontal plane at their crest and fold back around the cool pool sitting in the wave trough. As the wave crest folds back toward the coast, shallower depths are encountered and the vertical vorticity constraint requires that the anticyclonic motion along the streamline of the wave crest be augmented. Flow is to the north on the shoreward side of the event and to the south on the offshore side of the filament (Figure 22).

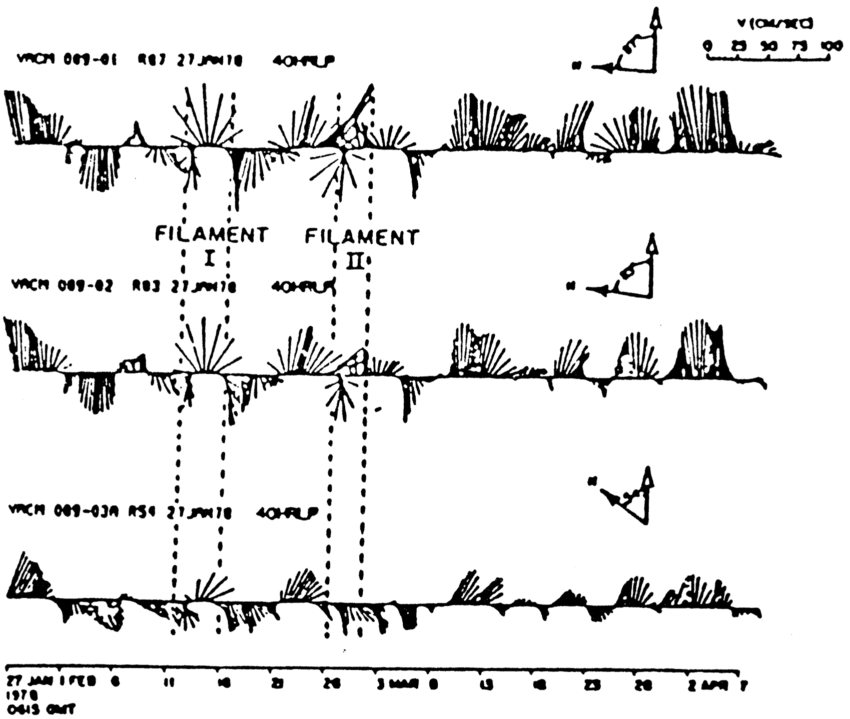

Figure 21. Current vector stick plots at 10(01), 22(02) and 42(03) meters of water at the Charleston 45 M isobath site.

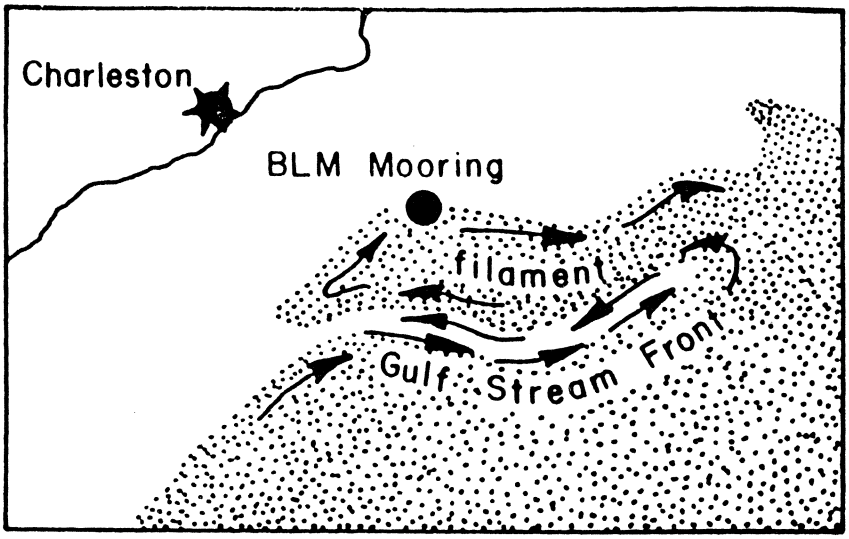

Figure 22. Gulf Stream filament observed in VHRR satellite imagery at 13:38Z on 12 February 1978. (Courtesy of Dr. R. Legeckis, NOAA/NESS). redrawn.

The warm Gulf Stream waters, which define the filament, deepen due to the downward vertical velocity produced by the increased negative relative vorticity. To the east (i.e. offshore, of the filament) and to the west (i.e. onshore) of the Gulf Stream front is a cold water mass which is cyclonically rotating and is, in fact, the trough of the mother wave. The filament formation occurs in concert, either as cause or effect, the wave trough realizes an intensified cyclonic torque and spins-up more intensely. The net effect is a rapid vertical ascension of isopycnals, a "doming up" phenomenon (Figure 20). As the filament advects north(east) ward along the Gulf Stream front, a series of shelf break/slope cold pool eddies are spun-up, forming an upwelled ridge, which, as a function of the intensity of cyclonic torquing, has a peak that varies in elevation, (cf. Figure 20).

Figures 23 and 24 represent frontal events observed at the Onslow and Raleigh Bay sites. The signature of filament passage can be either cyclonic or anticyclonic as a function of the amplitude of the event and its location relative to the current meter mooring array. Clearly if the mooring is located on the inshore side of the filament (Line 14), the vectors hardly rotate at all and temperatures rise. Curiously, the vector along Line 10 hardly rotates also, but in this case, the mooring is on the offshore side of the whole event and the temperature decreases markedly as the outer part of the cold core trough passes by. Line 14 will yield a slight anticyclonic rotation. Lines 11, 12 and 13 represent the intermediary and sometimes rapidly rotating case.

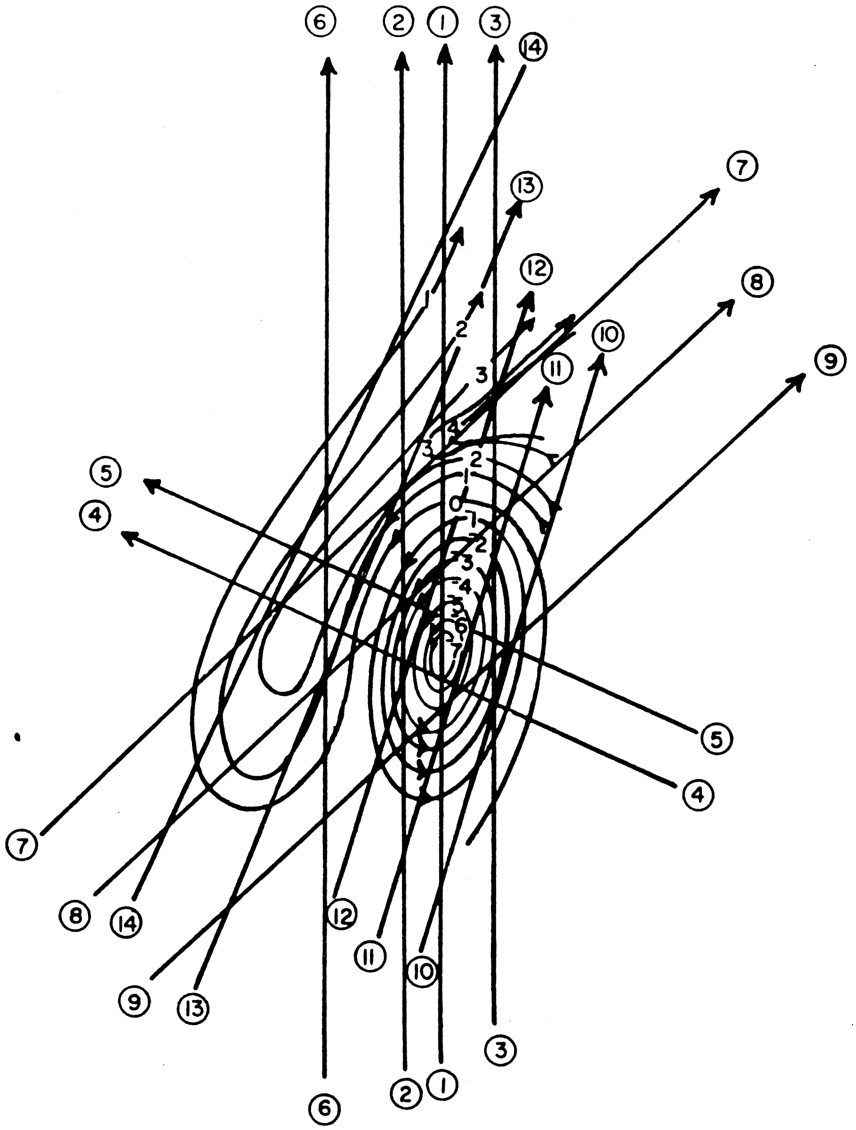

Figure 23. Snapshot of the streamlines of flow around the surface plane of a folded-back Gulf Stream frontal wave crest (a filament) and its associated trough. Numbered lines indicate possible passage by fixed current meter moorings.

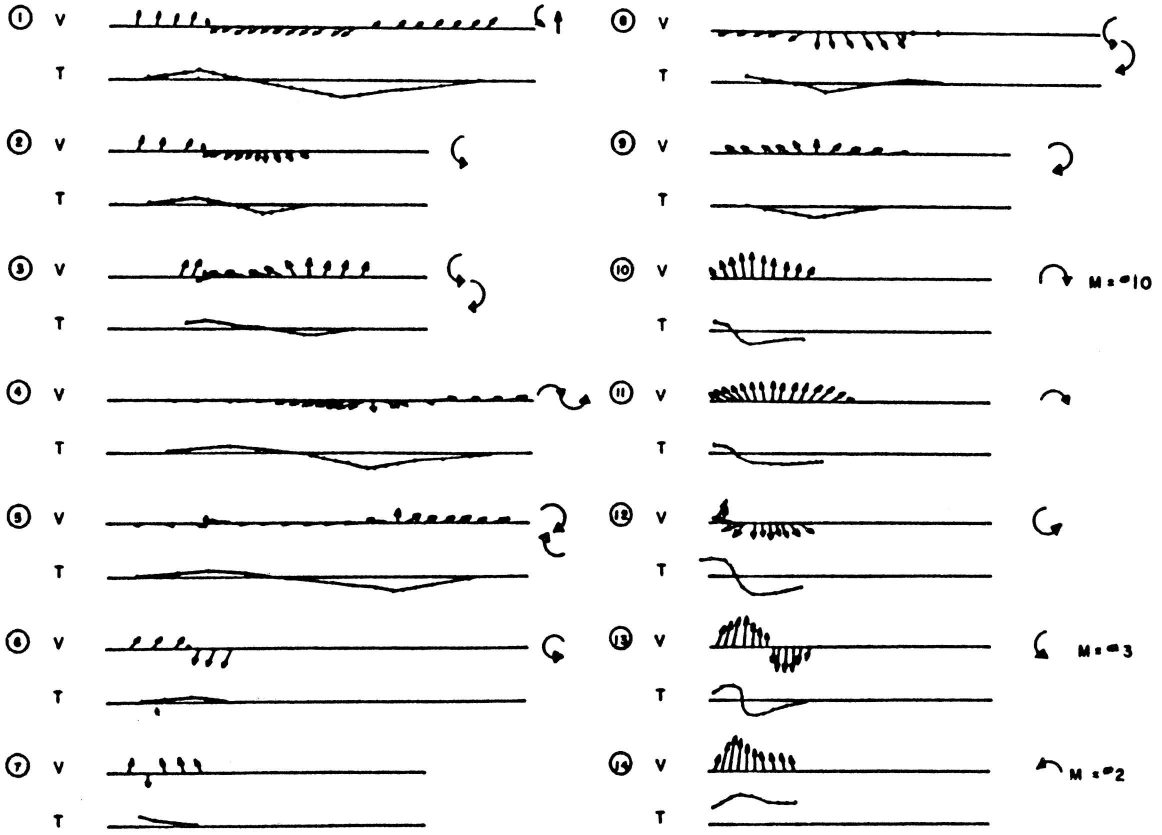

Figure 24. Time series of Eulerian currents and temperatures (derived from moorings) based on the passages of Lagrangian events shown in Figures 11, 12, 17, 18, 19, 22 and others manifested in NOAA/AOML VHRR products.

There are also secondary frontal features which appear in VHRR imagery in the CC. These secondary thermal boundaries appear to mimic the curvature of mid-shelf bottom isobaths and appear to reflect the existence of a boundary separating inner from mid-shelf waters. This secondary front has not been studied.

Penetration of Virginia Coastal Waters South of Cape Hatteras

The likelihood of the penetration of Virginia coastal waters southward into Raleigh and, possibly, Onslow Bay increases in the Fall season which is generally characterized by winds from the northeast (Weisberg and Pietrafesa, 1983). However, during the March-April 1979 period, the satellite imagery for 27 March indicated that cold virginia coastal waters had penetrated into, at least, Raleigh Bay (Figure 11). In the period 6-23 March, the winds were, on the average, from the north or northeast (Figure 14), setting up conditions favorable for the southward penetration of Virginia coastal waters observed on 27 March.

Salinity provides an excellent tracer for Virginia coastal waters off the North Carolina coast since the fresh water source of the Chesapeake Bay results in a several parts per thousand (^{o}/oo) salinity difference between these water masses. Annual mean salinities from the Chesapeake Bay, Diamond Shoals, and Frying Pan Shoals lightships are approximately 30^{o}/oo, 34^{o}/oo, and 36^{o}/oo respectively as shown in Figure 25. These mean differences are sufficiently large that the salinities remain distinctive even on the time scales of the low frequency fluctuations. From the relative fresh water inflow amounts from the Chesapeake Bay and Cape Fear Rivers, also shown in Figures 25, we observe that the only significant fresh water source for this study region exists northward of Diamond Shoals. Although the proximity of the Gulf Stream to Diamond Shoals is generally a barrier to communication of waters from the mid-Atlantic to South Atlantic bight regions under favorable wind and or Gulf Stream conditions waters will flow across this barrier. One such wind was observed during March 1979.

Figure 26 shows salinity as a function of time from moorings at two locations in Onslow Bay (moorings at two locations in Onslow Bay (moorings P and O of Figure 1). A rapid drop in salinity occurred at mooring P beginning around March 12. This salinity drop was followed some two weeks later by a similar drop at mooring 0 situated further southwest along the coast. Note that an even larger drop with a similar lag occurred at these two stations between April and May. Figure 27 shows the temperature/salinity (T/S) relationship at these stations as a function of time during the March event. The rapid switch in water properties is clear. Salinity declined rapidly by some 2-3^{o}/oo and temperature declined by 1-15^{o}/ooC resulting in a decrease in water density. Although the origin of this lighter and fresher water seems to be from the Virginia coastal waters, or waters at least north of Diamond Shoals, the mechanism by which salinity changed at sites P and O remains uncertain. The fact that there is a two week time lag between the onset of the event at O relative to P suggests southwestward advection. However the horizontal currents observed at these locations do not bear this out in a simple manner. Vertical advection downslope of lighter fresher water initially trapped shoreward by a Gulf Stream filament front may account for the observation. The entire salinity fluctuation was confined to the bottom half of the water column (depth ~33m) since the instruments at 17 m observed no comparable variations. Therefore a vertical salinity

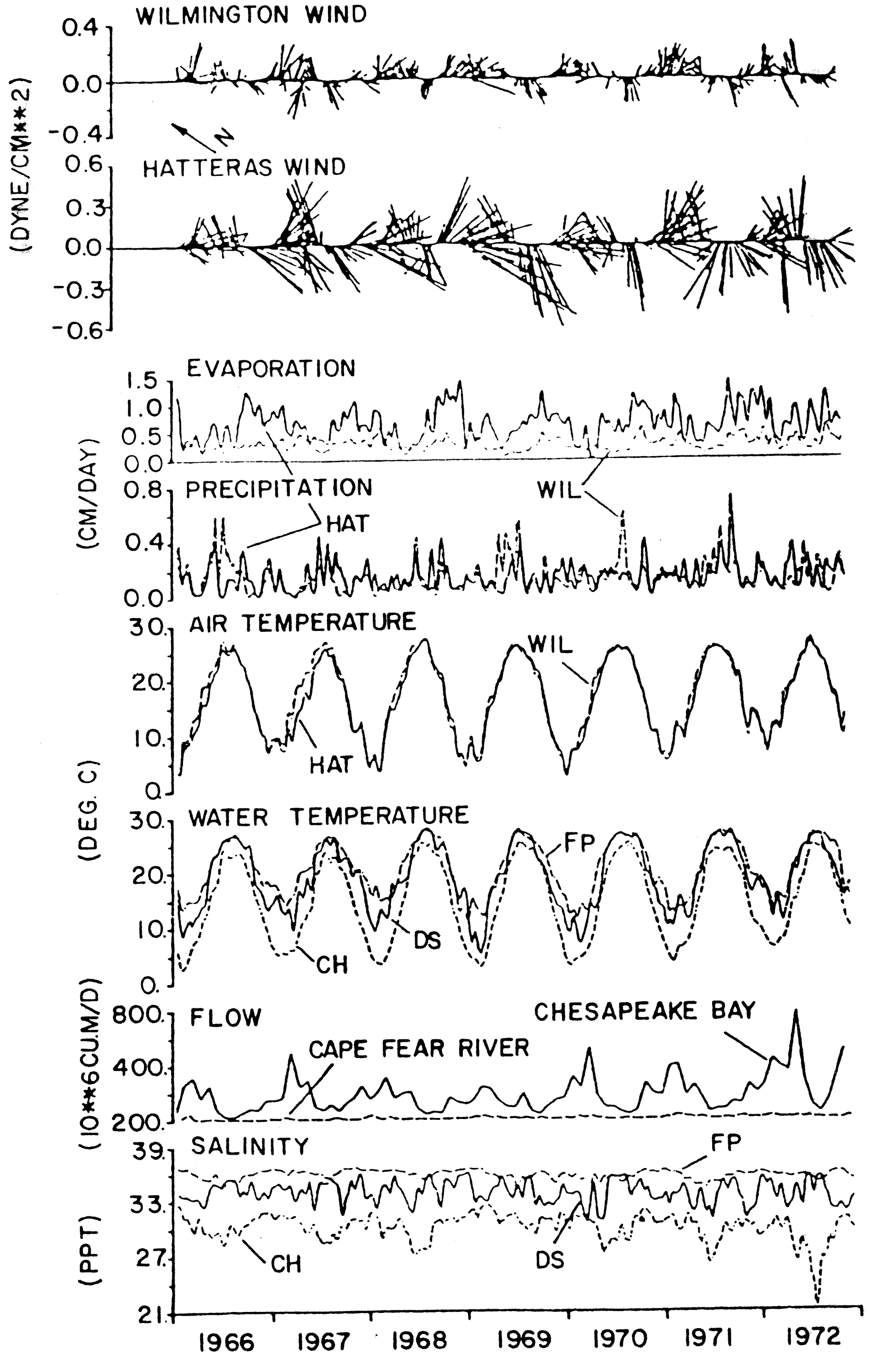

Figure 25. Weekly mean salinity and water temperature observed from 1966 to 1972 at the lightship stations offshore of the Chesapeake Bay, Diamond Shoals, and Cape Fear. Cape Fear River and Chesapeake Bay fresh water flow and Cape Hatteras and Wilmington, N.C. meteorological station data are also shown.

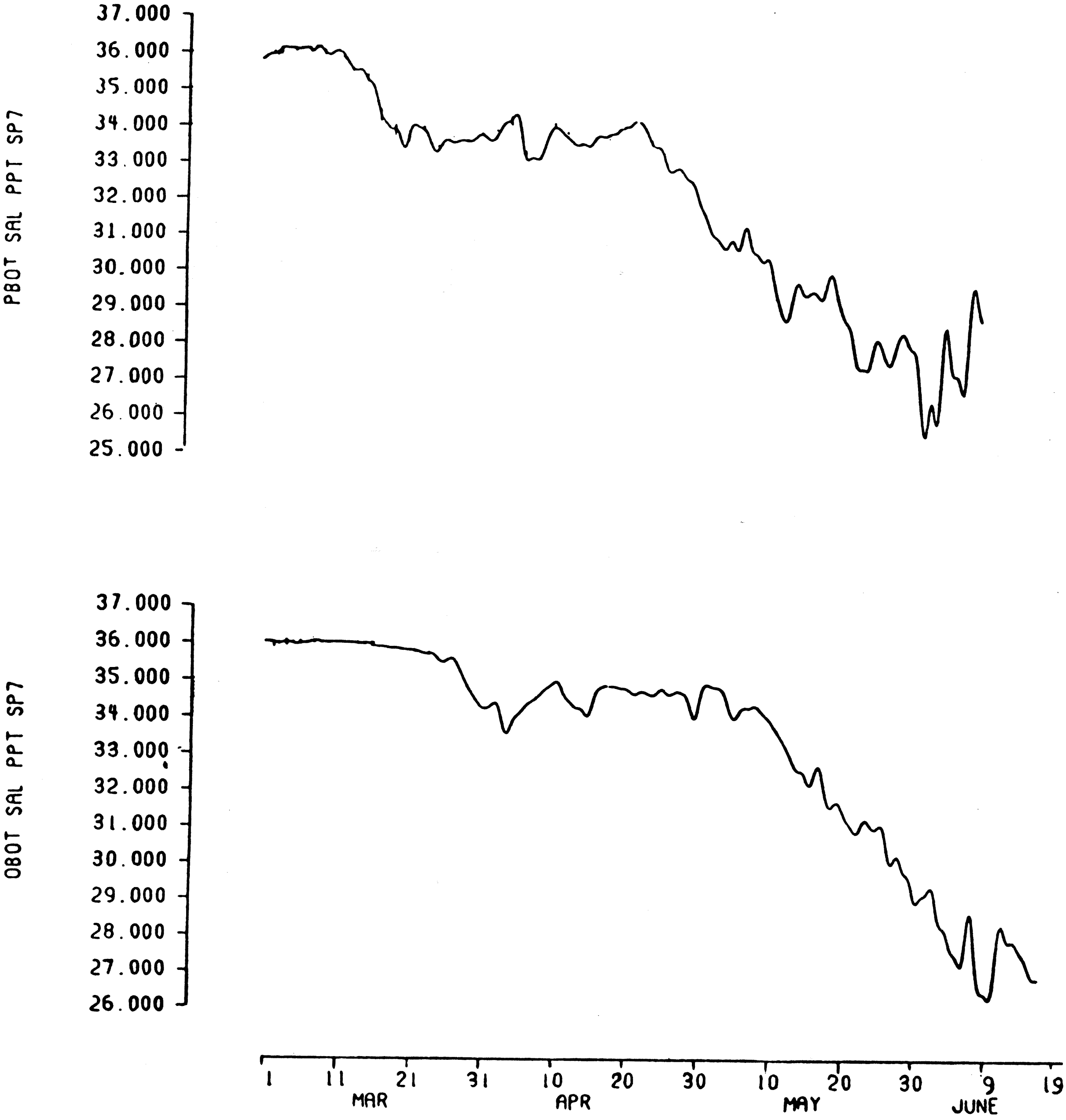

Figure 26. Salinity as a function of time measure 3 m off the bottom at moorings P and O.

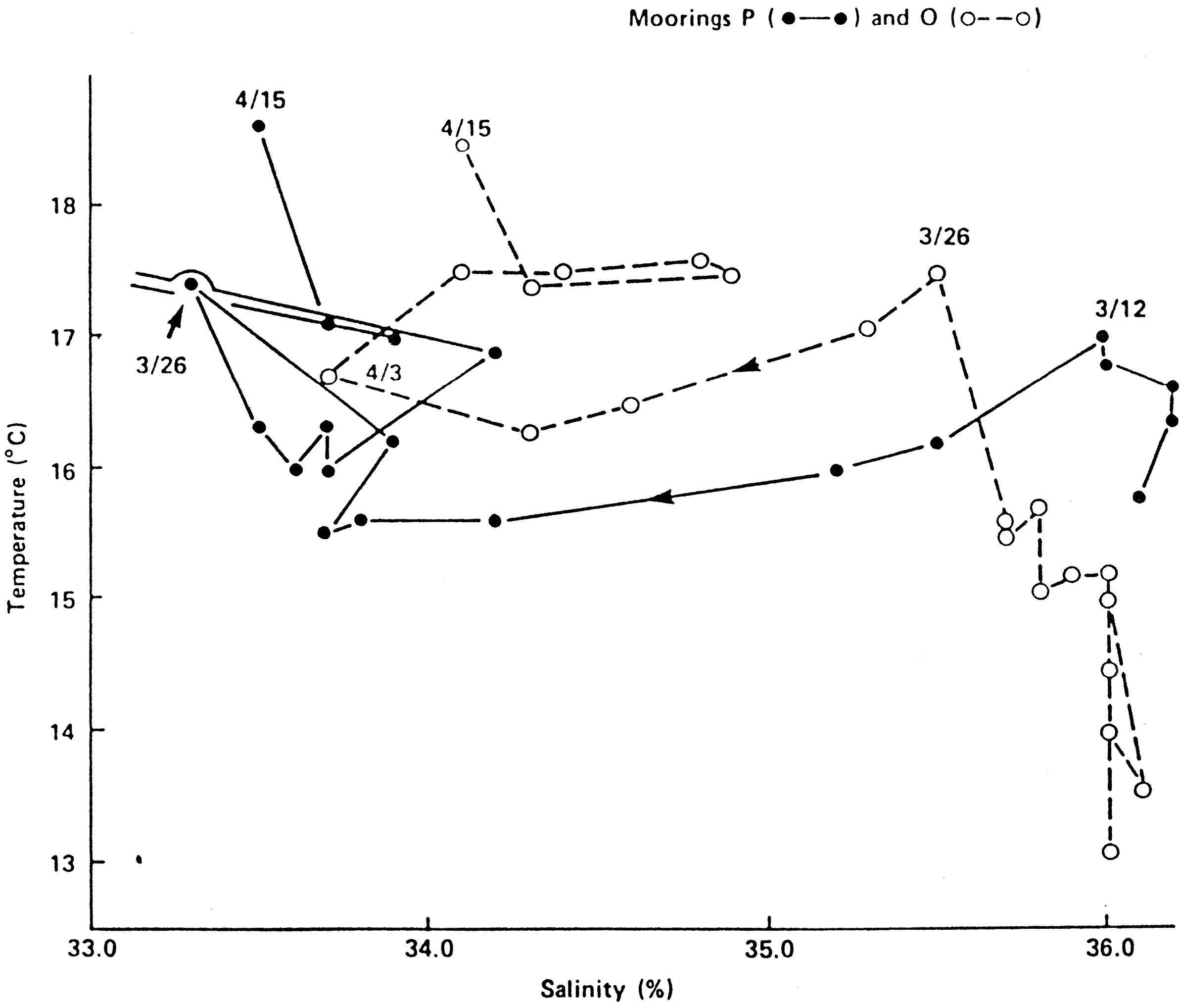

Figure 27. T/S curves as a function of time during the event from 3/4-4/15, 1979.

gradient 2-3°/oo existed over the water column.

The larger decrease in salinity observed beginning toward the end of April when salinity declined by around 7°/oo is probably of the same origin since there is a similar lag between P and O. Clearly, the water must have originated north of Diamond Shoals since there is no other source of such low salinity water. Again, the velocity vectors do not show a period of sustained alongshore or offshore flow; rather they oscillate with time scales shorter than the overall salinity event. Notice, however, that the salinity event, at least at mooring P, shows a step-like reduction in salinity which would be consistent with a fluctuating front with each fluctuation mixing fresher water into the region. Initial inspection of the vertical shear in horizontal velocity suggests a general consistency between a frontal interpretation and what is implied by the thermal wind relationship. The important points here are that Virginia coastal water does penetrate southwestward along the North Carolina coast as was suggested by Bumpus (1973) and mid to inner shelf fronts, separate from that of the GSF and the secondary frontal water masses, exist on the CC shelf.

Recruiting the Red Tide

During October, 1987, the dinoflagelate which constitutes the red tide, the scourge of the fishing industry as well as the tourist trade, made its appearance in Onslow Bay. This bug not only poisons fish, particularly filter feeders, thus rendering the creatures unfit for human consumption, but also creates noxious fumes which cause respiratory and eyesight problems in humans. Carolina Capes waters are not known to be infested with this particular form of dinoflagelate so the question asked was: What conditions were responsible for the outbreak of the red tide? The more appropriate related question is: Where did the red tide come from and what physical oceanographic conditions were present to assist the dinoflagelate population on its apparent maiden voyage into North Carolina coastal waters?

The origin of the red tide dinflagelate (RTD) was probably west Florida coastal waters. The RTD could then have very easily been entrained into the Gulf Stream and rapidly transported by the Gulf Stream some 1600 km within several weeks to Carolina coastal waters. Now, if a filament happened to be present then it would be a direct route from the Gulf Stream to the coast via one of the streamlines shown in Figure 20. Following a filament streamline takes a parcel from surface interior Gulf Stream waters right onto the mid to outer shelf on the shoreward side of the filament where the water parcel is now exposed to the direct wind stress driven as well as slope current regime. The parcels of RTD laden water can then be driven towards the coast where water masses may reside for periods of 2-3 months (Blanton and Pietrafesa, 1978). During the period 09 October - 07 November, 1987, the N.C. coast was buffeted by northeasterly winds and several large filaments. The conditions were perfect, as is explained in Pietrafesa, et al. (1988), for recruitment of the RTD from Gulf Stream frontal filaments onto the shelf to be advected across the shelf and retained near the coast. Figure 28 conceptualizes the scenario.

SUMMARY AND CONCLUSIONS

Hydrodynamics and hydrography on the CC shelf are controlled by atmospheric forcing from the top and Gulf Stream frontal events from offshore. Gulf Stream phenomena which affect the oceanography of the CC shelf include the deflection of the stream at the Charleston Bump and the subsequent creation of the Charleston Trough and frontal meanders and filaments. Atmospheric wind effects are most apparent in mid to inner shelf

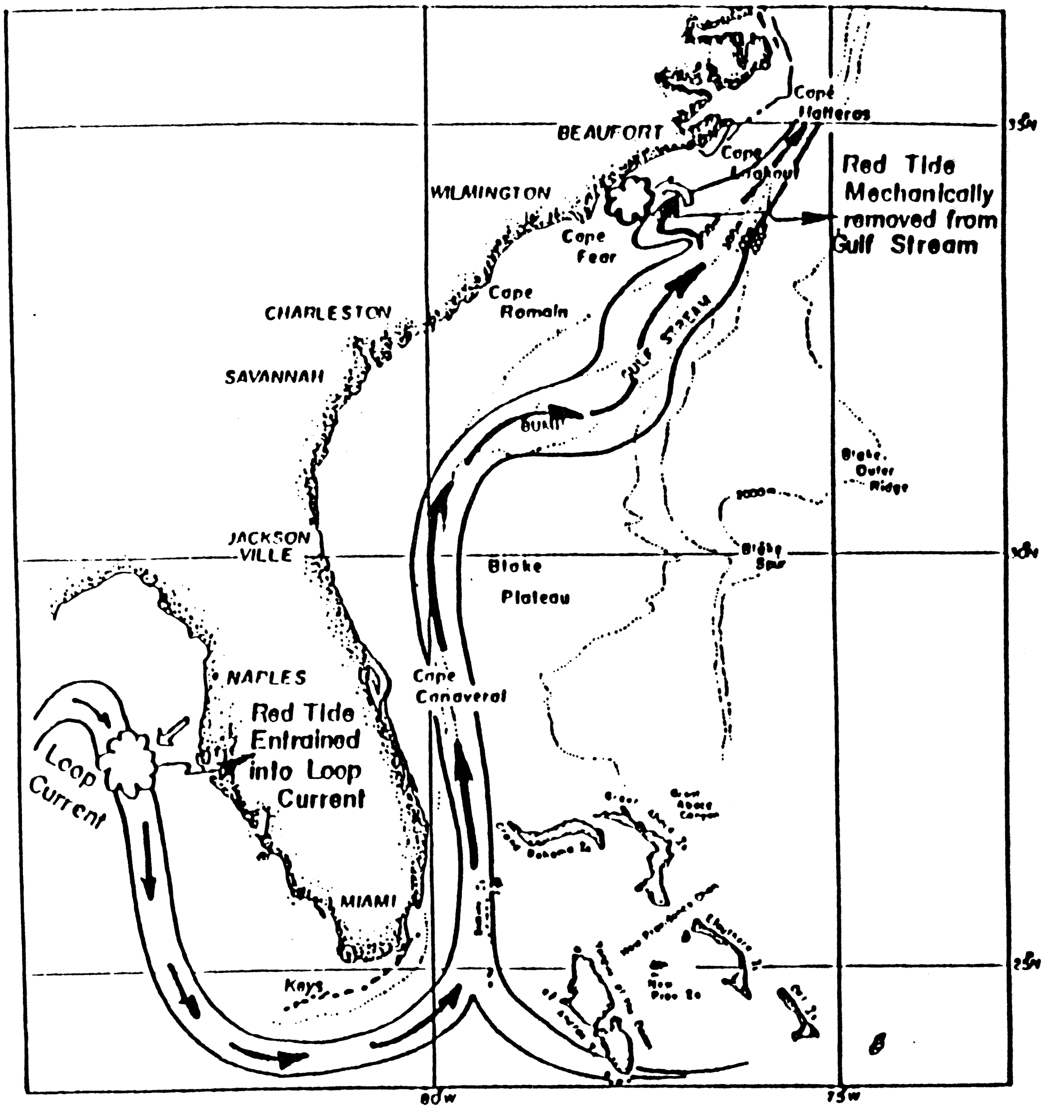

Figure 28. Recruitment and Retention of the Red Tide to N.C. Coastal Waters: A conceptual scenario based on VHRR and coastal wind data.

waters. In offshore waters wind effects are generally masked by GSF events.

The alongshore component of the wind provides the important forcing out to mid-shelf waters. Wind effects are both mechanically direct and indirect via the setup of coastal pressure gradients. The mid to inner shelf current field consists of a wind driven surface component and slope currents which extend throughout the water column and are strongly geostrophic coupled to both surface and mass field slopes. The bottom boundary layer consists of geostrophic and bottom stress induced current components.

Water masses are derived principally from the Gulf Stream via frontal event processes which not only advect warm, saline surface layer stream waters onto and along the mid to outer shelf but also create an upwelling ridge along the outer shelf, during their passage, within which offshore waters are advected up and onto the shelf. Georgian shelf waters are advected into the CC region during periods of persistent southwesterly winds while Virginian coastal waters penetrate the Diamond and Lookout shoals, from the north, during periods of persistent northerly winds.

In outer shelf waters, hydrographic fronts are formed by the Gulf Stream front, a generally progradational front (Pietrafesa, 1983). In mid shelf waters, a retrogradational front (ibid) can form consisting of inshore CC waters, or occasionally Virginia coastal water, on the coastal side and GSF waters on the offshore side. This front is not yet well understood.

Finally the Red Tide, a dinoflagelate, can be carried from Florida coastal waters by the Gulf Stream to North Carolina where the presence of warm core frontal filaments may allow the plant to be carried into shelf outer waters. Thereafter the plants may be carried towards the coast by wind induced or slope currents.

ACKNOWLEDGMENTS

This study was supported by the U.S. Department of Energy under Contract No. DE FG 09-85-ER 60376, and by the U.S. Department of the Interior under Contract No. 14-12-0001-30152. Gerry Janowitz, Bob Weisberg, Bobby Crissmand, Dave Amstutz and Fred Vukovich all participated in the DOI portion of the study and are thusly acknowledged.

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OVERVIEW OF NEOGENE AND QUATERNARY GEOLOGIC HISTORY, NORTH CAROLINA CONTINENTAL MARGIN (ONSLOW BAY)

Scott W. Snyder and Stanley R. Riggs
Department of Geology, East Carolina University
Greenville, North Carolina 27858

ABSTRACT

Neogene and Quaternary sediment patterns on the Onslow Bay continental shelf are, in large part, the product of eustatic sea-level fluctuations. The lower to middle Miocene Pungo River Formation was deposited during second-order supercycle TB2 (Haq et al., 1987). Eighteen fourth-order seismic sequences within the formation can be grouped into three third-order seismic sequences (Frying Pan, Onslow Bay and Bogue Banks), each of which corresponds to the maximum landward extent of a third-order coastal onlap event. Despite the influence of eustatic sea-level fluctuations on the depositional history of the continental shelf, not all known third-order coastal onlap events are represented by the Miocene sediments of Onslow Bay. In addition to relative position of sea level, factors such as topographic configuration of the shelf and flow path and intensity of the Gulf Stream influenced depositional-erosional patterns and the distribution of phosphatic vs. siliciclastic sediments. Explaining why specific onlap events are represented by deposits whereas others are not will require additional research. General lack of Pliocene deposits across the Onslow Bay shelf and in portions of the adjacent coastal plain region cannot be adequately explained solely by sea-level fluctuations. Gentle upward movement along the Mid-Carolina Platform High seems a more likely explanation for the present distribution of marine Pliocene deposits.

Quaternary deposits were also strongly influenced by high# frequency fluctuations of sea level. Widespread carbonates deposited during interglacial marine transgressions were later altered and partially eroded by subaerial and fluvial processes during glacial regressive phases. Where dissected, the resulting carbonate hardbottoms are bounded by exposed rock scarps which support a prolific marine biota. Unconsolidated sediments in low areas between the hardbottoms are the site of secondary mineralization, including minor reprecipitation of phosphate dissolved from underlying Pungo River phosphorites.

INTRODUCTION

Onslow Bay is a modern cuspate embayment in southeastern North Carolina bordered to the north by Cape Lookout and to the south by Cape Fear (Figure 1). The modern continental shelf in Onslow Bay extends from the barrier island system to approximately the 50-m isobath. The shelf has a maximum width of about 100 kilometers and consists of Upper Mesozoic and

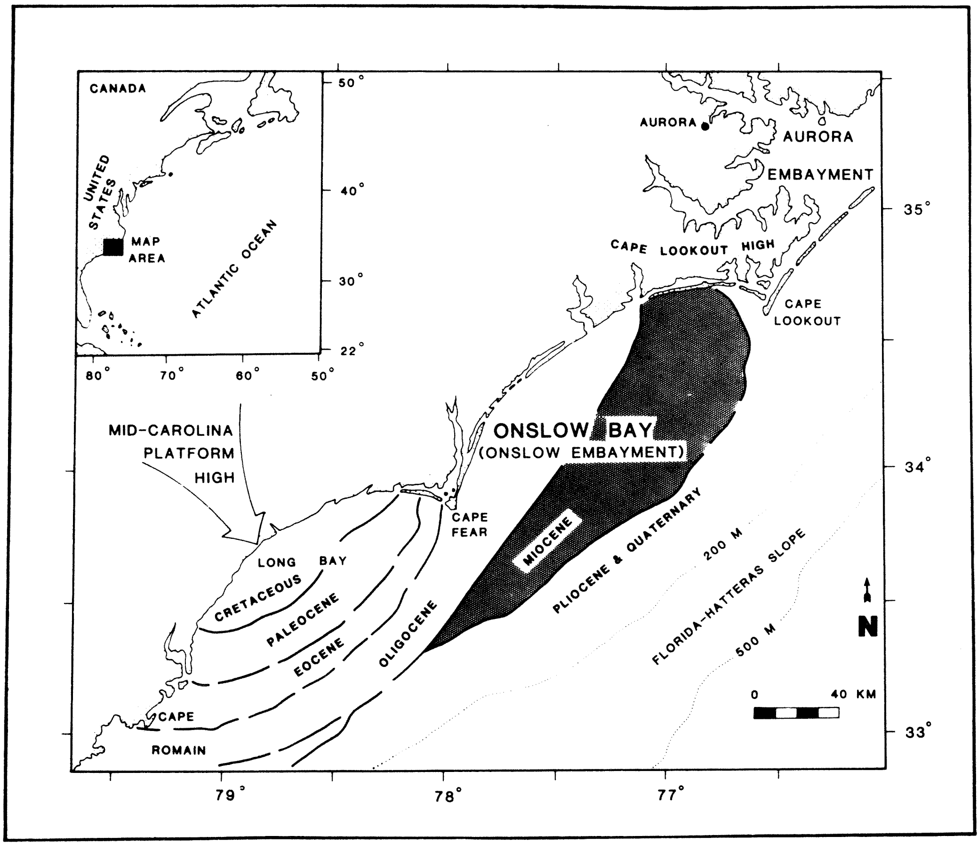

Figure 1. Locality map showing Onslow Bay in relation to the Mid-Carolina Platform High, Cape Lookout High and outcrop patterns of Upper Mesozoic/Cenozoic strata (after Stephen W. Synder (1982) from Scott W. Snyder et al., 1988a).

Cenozoic strata that have built outward and upward to produce its present configuration. This paper focuses on sediments representing the Neogene and Quaternary Systems of the Cenozoic Era. According to Haq et al. (1987), the Neogene System includes sediments deposited between 25.2 and 1.65 million years ago (mya) (Figure 2). The Miocene Series spans 20 million years (from 25.2 to 5.2 mya), while the Pliocene Series spans 3.55 million years (from 5.2 to 1.65 mya). The Quaternary System extends from 1.65 mya to the present day and includes the Pleistocene and Holocene Series, which are not differentiated for purposes of this report.

Over the past 20 million years the continental margin in the vicinity of Onslow Bay has been influenced by diverse and complexly interrelated geologic, biologic and oceanographic processes. It has been repeatedly inundated by advancing seas, subjected to episodes of marine scour and upwelling, blanketed

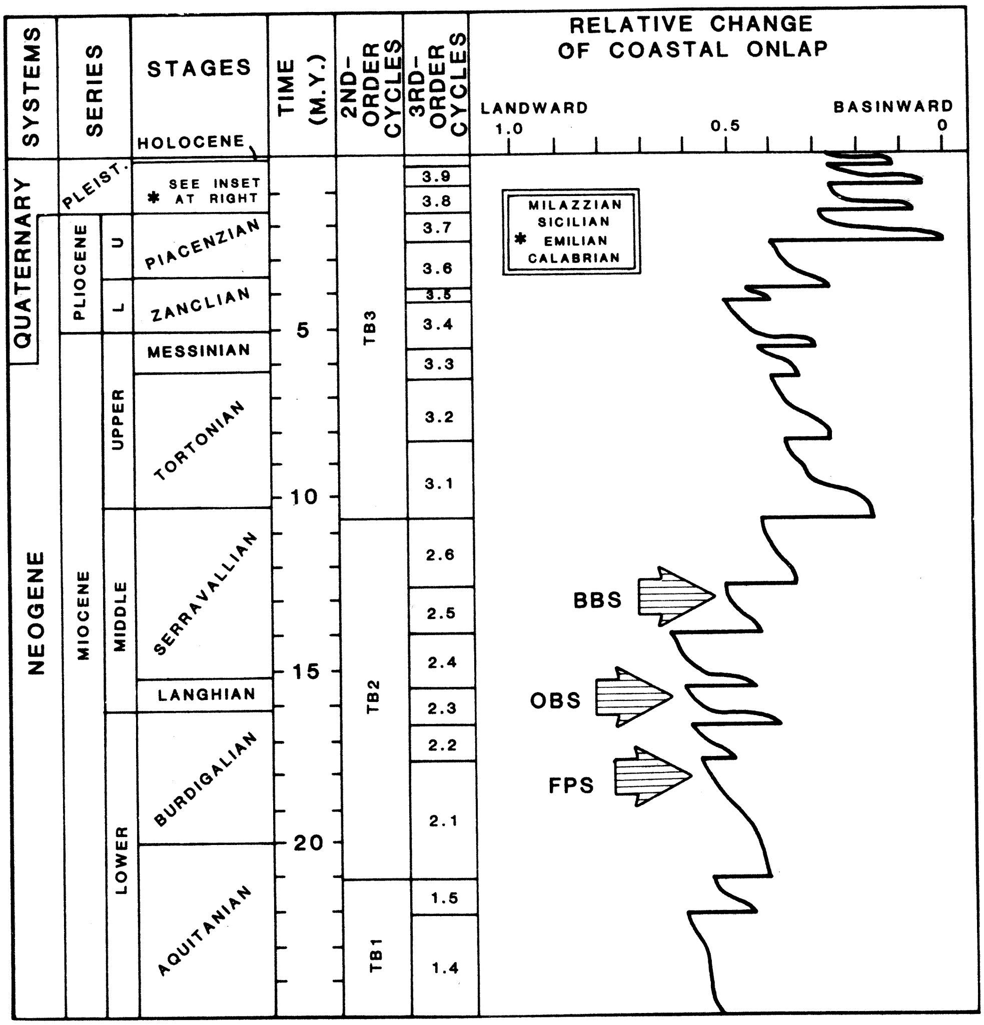

Figure 2. The Neogene sea-level cycle chart (modified from Haq et al., 1987) showing stratigraphic position of third-order Miocene sequences (Frying Pan, Onslow Bay, Bogue Banks) in Onslow Bay.

by deposits ranging from mostly authigenic minerals to predominantly siliciclastic sediments, and exposed to subaerial erosion and channeling during sea-level lowstands. Neogene eustatic sea-level fluctuations, imprinted upon the structural and stratigraphic framework produced during the earlier evolution of this passive continental margin, have controlled primary depositional features and sediment types, as well as postdepositional alteration and secondary mineralization. Superimposed upon patterns due to sea-level cyclicity are the effects of oceanographic and/or climatic changes that were not directly linked to eustacy. For example, Gulf Stream flow probably intensified during the early to middle Miocene in response to circulation changes in the Gulf of Mexico, which were triggered by tectonic events in Central America (Mullins et al., 1987). Intensification of Gulf Stream flow, in turn, profoundly affected the continental margin of Onslow Bay, contributing to an intricate, sometimes confusing composite geologic section.

Since 1979, geology of the Onslow Bay continental margin has been the object of seismic, sedimentological, mineralogical, chemical and paleontological analyses supported by the National Science Foundation (grants OCE-7908949, OCE-8110907, OCE-8342777 and OCE-8609161) and the North Carolina Sea Grant College (grants NA83AA-D-00012/R/A03 and NA85AA-D-SG022/R/A04) under direction of Stanley R. Riggs, Albert C. Hine and Scott W. Snyder. The purpose of this paper is to provide a general overview of this research and the geologic history of Onslow Bay. It is not intended to be comprehensive or to supply supporting data, which are available in references cited within the text.

Structural and Paleotopographic Framework

Onslow Bay is located on the northeastern flank of a broad region of pre-Jurassic continental crust called the Carolina Platform, a tectonic component of the trailing margin of North America that extends from Florida to Maryland (Klitgord and Behrendt,, 1979). The relatively flat and shallow (less than 1 km) central portion of the Platform is located near Cape Fear, North Carolina. Stephen W. Snyder et al. (1982) and Hine and Riggs (1986) argued that this shallow segment of the Platform, from which its margins descend into flanking embayments and troughs, should be termed the Mid-Carolina Platform High, rather than the Cape Fear Arch of traditional usage.

Distribution of post-Jurassic depositional sequences, including those of the Neogene and Quaternary, was controlled in large part by the configuration of the Mid-Carolina Platform High. Outcrops of post-Jurassic strata follow broadly concentric patterns around the eastern margin of this feature (Figure 1). Deposits along its northeastern flank formed the Neogene and Quaternary shelf sequences preserved in Onslow Bay.

During the Miocene, there were two depositional embayments along the North Carolina margin. The Onslow Embayment to the south was separated from the Aurora Embayment to the north by the Cape Lookout High (Figure 1), an elongate, east-west treading paleotopographic ridge formed by pre-Miocene sediment drift along the merge-point of the Gulf Stream and south-flowing shelf currents (Stephen W. Snyder, 1982; Popenoe, 1985). The Cape Lookout High remained a prominent topographic feature until nearly the end of Miocene deposition, when it was buried and the two depositional embayments it had separated were joined.

Studies discussed below concentrated on the feather-edge, updip limit of outcropping Neogene sediments in Onslow Bay. Only here could Miocene sediments be recovered by vibracoring (maximum core length of 9 m). Although Neogene and Quaternary sediments represent a small volumetric part of the entire Mesozoic-Cenozoic wedge which forms the North Carolina continental shelf, they record many significant geological events.

Neogene System

Miocene Series

Miocene sediments of the exposed North Carolina Coastal Plain occur only in the subsurface, where interbedded phosphatic clays, sands and carbonates 'were assigned to the Pungo River Formation (Kimrey, 1964). Pungo River sediments extend onto the continental shelf of Onslow Bay where they occur in outcrop and shallow subcrop beneath a widespread veneer of Quaternary sands and more limited exposures of Plio-Pleistocene carbonates (Blackwelder et al., 1982; Matteucci, 1984; Popneoe, 1985; Riggs et al., 1986).

Detailed seismic stratigraphic analyses of Neogene and Quaternary deposits extending from the outer coastal plain to the upper continental slope have delineated 18 distinct depositional sequences within the Miocene Pungo River Formation (Stephen W. Snyder, 1982; Stephen W. Snyder et al., 1982). Each such sequence is bounded above and below by an unconformity, and thus represents a depositional event within a discrete time--stratigraphic interval (Vail et al., 1977). Utilizing an extensive network of seismic reflection data collected along the Carolina continental margin (21,000 + km of high-resolution profiling), depositional sequences were traced in the subsurface and their outcrop pattern was mapped. These sequences strike generally north-northeast, forming a complex outcrop/shallow subcrop pattern in which younger sequences commonly truncate older ones (Figure 3). From their western updip limit, Pungo River sediments dip to the south-southeast, thickening to more than 500 m at the shelf edge (Riggs et al., 1985).

Seismic analyses provided the stratigraphic framework for biostratigraphic interpretation of sediments from 95 vibracores which penetrated the Pungo River Formation. The 18 depositional sequences mentioned above represent fourth-order seismic sequences which can be grouped into three third-order sequences, the ages of which can be resolved on the basis of biostratigraphic evidence (Figure 3). Age assignments are based upon planktonic foraminifera and nannofossils (Scott W. Snyder et al., 1988b), diatoms (Powers, 1988) and radiolarians (Palmer, 1988).

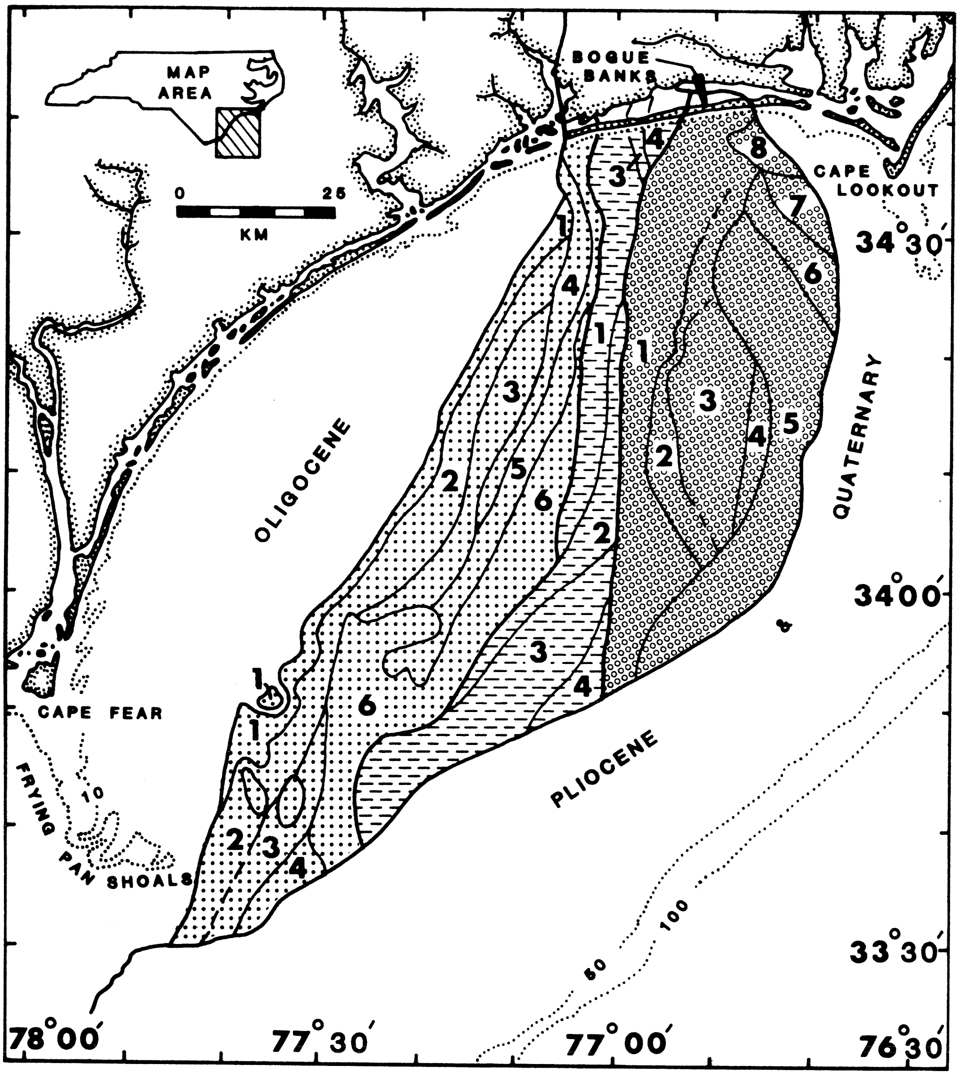

Figure 3. Map showing outcrop and shallow subcrop pattern of fourth-order seismic sequences within the Miocene section of Onslow Bay. Patterns differentiate third-order seismic sequences (Frying Pan - solid dots, Onslow Bay - dashes, Bogue Banks - open circles). Seismic interpretation by Stephen W. Snyder and A.C. Hine.

The stratigraphically lowest third-order sequence, dated as middle Burdigalian (upper lower Miocene), is termed the Frying Pan Sequence. It contains six fourth-order seismic sequences (FPS-1 through FPS-6) (Figure 3). The overlying Onslow Bay Sequence, dated as Langhian (lower middle Miocene), contains four fourth-order sequences (OBS-1 through OBS-4). The stratigraphically highest of the three third-order sequences is the Bogue Banks Sequence. It was deposited during the middle

Serravallian (middle Miocene) and contains eight fourth-order sequences (BBS-1 through BBS-8). Biostratigraphic constraints on the ages of the Frying Pan, Onslow Bay and Bogue Banks Sequences indicate that each was deposited during a third-order coastal onlap event (Haq et al., 1987), whereas the entire Pungo River Formation was deposited during a larger-scale, second-order Miocene marine transgression (Figure 2).

The Frying Pan, Onslow Bay and Bogue Banks Sequences each represent deposition associated with a sea-level highstand. Intervening unconformities were most likely developed during sealevel lowstands. The influence of eustatic sea-level oscillations in producing this depositional record would seem to be straightforward and obvious. However, Pungo River strata do not represent all of the Miocene coastal onlap events depicted in the chart of Haq et al. (Figure 2). We suggest two possible explanations for this:

1) Oceanographic factors, such as impingement of the westward migrating Gulf Stream on the continental margin (Pinet and Popenoe, 1985), may have resulted in sediment bypass/erosion during some episodes of coastal onlap.

2) Deposits emplaced during some episodes of coastal onlap were later removed by erosion, either by subaerial processes during sea-level lowstands or by submarine scour associated with migration of the Gulf Stream during subsequent marine transgressions (Pinet and Popenoe, 1985; Popenoe, 1985).

Resolution of specific mechanisms responsible for the Miocene record must await 1) acquisition of continuous cores from thicker, more complete downdip sections, and 2) better understanding of regional and global changes (tectonic, climatic, oceanographic) during the Miocene.

The preserved depositional record in Onslow Bay contains a variety of lithofacies. Successive seismic sequences may be composed of similar lithofacies, in which case there is no distinct lithologic change across the intervening stratal reflector (Mallette, 1986; Scott W. Snyder et al., 1988a). Lithologies change vertically through the Miocene section, but the generalized lithofacies patterns within the northern, central and southern portions of Onslow Bay tend to persist through time. A source area to the northwest supplied siliciclastic sediments to northern and central portions of the Bay, while authigenic sediments accumulated farther south. During deposition of the Frying Pan and Onslow Bay Sequences, carbonates (composed largely of molluscan and barnacle fragments) and quartz sands accumulated in northern Onslow Bay along the southern flank of the Cape Lookout High. Deposits of the Bogue Banks Sequence in the northern region changed to predominantly siliciclastic sands. The central portion of all three third-order sequences (Frying Pan, Onslow Bay and Bogue Banks) was dominated by siliciclastic sands and muds, with abundant dolomite in both the Onslow Bay and Bogue Banks Sequences. The slow accumulation of fine sediment in the latter two sequences was repeatedly interrupted by influx of sands from a point-source to the west-northwest, producing interbedded fine-grained and coarser-grained deposits. Grain-size of the siliciclastic sediments generally decreased southward, indicating increased distance from the source area. During deposition of the Bogue Banks Sequence, phosphatic sands accumulated in the north and central portions of the Bay. In southern Onslow Bay, where only the Frying Pan Sequence has been extensively sampled, sediments consisted of largely authigenic components. Rich basal phosphorate deposits were gradually replaced by organic-rich, zeolitic muds (probably derived from biogenic silica) and deposition culminated with fossiliferous, fine quartz sands.

In reconstructing ancient depositional environments, the contrast between conditions favoring siliciclastics and authigenic phosphate sediments is of primary interest. Concentration of authigenic sediments occurs only where they are not overwhelmed by the influx of siliciclastic materials. Such conditions existed in southern Onslow Bay, far removed from the source area of siliciclastic sediments that lay to the northwest. However, formation of extensive sedimentary phosphorites also requires nutrient enrichment far beyond that found in most marine environments. Riggs (1984) demonstrated that interaction of the ancient Gulf Stream with topographic features of the continental margin during marine transgression could induce large-scale coastal upwelling. These upwelling events, in areas of minimum siliciclastic sediment input, were responsible for phosphate formation in southern Onslow Embayment during deposition of the Frying Pan Sequence. Smaller-scale phosphogenic episodes occurred in northern and central Onslow Embayment during deposition of the Bogue Banks Sequence.

Paleontological studies based on benthic foraminifera (Scott W. Snyder et al., 1988c) and diatoms (Powers, 1988) indicate that phosphatic intervals were indeed associated with episodes of nutrient enrichment. Although Miocene deposits accumulated in relatively shallow waters (mid to outer continental shelf), deeper, colder, more nutrient-enriched water masses occasionally invaded Onslow Embayment, probably through upwelling episodes like those described by Riggs (1984). Sediments containing appreciable amounts of phosphate yield benthic foraminiferal assemblages numerically dominated by forms known to thrive under conditions of nutrient influx , organic enrichment and oxygen depletion (Scott W. Snyder, 1989). These same sediments also contain diatom assemblages enriched in meroplanktonic and planktonic species known to be associated with modern upwelling systems (Powers, 1988). Conversely, benthic foraminiferal and diatom assemblages in siliciclastic lithofacies indicate well oxygenated bottom waters with reduced levels of nutrient content.

Phosphorate sediments in the Frying Pan Sequence of southern Onslow Bay and the Bogue Banks Sequence of central Onslow Bay (Figure 4) yield faunas and floras indicative of nutrient enrichment. Phosphatic sands in the Bogue Banks Sequence of northeastern Onslow Bay (Figure 4) are not so clearly associated with upwelling. Benthic foramininferal faunas suggest well-oxygenated bottom waters with only modest levels of organic enrichment (Scott W. Snyder et al., 1988c). Perhaps these phosphate grains are reworked, rather than being formed <u>in situ</u>.

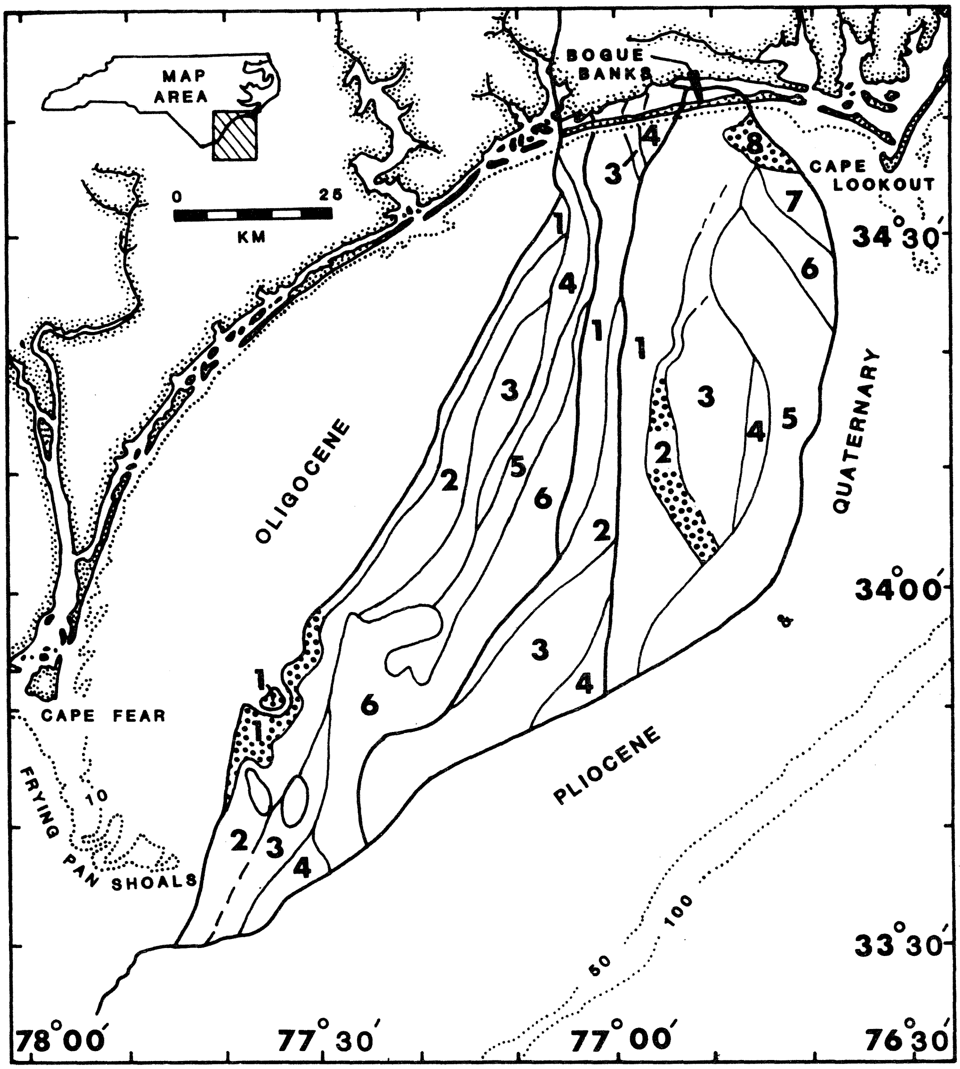

Figure 4. Phosphate depocenters (indicated by dotted pattern) shown in relation to seismic stratigraphic framework of Miocene deposits in Onslow Bay.

The Miocene deposits of Onslow Bay are largely the product of high-frequency eustatic sea-level fluctuations and oceanographic changes triggered by such changes. Depositional episodes correlate with global coastal onlap events. Explanation as to why all of the known Miocene onlap events are not recorded in Onslow Bay requires further research. The composition of deposits that have been preserved (siliciclastics vs. carbonate vs. phosphate) depends on the interaction of numerous factors, including relative position of sea level, rate of sea-level change, configuration of the shelf margin, proximity to shelf margin and to source areas of siliciclastic sediments, flow path and intensity of the Gulf Stream and its interaction with the margin, nature of deeper water associated with upwelling, etc. Some of these factors are, in turn, dependent on global and regional changes in climate and oceanic circulation. It is not surprising that the resulting Miocene depositional record along the North Carolina margin is so complex.

Pliocene Series

Pliocene sediments are absent throughout nearly all of Onslow Bay (Figure 1). They form a veneer of siliciclastic sands and carbonates along the modern shelf edge, and extend onto the present-day shelf of Onslow Bay only in the northeastern corner.

Absence of Pliocene deposits in Onslow Bay is consistent with the distribution of equivalent-aged strata on the emerged North Carolina Coastal Plain. Except for scattered outliers (such as at Natural Well, Bear Bluff, etc.), marine deposits of Pliocene age are absent across the coastal plain from the vicinity of Cape Lookout to Cape Fear, whereas the Pliocene Yorktown and Duplin Formations are widely distributed north of Cape Lookout and southwest from Cape Fear into South Carolina, respectively (Brown et al., 1985). In these latter areas, marine Pliocene sediments extending westward across the coastal plain record a major marine transgression, as suggested in the chart of Haq et al. (1987) (Figure 2).

Lack of Pliocene deposits across the Onslow Bay continental shelf and portions of the adjacent coastal plain cannot be adequately explained solely by eustatic sea-level fluctuations. Perhaps Pliocene sediments, once more extensive across the Onslow Bay shelf, were eroded during subsequent sea-level lowstands. However, the extensive marine Pliocene deposits north of Cape Lookout and south of Cape Fear suggest that Onslow Bay and the adjacent coastal plain region may not have been extensively inundated during the Pliocene. Gentle upward movement, perhaps initiated in the late Miocene, of the Mid-Carolina Platform High (= Cape Fear Arch of traditional usage) seems a more likely explanation for the present distribution of marine Pliocene deposits. Our data are not sufficient to either demonstrate or contradict either of these possibilities.

Quaternary System

The Quaternary System includes the Pleistocene and Holocene Series (Figure 2). These series are not differentiated for the purposes of this report due to difficulties in distinguishing them in sediments of Onslow Bay. There are several reasons for this:

1) discontinuous nature of the Quaternary sediment cover,
2) extensive resuspension and vertical mixing of the surficial veneer of sediment during storms,
3) lack of planktonic fossils suitable for differentiating Pleistocene from Holocene deposits,
4) abundant relict Pleistocene materials within Holocene deposits due, in part, to limited sediment supply from modern rivers.

Two aspects of Quaternary sedimentation are of primary interest:

1) the formation and subsequent erosional history of carbonate hardbottoms and their influence on modern biological communities,
2) the distribution of and sources for secondary minerals (e. g., phosphate and iron) within unconsolidated, quartz-rich surficial sands.

Hardbottoms

Extensive and morphologically complex hardbottoms crop out across the inner and middle continental shelf of Onslow Bay. Hardbottoms are of three types:

1) calcareous quartz sandstones,
2) quartz-rich, molluscan-moldic, fossiliferous limestones,
3) extensively bored, fossiliferous calcarenites (Mearns, 1986).

The first two types are associated with Neogene strata, whereas the third is part of the Quaternary System which lies unconformably above Neogene sediments. The focus here is upon hardbottoms composed of the Quaternary calcarenites because their more extensive exposure and greater vertical relief make them more important in terms of their influence on modern biological communities.

Using high-resolution seismic and sidescan sonar profiling, the general distribution of hardbottoms which crop out on the modern shelf of Onslow Bay has been mapped (Mearns, 1986; Riggs et al., 1986). Quaternary hardbottoms are generally extensive, unbroken, flat surfaces; however, where dissected by erosion they usually rise 2 m or more above the surrounding sea floor. They are concentrated in southern Onslow Bay. Their upper surfaces range from smooth to irregular and frequently are covered with an ephemeral, highly mobile modern sand sheet. Where dissected they form extensive mesa-like platforms of carbonate rock bounded by highly eroded vertical scarps. Most scarps probably originated through fluvial erosion during sea-level lowstands. Once initiated, scarps are modified by submarine biological, chemical and physical processes. Vertical scarps are the most important aspect of hardbottoms.

Calcarenites exposed along vertical scarps are subjected to intense bioerosion, mostly by endolithic lithophagid and gastrochaenid bivalves (Carter and Mearns, 1986). These borers obliterate the calcareous rock fabric by chemical dissolution and riddle the rock wall with boreholes. The more indurated upper portion is protected by encrusting organisms. The net effect is for bioerosion to undercut the scarp, forming an overhang which eventually collapses due to wave surge pressure. With each successive episode of undercutting and collapse, the edge of the hardbottom recedes, and rock debris accumulates along the base of the escarpment as a rubble ramp (Mearns, 1986). Based on the width of the accumulated rubble, Mearns demonstrated that Quaternary scarps in southeastern Onslow Bay have receded as much as 80 m during the last 9000 years of Holocene sea-level rise.

Several types of margins are developed along hardbottoms (Figure 5). Vertical scarps that rise up to 8 m above adjacent unconsolidated sediments host a rich bottom biota including algae, sponges, corals, epifaunal and infaunal biavles, assorted vagrant benthic organisms and a variety of fishes. With increasing bioerosion and scarp recession, the zone of massive boulder debris increases. The resultant increase in surface area of exposed rock sustains a larger, more prolific bottom biota. The northeastern margins of hardbottoms are usually ramps composed of unlithified sands (Figure 5). They are gently sloping surfaces that result from transport and deposition of Holocene sands. Hardbottom margins with unconsolidated sediment ramps do not support the rich biota associated with escarpments and zones of boulder debris. Because the biota supported by scarps serves as a food source for a variety of invertebrates and fishes, knowledge about the nature and distribution of hardbottom margins is important to understanding productivity on the continental margin.

The geological origins of hardgrounds and their associated margins are, like the underlying Miocene deposits, linked with changes in eustatic sea level. Rises and falls in sea level during the Quaternary were controlled by glacial retreats and advances. Marine transgressions (interglacials) were marked by warming climatic conditions, increased vegetative cover on adjacent lands areas, and decreased terrigenous sediment input. Siliciclastic sedmentation was limited to nearshore environments whereas carbonate sediments predominated in more offshore

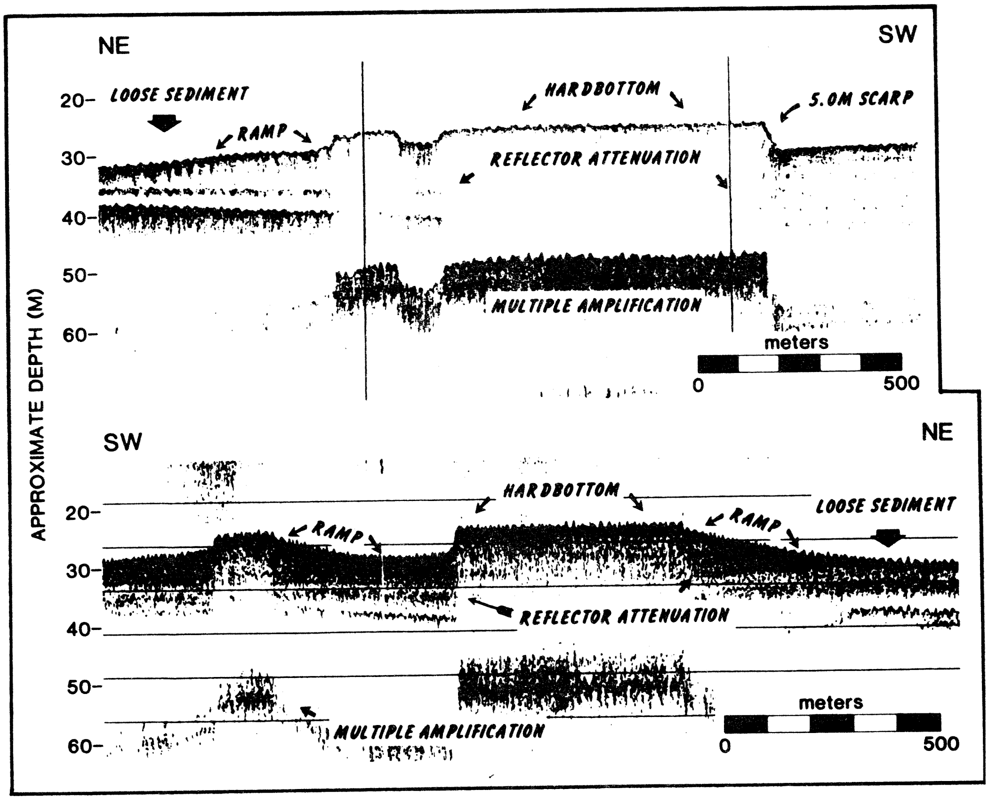

Figure 5. Seismic profile across Quaternary hardbottom showing nature and orientation of margin types (from Hine and Riggs, 1986).

environments (Riggs, 1984). Marine regressions (glacials) were characterized by fluvial channeling and erosion by the migrating shoreface, which dissected and removed much of the previously deposited volume of shelf sediment (Hine and Snyder, 1985). Subaerial exposure of the shelf during maximum sea-level lowstands also indurated and diagenetically altered remaining sediments (Riggs, 1984). Once formed and partially eroded by a combination of subaerial and fluvial processes, hardground scarps recede by the process of marine bioerosion during the subsequent sea-level highstand. Repetition of this sequence of events occurred throughout the Neogene and Quaternary. It is, however, most dramatically exemplified by the younger and consequently better preserved and exposed carbonate hardbottoms of the Quaternary.

Secondary Mineralization

The Quaternary sand sheet, irregularly distributed across the erosional surface capping Neogene strata, is the site of rather interesting mineralization processes. Some minerals in these sands are not primary (i.e., formed at the time of sediment deposition), but rather are being secondarily deposited after dissolution and transport from other sediment sources.

In southern Onslow Bay, the Quaternary sands contain orange phosphate grains which are petrologically and chemically distinctive from dark brown phosphates of the underlying Pungo River Formation. Orange grains have been extensively altered during mechanical reworking and incorporation into the younger sands. Phosphate content in the Ouaternary sands is highly variable, with P_2O_5 content ranging from negligible to 21.7% (Riggs et al., 1986). The sands range in thickness from 0 to 3 m and occur largely between mesas capped by carbonate rock (the hardbottoms discussed previously).

Distribution of phosphatic Quaternary sands provides insight into the mechanism of phosphate formation. Figure 6 shows the distribution of sands which contain 3% or more P_2O_5 superimposed upon the seismic sequences of the underlying Pungo River Formation. The richest phosphorites in the Miocene deposits of Onslow Bay occur in the southern portions of seismic sequence FPS-1 (Riggs et al., 1985). Note that the 3% P_2O_5 contour in Quaternary sands approximates the outline of the phosphorate deposits of FPS-1. This contour suggests that the majority of the phosphate is being mechanically reworked from FPS-1 and re-deposited in overlying sands.

However, uranium-series age dates (Riggs et al., 1982 and 1983) suggest the presence of a component that may be younger than 150,000 years. During mechanical reworking, some of the phosphate was evidently dissolved and reprecipitated to produce the minor occurrences of young, glossy-black phosphate grains. Uranium-series dates reflect the time of reprecipitation of these grains. This interpretation is supported by the fact that dissolution continues on the modern seafloor where phosphatic Miocene sediments are exposed, as evidenced by the release of soluble reactive phosphate (SRP) into the benthic boundary layer. Mean SRP at 1 cm above the sediment-water interface ranges up to 2.5 times that at 3.5 m (T. Tisue, unpubl. data), strongly suggesting release from the sediment. Similar SRP gradients do not occur where exposed bottom sediments are nonphosphatic.

Foraminifera within the same portion of the Quaternary sand sheet are also being permineralized, but demonstrate that phosphate is not the only, or even the major, mineral involved (Riggs et al., 1984). Altered specimens of miliolid foraminifera show gradational surface discoloration (white to dark yellow-brown) that progresses from late- to early-formed chambers. The percentage of extensively altered specimens varies directly with phosphate concentration in the sand fraction. Nearby nonphosphatic sands are devoid of such discolored specimens. Microprobe analyses of polished thin-

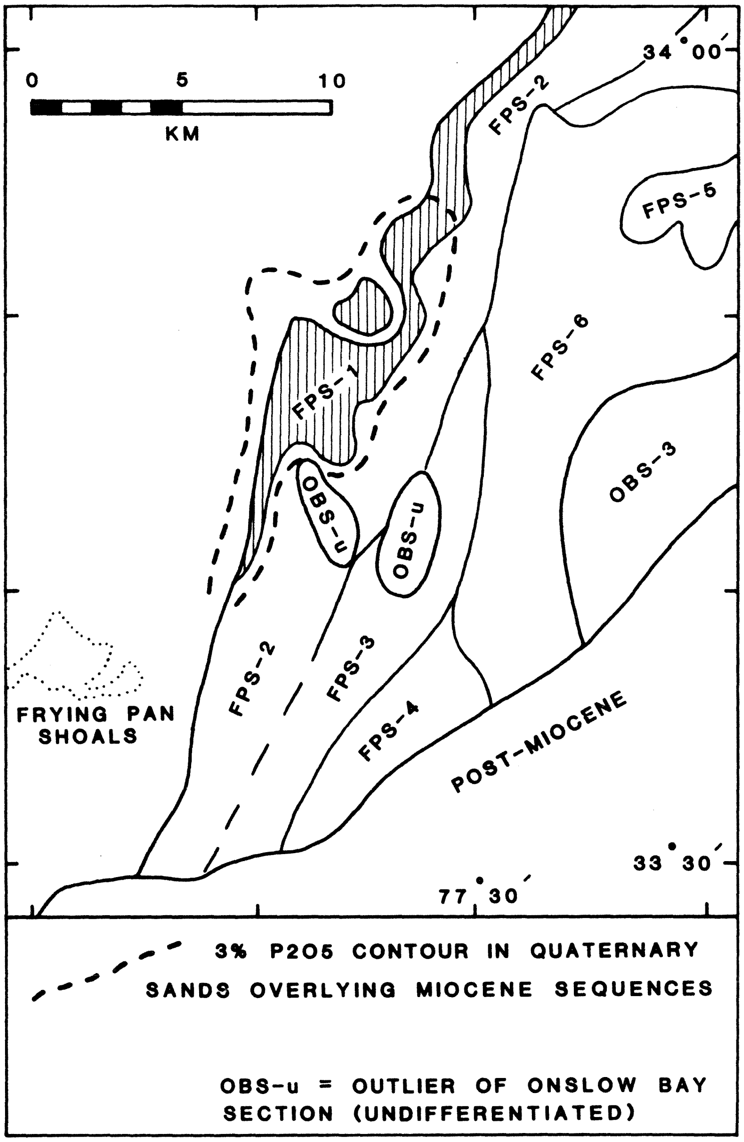

Figure 6. Distribution of phosphatic sediments in Quaternary sand sheet (modified from Hine and Riggs, 1986).

sections from completely discolored specimens indicate that alteration involves a decrease in %CaO and concomitant enrichment in %FeO and %P_2O_5. However, the degree of enrichment in %P_2O_5 (maximum of 0.8%) is minor compared to that for FeO (maximum of 18%). Nevertheless, such phosphate enrichment occurs only where the underlying sediments are phosphorites. Clearly, underlying deposits are supplying a complex assortment of elements that may precipitate in various mineral forms within Quaternary sands.

Secondary mineralization in Quaternary sands exemplifies the complex digenetic history of continental shelf deposits. Although this type of diagenesis is linked with eustatic sea-level fluctuations, its net effect is to alter and obscure the primary depositional record. The sedimentary record becomes proportionately more complex and difficult to unravel with each digenetic episode. Many such episodes characterized both the Neogene and Quaternary deposits. Any given stratum may have been repeatedly altered by successive digenetic events.

SUMMARY

The history of the Onslow Bay continental margin is complex, with regard to both primary depositional events and subsequent episodes of erosion and diagenesis. Unraveling its history requires multidisciplinary research efforts and recognition that traditional "layer-cake" stratigraphic concepts are not applicable to this type of continental margin depositional system.

ACKNOWLEDGMENTS

We gratefully acknowledge the contributions of A. C. Hine, Stephen W. Snyder and several masters-level students from the University of South Florida. Their collective efforts produced the seismic stratigraphic framework summarized in this paper. Numerous graduate students at East Carolina University contributed to the present understanding of litho- and biostratigraphic relationships. We also extend our thanks to an anonymous reviewer for suggestions which improved the manuscript.

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HYDROGRAPHY AND SEDIMENTATION ON THE CONTINENTAL SLOPE AND RISE OFF NORTH AND SOUTH CAROLINA

Thomas C. Johnson
Department of Geology, Duke University Laboratory
Beaufort, North Carolina

ABSTRACT

The continental margin off North and South Carolina is very complex in terms of its hydrography and sedimentation. The north flowing Gulf Stream intersects the deeper Western Boundary Undercurrent (WBUC) flowing southwards to create a complex structure of salinity, temperature and turbidity. Sediments that accumulate on the continental slope and rise are subject to scour, erosion and transport by these two major current systems. In addition, there is widespread downslope transport of sediment by mass wasting. Much of the deep water circulation pattern was established around 35 million years ago (ma). Distinct erosional pulses occurred at 17, 11-12 and 2-3 ma. The onset of glacial/interglacial conditions that are characteristic of the Pleistocene began at about 2.4 ma. The WBUC has varied significantly in strength during the past 100,000 years. It decreased steadily from about 30,000 to 12,000 years ago (ka). At 12 ka there was a major resurgence of the WBUC, marking the end of the last major ice age.

INTRODUCTION

The North Carolina continental margin marks an important oceanic boundary in the western North Atlantic. It separates a temperate environment to the north of Cape Hatteras from a subtropical environment to the south. A wide diversity of flora and fauna are found on the North Carolina shelf in part due to the convergence of temperate and subtropical species (Kirby-Smith, this vol.). Cape Hatteras marks the boundary between carbonate-rich shelf sediments off the southeastern coast and carbonate-poor shelf sediments off the middle Atlantic and New England States (Milliman et al., 1972). In the deep waters farther offshore, the Gulf Stream overrides the Western Boundary Undercurrent (WBUC) (Figure 1), creating a dynamic and complex hydrographic environment that strongly impacts on the morphology of the sea floor and the texture of the bottom sediments.

The purpose of this paper is to provide an overview of the deep-water circulation and its impact on sedimentation on the North Carolina continental slope and rise. In addition, results of paleoceanographic studies conducted upstream and downstream from North Carolina will be presented that summarize our present knowledge of the history of the WBUC in the western North Atlantic basin.

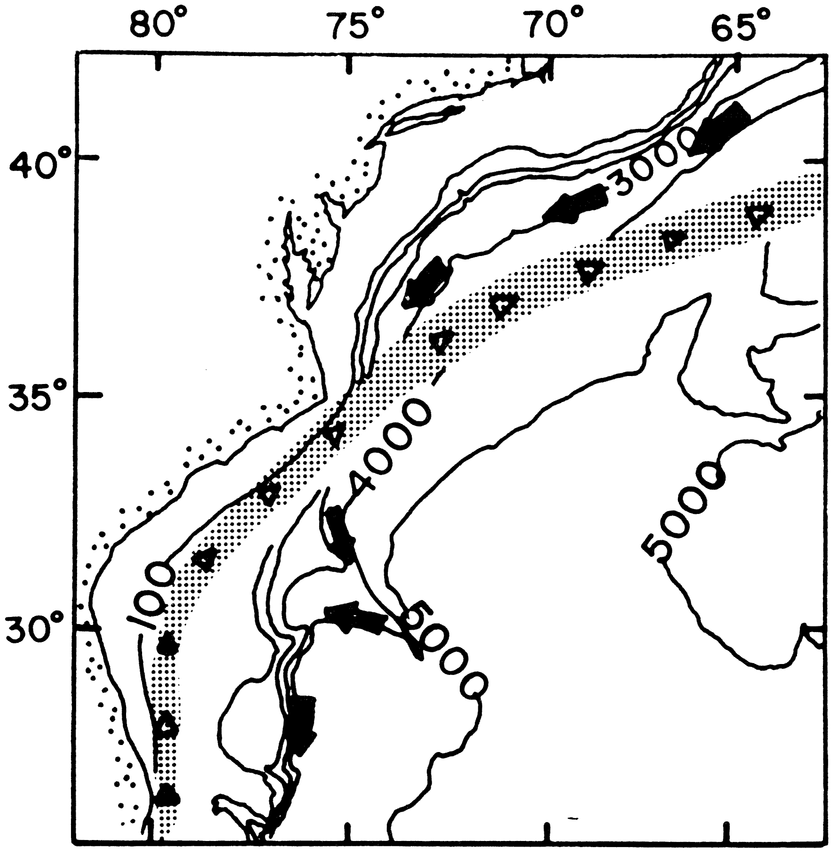

Figure 1. Location of the Gulf Stream (stippled) and Western Boundary Undercurrent (heavy arrows) off the east central U.S. continental margin (after Richardson, 1977).

Geological Setting

The continental margin off North Carolina is relatively narrow compared to most of the east coast, and has complex structure and morphology. Tertiary sediments outcrop on much of the Carolina shelf and dip and thicken in a seaward direction. They are exposed or covered by only a thin blanket of sediment on the continental slope as a result of erosion by bottom currents (Hutchinson et al., 1982; Riggs, 1984; Riggs et al., 1985). The Tertiary deposits are overlain by a thin and patchy veneer of Quaternary sediments on the shelf (Riggs et al., 1985) and they overlie a thick sequence of Jurassic and Cretaceous rift and post-rift sediments. The Mesozoic units are up to 10 km thick in the long, linear Carolina Trough that underlies most of the Carolina slope (Dillon et al., 1982; Paull, this volume). The trough is bounded on the landward side by a growth fault and on the seaward side by a series of salt diapirs that appear to have been active since the Jurassic (Dillon et al., 1982; Hutchinson et al., 1982). The salt diapirs penetrate the continental slope in some areas at a depth of about 2500 m, creating a hummocky topography and sediments with high salinity in the pore waters (Paull, this volume).

The Hatteras, Pamlico and Albemarle Transverse Canyons incise the continental slope and rise off North Carolina north of Cape Hatteras (Rona et al., 1967; Newton and Pilkey, 1969; Cleary et al., 1977) (Figure 2). No major canyons are found south of Cape Hatteras, either exposed or buried (Pilkey et al., 1971).

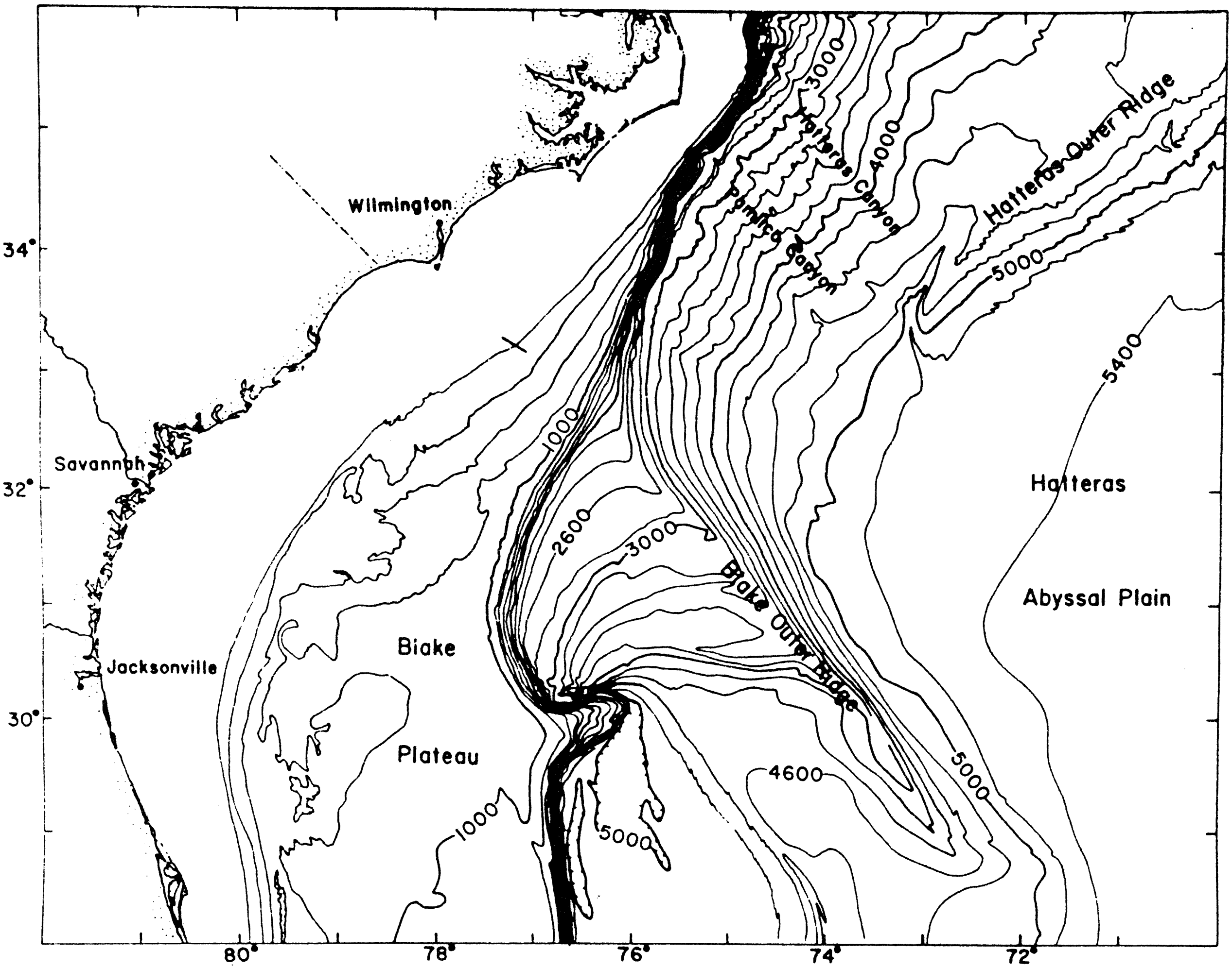

Figure 2. Bathymetry of the continental margin off the southeastern United States. Contours in meters.

The Tertiary and Pleistocene sediments on the outer shelf and upper slope lie in a series of prograding sedimentary lenses that are bounded by erosional or non-depositional surfaces (Pilkey et al., 1971) (Figure 3). This complex morphology and structure is the result of Gulf Stream dynamics causing repeated erosion and deposition on the outer shelf. Similar structure is observed in the outer shelf sediments of Cretaceous age, suggesting that a strong western boundary current similar to the Gulf Stream was already established early in the history of the Atlantic basin.

The upper slope morphology is further complicated by the occasional build-up of carbonate reefs just seaward of the shelf break (Menzies et al., 1966; Pilkey et al., 1971; Hine and Riggs, 1986). A prominent notch in the sea floor (Figure 4) that originally was attributed to reef construction by Menzies et al. (1966) was subsequently found in most places to be caused by erosion and deposition associated with the Gulf Stream (Pilkey et al., 1971).

Echo soundings from 3.5 kHz seismic systems from the Carolina continental slope and rise have been classified and mapped to better delineate the physical processes that control sediment distribution and sea-floor morphology (Vassallo et al., 1984). Damuth (1980) classified the echo character of 3.5 kHz records into those with single or multiple reflectors, smooth, hyperbolic or irregular seafloor, parallel or non-parallel sub-bottom reflectors, etc. Certain features are considered characteristic of turbidities, others of debris-flow deposits, and still others of contourites. None of the echo types are uniquely ascribed to one process, however, and in the final analysis, the distribution of a particular echo type is most indicative of the process that formed it. If the pattern of distribution is parallel to bathymetric contours, then it quite likely is controlled by contour currents. If, on the other hand, the feature is linear in a direction perpendicular to the contours it probably is the result of downslope sediment transport (Stowe and Lovell, 1979).

The distribution of four echo types off the Carolinas illustrates the relationship between distribution and process (Figure 5). Profiles with regular hyperbolae tangent to the sea floor usually indicate wavy bedforms formed by contour currents (Damuth, 1980; Flood, 1980). Many of the areas of these bedforms in the depth range of 3000 to 4000 m are elongate parallel to the bathymetry and most likely reflect the effects of the Western Boundary Undercurrent (WBUC). The fields of tangential hyperbolae in the vicinity of the Hatteras Transverse Canyon, however, are aligned perpendicular to the regional bathymetry and suggest an origin associated with turbidity currents. The distribution of sea floor with weak, indistinct echoes, usually attributed to debris-flow deposits (Embley, 1980), are indeed elongate perpendicular to the bottom contours

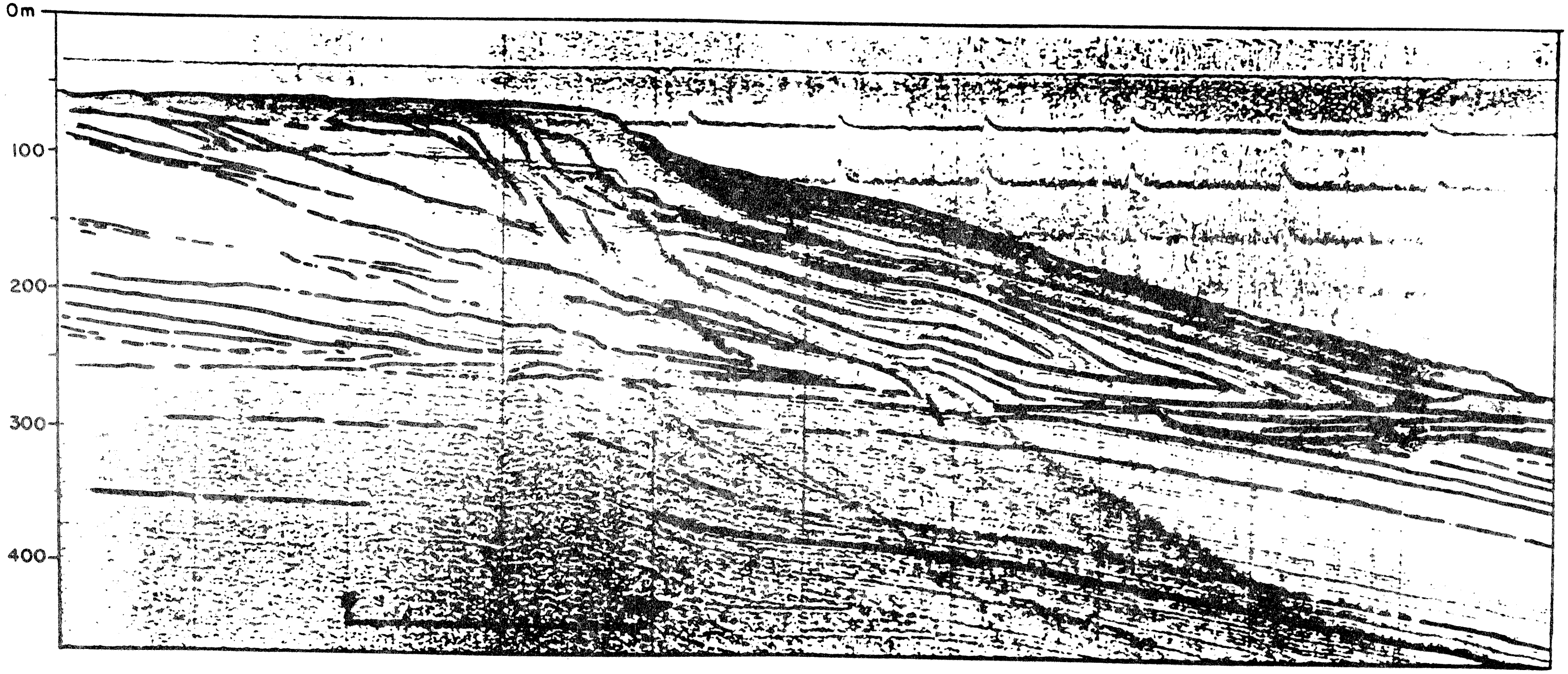

Figure 3. Single-channel, seismic reflection profile of the outer continental shelf and upper slope obtained by the R/V CAPE HATTERAS approximately 60 km southeast of Wilmington, N.C. The prograding sediment lenses of the outer shelf are the result of repeated erosion and deposition under the influence of the Gulf Stream.

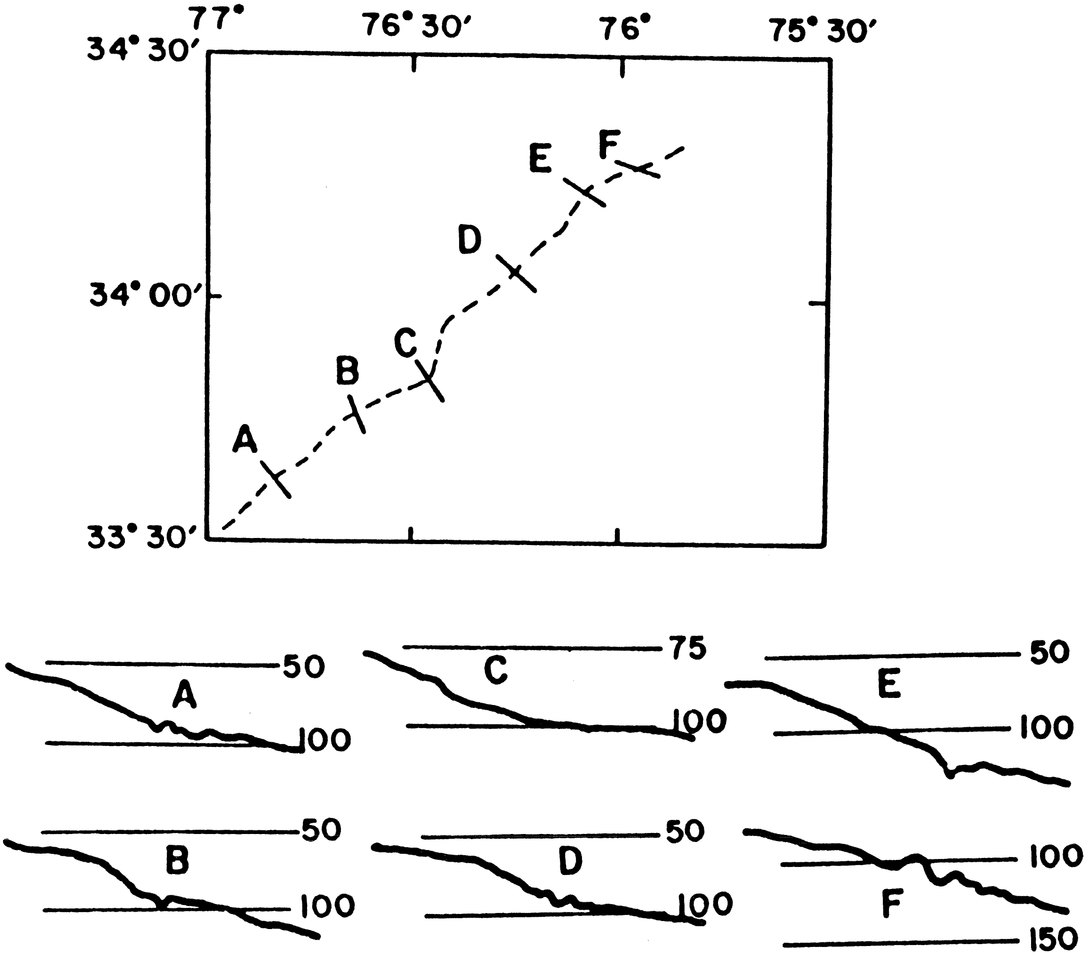

Figure 4. Bathymetric profiles of the upper slope at six locations off North Carolina, showing an erosional feature resulting from the Gulf Stream dynamics that originally was interpreted to be a carbonate reef. Depths are in meters. (after Menzies et al., 1966).

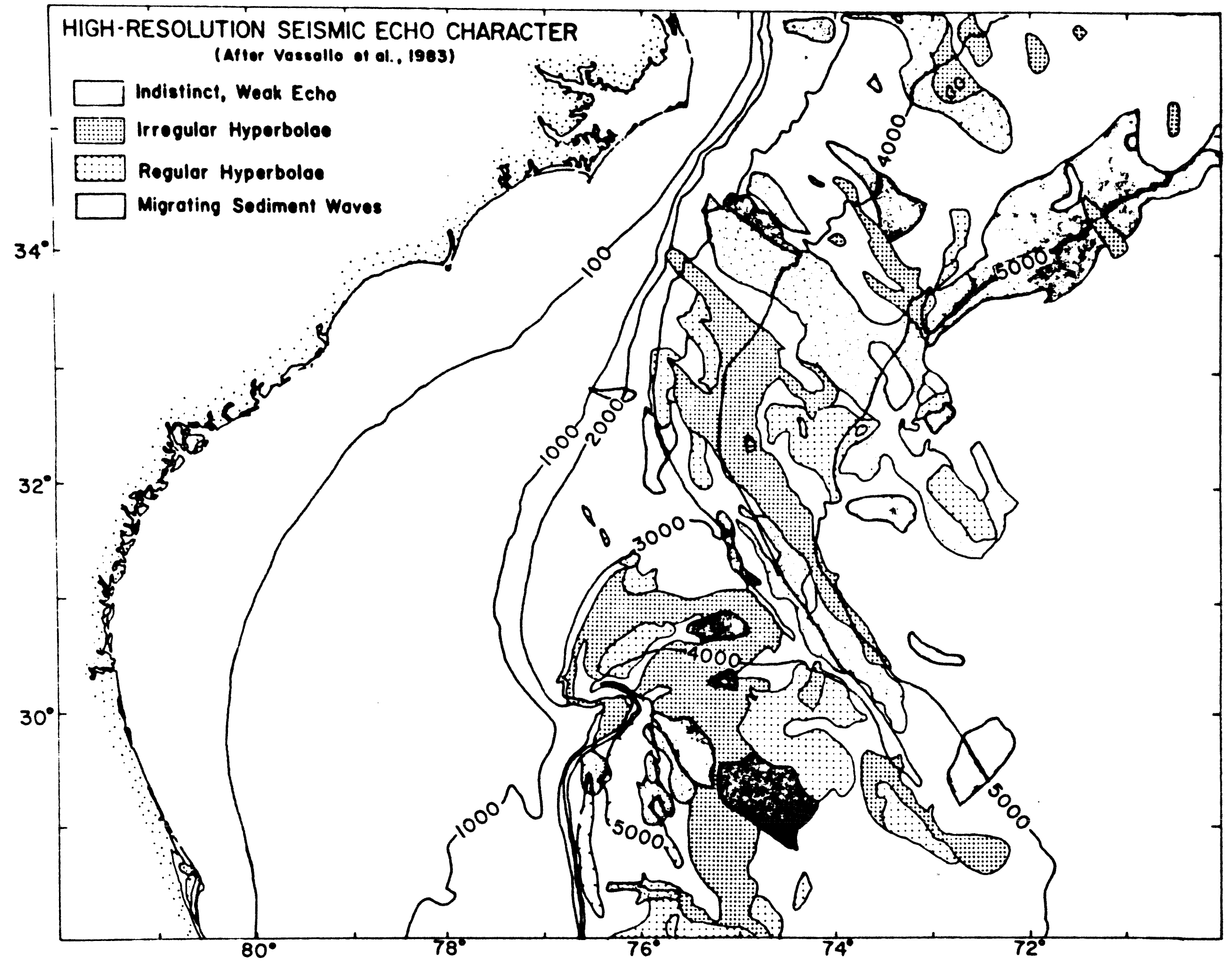

Figure 5. The distribution of four echo types off the Carolinas (after Vasallo et al., 1983).

in most areas. However, on the crest of the Hatteras Outer Ridge and on the northwest flank of the Blake Outer Ridge, this echo type is elongate parallel to the contours, suggesting the presence of bottom currents strong enough to influence sea floor morphology.

Based on echo character analysis, most of the continental rise off North Carolina appears to be influenced more by transport of sediment downslope rather than along slope by contour currents (Figure 5). Exceptions to this transport process are the Hatteras Outer Ridge and south of the latitude of Wilmington where the contours curve off to the southeast on the Blake Outer ridge. Here, strong lineations parallel to bathymetry indicate that contour currents strongly affect the distribution of sediments.

Seismic reflection profiles and results from the Deep Sea Drilling Project show that Quaternary sediments are deposited on the crest and lower flanks of the Blake Outer Ridge, but that the WBUC erodes the upper flanks of the ridge (Figure 6).

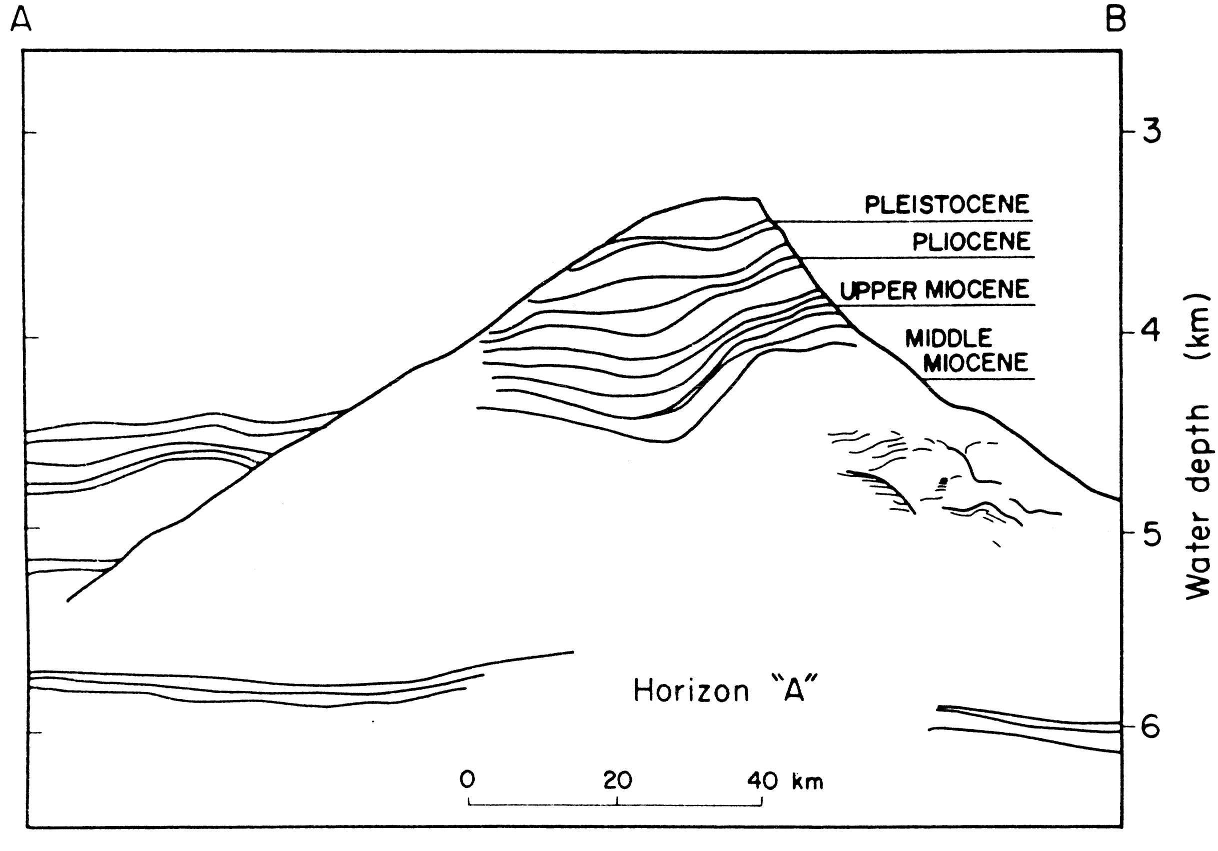

Figure 6. Line drawing of seismic reflection profile across the Blake Outer Ridge at about 30° North. (after Ewing and Hollister, 1972).

Hydrography

The deep circulation of the western North Atlantic can be divided into two components: the thermohaline-driven Western Boundary Under Current (WBUC) that transports about $10^7 m^3$/sec of water southward along the North American continental slope and rise, and two major gyres farther offshore that are associated with the Gulf Stream and North Atlantic Current (Worthington, 1976; Hogg, 1983). Worthington (1976) portrayed the two gyres as anticyclonic. Subsequent papers by Wunsch and Grant (1982), Hogg (1983) and Hogg and Stommel (1985) report the southern gyre to be anticyclonic and the northern gyre to be cyclonic. In either case, the deep-water circulation off North Carolina is of critical importance to the system for it is the region of intersection of the WBUC and the Gulf Stream gyre (Figure 1). Consequently, the outer continental margin of North Carolina has some of the most dynamic and complex deep-water flow of anywhere in the world ocean.

The Gulf Stream flows northeastward along the shelf break and upper slope from Florida to Cape Hatteras. Here it is deflected eastward into the deep North Atlantic and overrides the WBUC. Surface current speeds in the Gulf Stream are strong and variable off the Carolinas, frequently in the range of 50 to 100 cm/sec (Pietrafesa and Janowitz, 1980; Pietrafesa, 1983; Bane et al., 1981; Lee et al., 1985; Pietrafesa et al., 1985). The Gulf Stream remains strong (>40 cm/sec) to a depth of about 800 m, below which it drops off significantly. The stream maintains its identity all the way to the sea floor in water depths greater than 4000m northeast of Cape Hatteras, although bottom currents at these depths typically are slower than 10 cm/sec (Richardson, 1985; Joyce et al., 1986).

Volume transport (not to be confused with velocity) in the WBUC is an order of magnitude less than in the Gulf Stream gyre, yet the former generates bottom currents on the lower continental slope that are strong enough to erode, transport and redeposit sediment in large drift deposits (Heezen et al., 1966; Laine et al., 1986; McCave and Tucholke, 1986).

Hydrographic profiles along a NW-SE section approximately 90 km northeast of Cape Hatteras clearly show the complex water structure (Figure 7). Temperature and salinity isopleths slope in response to different water source areas and the dynamics of the interfingering WBUC and Gulf Stream (Figure 7 a, b). The oxygen profile shows two distinct depth ranges on the slope with high oxygen concentrations (>6.1 m./1) associated with the WBUC (Figure 7c). The velocity profile, derived from calculations based on geostrophy and mass balance of the hyrographic data, coupled with direct current measurements to derive the level of no motion, shows that the WBUC is split into shallow and deep components by the northeasterly flowing Gulf Stream (Figure 7D). Along this section the axis of the Gulf Stream already has been deflected seaward away from the shelf break. Southwestward flowing water with a mean velocity of less than 5 cm/sec extends from about 1000m to 3000m. The Gulf Stream impinges on the bottom between 3000m and 4200m with mean speeds perhaps as high as 10-20 cm/sec. The main core of the WBUC is farther offshore in a depth range of 4200-4600 m, with a mean speed exceeding 20 cm/sec (Figure 7d).

The hydrographic structure and computed velocity field directly off Cape Hatteras, approximately 90 km south of the section portrayed in Figure 7, is very similar to that described above, except the shallow, high-velocity core of the Gulf Stream lies to the west of its deeper section, overrides the WBUC, and impinges on the upper continental slope (Richardson and Knauss, 1971). Turbidity measurements made along the same transect show three distinct regions of high suspended sediment concentrations (Betzer et al., 1974) (Figure 8). The shallowest, centered at about 1000m, is associated with the northward flowing, high velocity core of the Gulf Stream. The two lower zones of high turbidity are associated with the two southwesterly flowing segments of the WBUC that are split by the deeper portion of the Gulf Stream where it impinges on the sea floor. Direct measurements of the bottom currents by Betzer et al. (1974) do not agree with the computed velocity field based on geostrophy. The current meters measured stronger southwesterly flow in the depth interval of the shallower portion of the WBUC than in the deeper portion, and they measured fairly strong southwesterly flow where the deep Gulf Stream should have been carrying bottom water to the northeast. These discrepancies underlie the complexity of the hydrography off Cape Hatteras, and may result from temporal variability on a time scale of days to weeks that is associated with Gulf Stream meanders and eddies. The eddies or rings can extend to the deep-sea floor and create "abyssal storms". These can generate current speeds in excess of 25 cm/sec and high turbidity events that may last for one to two weeks (Hollister et al., 1984; Hollister and McCave, 1984).

There have been no extensive hydrographic surveys off the Carolina margin between Cape Hatteras at 35°N and the Blake Outer Ridge at about 31°N. An analysis of the sea-floor photographs off North Carolina between 36°N and 32°N by Rowe and Menzies (1968) indicates that the bottom currents are flowing in a manner similar to that described off Cape Hatteras. There is strong northeasterly flow associated with the Gulf Stream between the shelf break and 1000m depth, substantial south-westerly flow associated with the WBUC between 1200 and 3100 m depth and also between about 3900 and 4600 m. These probably represent the upper and lower segments of the WBUC, respectively, and they are separated by a region between 3100 and 3900 m where the bottom photos showed no evidence of bottom currents. Only two of 21 bottom photographs from deeper than 5000 m showed any evidence of bottom currents. One at 5080 m showed southwesterly flow and one at 5260 m showed northeasterly

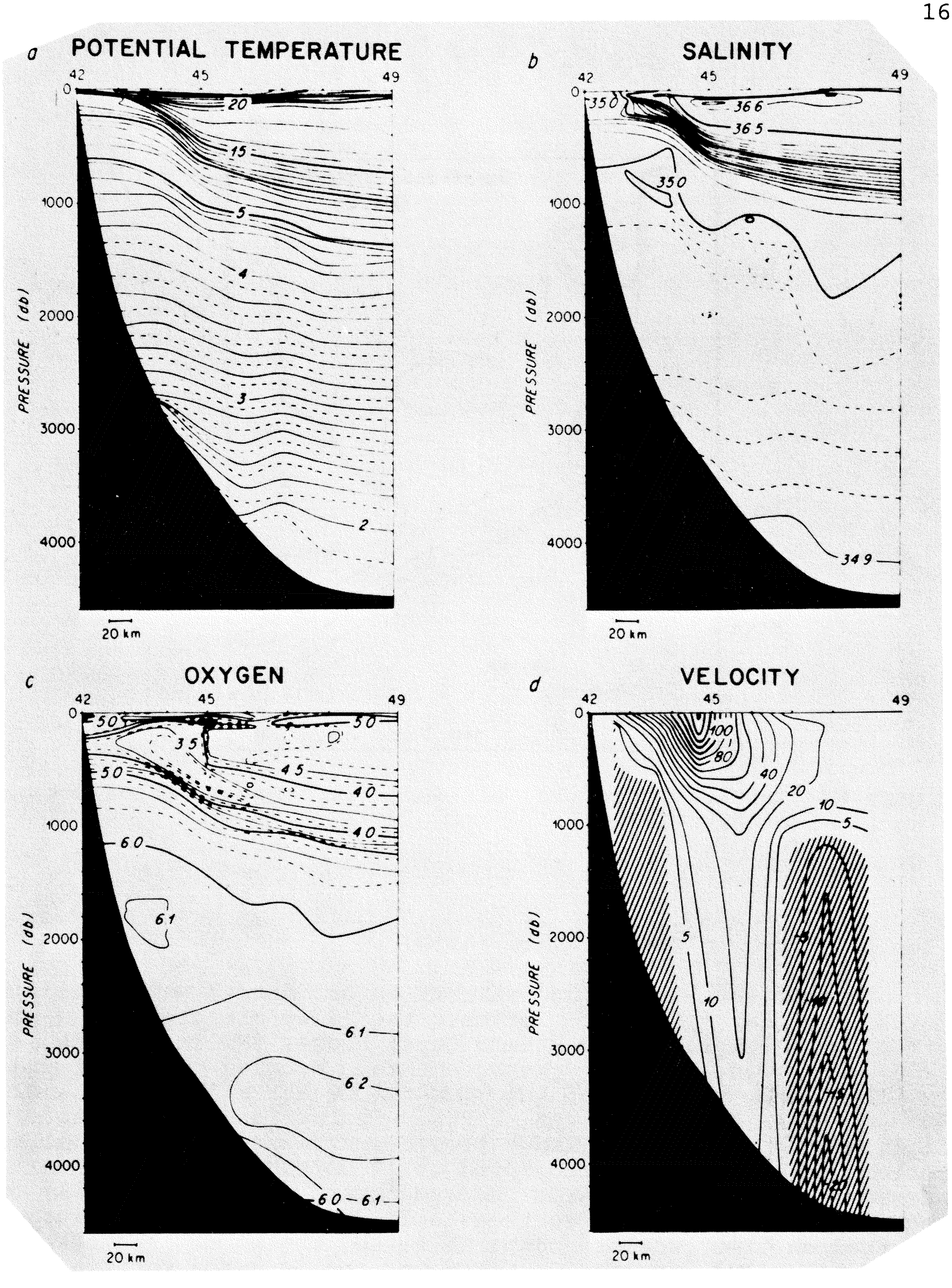

Figure 7. Profiles of potential temperature, salinity, oxygen and current velocity off Cape Hatteras. Shaded regions in the velocity profile denote southerly flow of the WBUC. (Modified from Joyce et al., 1986).

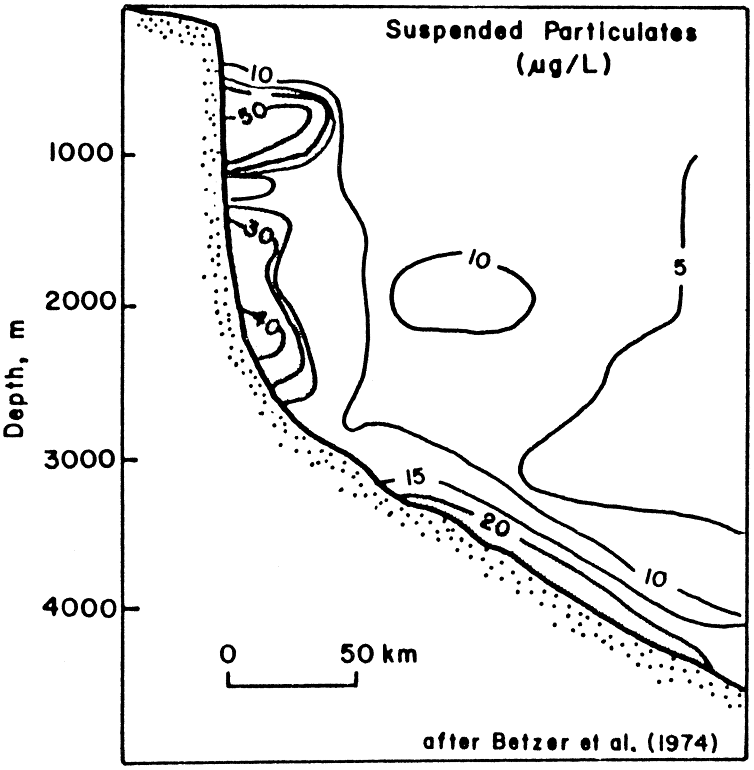

Figure 8. Turbidity profile off Cape Hatteras. (after Betzer et al., 1974).

flow of Antarctic Bottom Water (AABW).

Farther south at 31°N, current meter arrays were deployed for a one year period to measure the deep circulation in the vicinity of the Blake and Bahama Outer Ridges (Mills and Rhines, 1974). These direct measurements, coupled with tritium profiles, show the core of the WBUC to be at a depth of about 4000 m (Jenkins and Rhines, 1980). The current on the eastern flank of the Blake Outer Ridge flowed southeastward parallel to bottom contours at a mean speed of 21 cm/sec, and periodically surged to 40 cm/sec towards the southeast and occasionally to very slow flow in a northeasterly direction. These surges occurred on time scales comparable to those of the benthic storms described earlier. There was no evidence for the WBUC being split into upper and lower components, probably because the outer flank of the Blake Outer Ridge is well seaward of the Gulf Stream.

The WBUC continues around the nose of the Blake Outer Ridge, flows northwestward along its western flank and then follows the contours around to a southerly direction as it flows along the eastern flank of the Blake Plateau (Amos et al., 1971; Mills and Rhines, 1974).

Sediment Cover

The sediments on the continental slope and rise are predominantly brown to gray to reddish-gray lutites. In most regions they contain a small percent (typically <5%) of sand and 20-50% silt. The upper slope south of Cape Hatteras contains a much higher percent sand than in other areas due to the influence of the Gulf Stream, and shows a progressively finer mean grain size with increasing water depth (Doyle et al., 1979). Klasik and Pilkey (1975) examined 17 piston cores collected along the 3500 m isobath from Cape Hatteras to the Blake Outer Ridge and found the percent silt to decrease steadily from about 50% in the north to 20% in the south.

Most piston cores recovered from the slope and rise show few sedimentary structures other than burrow mottling. In the immediate vicinity of the submarine canyons off Cape Hatteras and to the north, graded turbidites are common. Cores that are not from these areas, however, rarely have sand layers. Field and Pilkey (1971) found the sand units not associated with the canyons to differ from the turbidites in their lack of graded bedding, finer grain size and better sorting. These sand layers and other textural banding in cores (i.e. silt layers) are attributed to the winnowing effects of contour currents.

The mineralogy of the deposits on the slope and rise is distinctly different from the shelf sediments. The sand fraction contains a higher feldspar-to-quartz ratio and more mica than the shelf sands, indicating a source predominately to the north of Cape Hatteras (Field and Pilkey, 1971). The heavy mineral fraction of the sands shows two dominant assemblages, an epidote-rich assemblage south of Cape Fear that is characterized by relatively high occurrences of epidote, pyroxenes, amphiboles and tourmaline, and an epidote-poor assemblage north of Cape Fear that has relatively high concentrations of staurolite, garnet and zircon (Pilkey, 1963). A close areal relationship exists between several heavy mineral distributions and the locations of the capes and shoals suggesting that these shelf features affect the transport pathways of sands from the shelf to the slope and rise (Pilkey, 1963). The abundance of calcite increases progressively form north to south, with values typically less than 10% north of Cape Hatteras and higher than 30% to the south (Doyle et al., 1979). The calcite is primarily biogenic planktonic foraminifera in the sand fraction and coccoliths in the silt and clay fractions.

The clay mineralogy is dominated by illite and smectite, with lesser amounts of kaolinite and chlorite. The relative abundance of kaolinite increases from north to south (Klasik and Pilkey, 1975). A significant temporal shift in clay mineralogy occurred on the continental rise during the last deglaciation. The smectite/chlorite ratio drops in many cores from about 5:1 in Holocene sediments to about 2:1 in the Pleistocene, and the kaolinite/chlorite ratio shifts from slightly greater than one to slightly less than one over the same interval (Klasik and Pilkey, 1975). These changes probably reflect a shift in the relative importance of local and distal sources of clays with fluctuations in sea level and global climate.

Authigenic pyrite is abundant in the slope and rise sediments, often occurring as casts of burrows, Foraminifera and Radiolaria. Authigenic siderite, ankerite, limonite and greigite also have been found in slope sediments (Doyle et al., 1979). Glauconite and phosphorite grains are also present on the slope and rise in minor quantities and are interpreted to be of detrital origin (Field and Pilkey, 1971; Doyle et al., 1979).

Sedimentation rates have been measured in very few cores from the North Carolina slope and rise. Klasik and Pilkey (1975) obtained rates of 12 and 13 cm/1000 y in two piston cores from 3500 m depth near the Hatteras submarine canyon and by correlation of carbonate profiles, inferred that the sedimentation rate on the 3500 m isobath decreased steadily southward. Doyle et al. (1979) obtained a sedimentation rate of 22 cm/1000 y on the continental slope off Delaware and Johnson et al. obtained sedimentation rates of about 20 cm/1000 y in two piston cores from the crest of Blake Outer Ridge. As more cores are dated, rates in the range of 10 to 20 cm/1000 y probably will be found to be representative of hemipelagic sedimentation off North Carolina except in regions strongly impacted by debris flows, turbidity currents and contour currents. The north-south gradient in sedimentation rates is attributed to the interfingering of the Gulf Stream and WBUC off Cape Hatteras creating conditions favorable for deposition of sediment carried in the two current systems (Klasik and Pilkey, 1975).

Paleocirculation

The deep-water circulation of the North Atlantic has varied considerably through time as the ocean basin has changed shape in response to sea-floor spreading and as the hydrography (i.e., distributions of water salinity and temperature) has altered with tectonic and climatic change.

Extensive analyses of seismic reflection profiles and sediments recovered by deep-sea drilling in the North Atlantic have revealed a history of deep-sea circulation that, while still vague in detail, is remarkably coherent in its broadest aspects. The Cretaceous record is summarized by Arthur and Dean

(1986) and the Tertiary history is described in Tucholke and Mountain (1986). These syntheses are briefly summarized below.

The late Jurassic-early Cretaceous Atlantic basin was narrow, strongly influenced by continentally-derived sediment, and had a relatively deep calcite compensation depth (CCD). By mid-Cretaceous times the basin had spread to a width that resulted in significantly less continental influence on sedimentation. There was an increase in deep-water circulation and the consequent development of some localized, lensoid sediment drifts. Organic-rich black shales were widespread in both early and middle Cretaceous times, however, indicating that deep-water stagnation must have been widespread during most of this time. These conditions extended into the late Cretaceous, although the mass accumulation rate of organic matter decreased significantly, and the CCD, which had been as shallow as 2800 m in mid to late Cretaceous times, plummeted briefly in the latest Cretaceous to about 5000 m. These fluctuations in the CCD and accumulation rates of organic carbon, as well as a widespread hiatus of mid-Cretaceous age, indicate that the deep water of the western North Atlantic changed significantly in degree of oxygenation, pH and intensity of circulation through time.

The Tertiary/Cretaceous boundary is marked by an uncomformity in most continental shelf regions of eastern North America, just as it is in many other areas worldwide. The Paleocene units that have been recovered by ocean drilling contain abundant turbidites and interbeds of organic-rich sediments, indicating stagnant conditions. By Eocene times, biosiliceous sedimentation became widespread in the western North Atlantic, a condition attributed by some to the coincidental development of strong Gulf Stream flow. There is some evidence for bottom current influence on deep-sea sedimentation, particularly in the Labrador Sea, but it is not extensive. The first major, basin-wide intensification of deep-water circulation occurred in the latest Eocene/early Oligocene. A widespread erosional unconformity is found along the entire continental slope and rise off North America (Reflector A^u), dated at about 33-37 million years ago (Ma). This erosional pulse was in response to the tectonic opening of a deep link between the Arctic and North Atlantic basins, thereby creating a substantial northern source of bottom water, coupled with global cooling and the establishment of some continental ice sheets (Miller and Tucholke, 1983). After the early Oligocene, sedimentation in the North Atlantic became more complex as the global climate became progressively cooler, continental glaciation intensified, high-latitude production of bottom water increased, sea level fluctuations became more dramatic, and deep-water pathways for abyssal circulation became better developed. Except for relatively brief periods of erosional pulses, however, bottom currents were generally slower than they had been during the lower Oligocene erosional phase, and substantial current drift deposits like the Hatteras and Blake Outer Ridges began to develop.

The late Tertiary is marked by three erosional pulses: in the late early Miocene, at about 17 Ma, the late middle Miocene at 11-12 Ma, and the late Pliocene between 2 and 3 Ma. These erosional pulses created the seismic reflectors designated as R2, Merlin and Blue, respectively (Tucholke and Mountain, 1986). These events also are observed in major shifts in the δC-13 content of benthic Foraminifera (Miller and Fairbanks, 1985). The causes of the Miocene erosional pulses are not clearly understood at this time. They undoubtedly will be tied into changes in global climate and morphology of deep-sea passageways to sources of dense bottom water as more data on these parameters are obtained.

The late Pliocene erosional pulse marks the transition to Pleistocene conditions of major continental ice sheets waxing and waning in response to the Milankovitch cycles of insolation to the northern Hemisphere. This record is clearly shown in the mean grain size record of detrital silt in DSDP Site 533 on the Blake Outer Ridge (Johnson and Johnson, 1987; A. Johnson 1987 (Figure 9). The changes in grain size record fluctuations in intensity of the WBUC on the crest of the Blake Outer Ridge. Prior to about 2.4 Ma the grain size record shows relatively small ampitude variability about a mean size of 14.5 µm. At 2.4 Ma there is a major shift to coarser size and, above that level, a Pleistocene record of high-amplitude variation about a coarser mean size of about 16 µm.

The extent to which the high-amplitude variability in grain size (or WBUC behavior) is tied to fluctuations in continental ice sheets is still being resolved. There is abundant evidence from geochemical and paleontological analyses of benthic foraminiferal assemblages in the deep North Atlantic that indicates that bottom waters were not as well mixed during the last glacial maximum compared to the Holocene (e.g., Schnitker, 1974; Boyle and Keigwin, 1985). Grain size analyses of the detrital silt fraction in two piston cores from the Blake Outer Ridge support this theory, and indicate that the WBUC accelerated dramatically around 12 thousand years ago (Ka), presumably marking the time of change from glacial to Holocene conditions in the deep, western North Atlantic (Lynch, 1986; T. Johnson et al.) (Figure 9). The tie between deep-water circulation and glaciation prior to the last glacial maximum is not so clear. Grain size variations between the two piston cores do not appear to be synchronous between 30 and 100 ka, suggesting that the axis of the WBUC migrated up and down slope in addition to or perhaps instead of changing speed through that time period (Figure 9). The high-resolution records in the two piston cores do not extend back to the previous major interglacial (oxygen-isotope state 5e), however. It is possible that we will find a coherent shift in WBUC strength across the

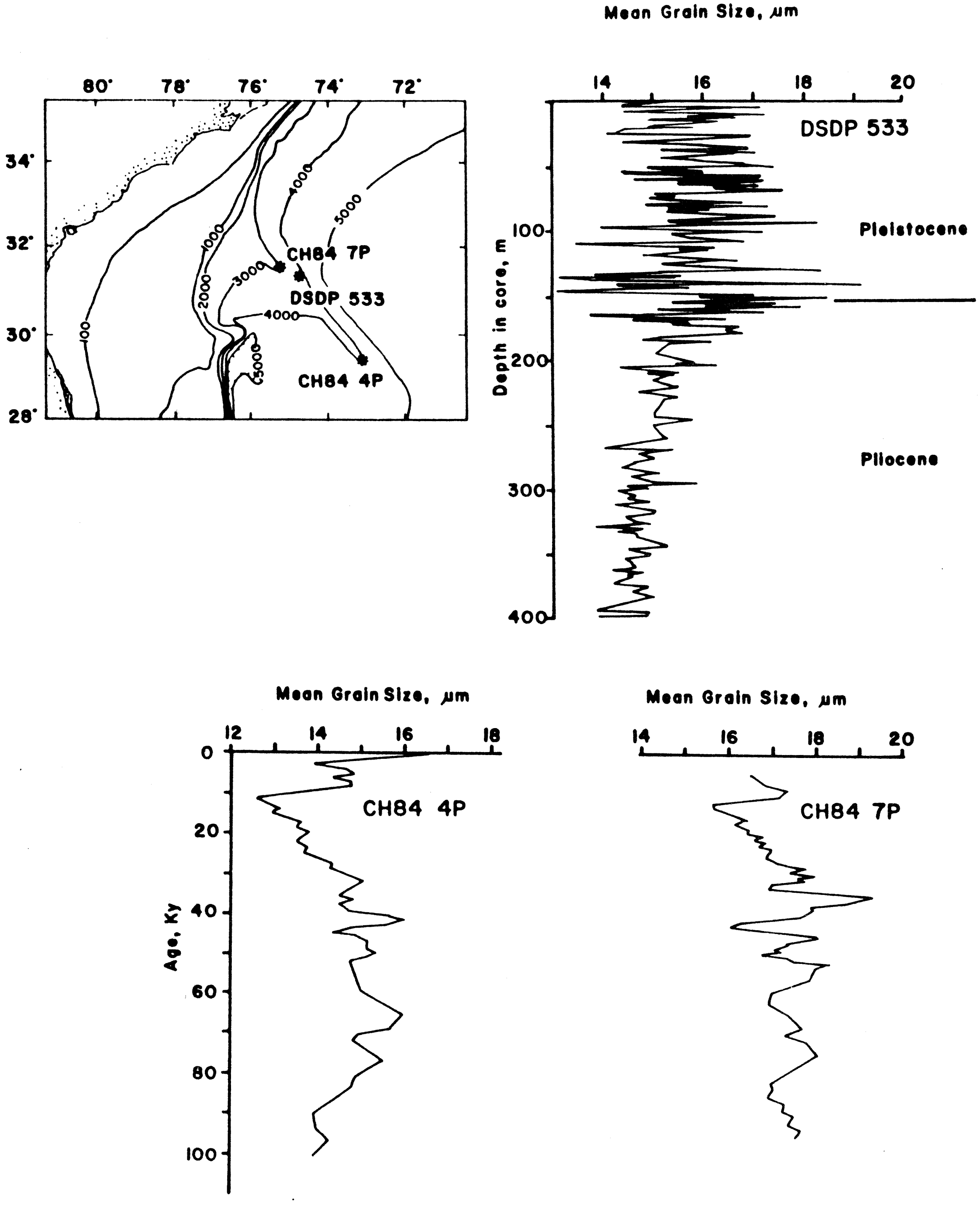

Figure 9. Mean size of the detrital silt fraction on the Blake Outer Ridge in DSDP Site 533 and two piston cores, CH84-4P and CH84-7P.

boundary of that interglacial and the previous glacial period that is comparable to what is observed at the 12 ka boundary. If so, the influence of Pleistocene climate change on the deep North Atlantic circulation will be better understood.

Grain size analyses of piston cores obtained from the continental slope off New Jersey, similar to the analyses of Blake Outer Ridge cores, have not shown as coherent a pattern of change from glacial to interglacial conditions as the Blake Outer ridge cores (Ledbetter & Balsam, 1985). The reasons for this discrepancy could be in a spatial variability in the response of the WBUC to glaciation. More piston cores from the continental rise off North America, particularly off the Carolinas, need to be analyzed to resolve the relationships between the deep western boundary currents, deep-water chemistry and climatic change.

CONCLUSIONS

Sedimentation on the continental slope and rise off the Carolinas is influenced strongly by downslope gravitational processes and by strong bottom currents associated with the Gulf Stream and southward-flowing North Atlantic Deep Water. The intersection of the Gulf Stream with the Western Boundary Undercurrent (WBUC) off North Carolina creates a complex hydrographic structure that varies in time and space. In general, the Gulf Stream erodes and strongly influences sedimentation on the outer shelf and the upper 1000 m of the continental slope. The WBUC is bisected by the Gulf Stream and transports sediment southwards in depth ranges of 1000 to 3000 m and about 4200-4600 m off Cape Hatteras. Farther south and seaward of the Gulf Stream on the Blake Outer Ridge, the WBUC is a single rather than bifurcated current, and is centered at a depth of about 4000 m. Echo soundings from the Carolina continental margin reveal that seafloor morphology is strongly affected by the Gulf Stream in the upper 1000 m, and by contour currents on the crest and flanks of the Hatteras and Blake Outer Ridges. Most other regions are strongly affected by downslope transport of sediment as well as by contour currents.

Many aspects of the modern deep-water circulation pattern probably were established around 35 million years ago. Distinct erosional pulses of intensified deep-water circulation occurred since then at 17, 11-12 and 2-3 Ma. The latest event is more precisely dated at about 2.4 Ma and marks the onset of glacial/ interglacial conditions characteristic of the Pleistocene.

The WBUC has varied significantly in strength and depth of maximum speed during the past 100,000 years. It decreased steadily in velocity during the last ice age from about 30 ka to 12 ka, at which time there was strong intensification of deep-water circulation as Norwegian Sea overflow water once again spilled into the western North Atlantic basin.

ACKNOWLEDGEMENTS

I thank Capt. Richard Ogus and the entire crew of the R/V CAPE HATTERAS for their excellent assistance in coring the Blake Outer Ridge. Numerous discussions with my graduate students, Lisa Lynch and Andrea Johnson, and results of their thesis research on the Blake Outer Ridge have helped in the development of ideas presented in this paper. This work was supported by NSF Grant OCE-85-10840 and ship-time support provided by the Duke/UNC Oceanographic Consortium.

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Chapter 5. Continental Shelf Biota

Chairperson - Dr. Thomas Johnson

A COMPARISON OF PHYTOPLANKTON AND BENTHIC MICROALGAL PRODUCTION IN NORTH CAROLINA CONTINENTAL SHELF WATERS

Lawrence B. Cahoon
Department of Biological Sciences
University of North Carolina at Wilmington
Wilmington, North Carolina 28403-3297

ABSTRACT

Production by phytoplankton and benthic microalgae was measured and compared in North Carolina Continental shelf waters at thirteen times in 1985 and 1986. Benthic microalgal production was estimated from changes in dissolved oxygen concentrations in light and dark chambers placed on the bottom by SCUBA divers. Phytoplankton production was measured in situ by the 14-C method.

Benthic microalgal production ranged from 1.8 to 47.2 mg C m-2 h-1 (mean: 16.7), while phytoplankton production integrated over the water column ranged from 2.9 to 71.0 mg C m-2 h-1 (mean: 26.3). Thus, benthic microalgal production is a significant source of fixed carbon to this continental shelf ecosystem. Benthic microalgae are a concentrated food source for shelf herbivores that has been ignored until now.

INTRODUCTION

Sverdrup's classic explanation of the processes driving the annual spring diatom bloom in the North Atlantic represents a model of the interaction between mixing and light flux in controlling phytoplankton production that is applicable to all aquatic ecosystems (Sverdrup, 1953). Sverdrup showed that phytoplankton population growth is controlled by the relationship between the depth of the surface mixed layer and the depth at which integrated phytoplankton production is just equal to integrated phytoplankton respiration, a depth he termed "critical depth." Critical depth is primarily a function of light flux through the water column, which is a function of season, latitude, and the light extinction properties of the water. When critical depth is greater than the depth of the surface mixed layer, phytoplankton populations in the surface mixed layer will expand. When mixing processes drive the lower limit of the surface mixed layer below critical depth, phytoplankton populations in the surface mixed layer will decline.

Continental shelves are a special case with respect to the interaction of mixed layer depth and critical depth. By definition, continental shelf waters are shallow, so the sea bottom itself often acts to limit the maximum depth of the surface mixed layer. Thus, the conditions favoring phytoplankton growth are more frequently satisfied in continental shelf waters, making these waters more productive on average than nearby slope waters, which in the temperate zone have no permanent pycnocline to restrain the depth of the surface mixed layer.

When water clarity is high in continental shelf waters, critical depth effectively exceeds the depth of the mixed layer, which can only extend to the sea bottom, meaning that positive primary production can occur throughout the entire water column and on the bottom. This leads to the hypothesis that clear shelf waters should support high benthic primary production.

Primary production must be supported by a nutrient source or sources, as well as by sufficient light levels. In the North Atlantic ecosystem, nutrients are supplied to the surface waters by the annual winter overturn of the water column and by regeneration of nutrients by planktonic grazers. Continental shelf waters have different but comparably adequate nutrient sources. Runoff from coastal rivers and outwelling from estuaries may supply nutrients in one form or another (Turner et al., 1979). Regeneration of nutrients is also likely to be important, especially release of nutrients from shelf sediments (Rowe and Smith, 1976; Hopkinson and Wetzel, 1982). In addition, coastal upwelling can provide nutrients. Thus, nutrients may be adequately available to support benthic primary production in continental shelf waters.

Several observations suggest that benthic primary production may be important in North Carolina continental shelf waters. First, water clarity is frequently high in shelf waters, owing perhaps to intrusion of clear Gulf Stream waters or to long periods of calm weather, which allows particulates to settle out of the water (Table 1). Second, extensive work by Searles and his students documents the abundance and growth of benthic macroalgae across the North Carolina continental shelf (Schneider, 1976; Schneider and Searles, 1979; Peckol, 1982). Summer biomass peaks suggest that these months may coincide with optimal conditions for benthic primary production (Peckol, 1982; Peckol and Searles, 1984). Most of the shelf bottom is covered with at least a veneer of unconsolidated sediment, which could be a substrate for the growth of microalgae. Therefore, I have tested the hypothesis that benthic microalgal production could make a positive and important contribution to total continental shelf primary production, especially when water clarity is high.

The data reported here are only a portion of the total collected during a larger project investigating the role of sediment-water column interactions in the continental shelf ecosystem of North Carolina. I have confined this paper to a comparison of benthic and planktonic primary production and the relationship of these, especially benthic production, to light flux through the water column.

Table 1. Quantum flux measurements at the bottom along a north-south transect from Beaufort, North Carolina, May 1984. Light extinction coefficient, k, was calculated assuming surface incident radiation to be 2350 uEinsteins m^{-2} s^{-1}.

Location	Depth (m)	Flux (uE m^{-2} s^{-1})	k
Turning Basin	11.5	0	1.32
1 mile south	6.3	54	0.60
2.5 miles south	11.0	189	0.23
6 miles south	17.0	340	0.11
10 miles south	19.0	362	0.10
12 miles south	20.0	152	0.14

METHODS AND MATERIALS

Benthic primary production has been measured by a variety of techniques. I chose to use in situ incubations of clear and opaque benthic chambers coupled with measurements of oxygen flux. First, in situ studies conducted with care are the most realistic and least subject to handling artifacts. Chamber incubations lent themselves most readily to estimation of areal productivity. Finally, oxygen exchange in clear and opaque chambers is a simple extension of the classical light/dark bottle method; preliminary experiments established that this method would have appropriate sensitivity.

Divers using SCUBA, SCUBA-Nitrox, or surface-supplied air placed and sampled benthic chambers, which were plastic domes, 30 cm diameter with a 10 cm hole in the top (Figure 1). Diving support was provided by the National Undersea Research Program's vessel, R/V SEAHAWK. Divers were routinely able to place or retrieve and sample from 6 to 8 chambers on a dive. Chambers were placed carefully so as to minimize disturbance of the sediment-water interface. Chamber tops, which incorporated a whirling-cup-rotor stirring device, were sealed onto the chambers after placement using clear silicone sealer (Figure 1). Chambers were set out in a single row, uniformly spaced, with clear and opaque chambers alternating. Water samples for analyses of oxygen content by the Winkler method (Strickland and Parsons, 1972) were withdrawn by 60 ml plastic syringes after flushing 2-3 times. The chamber retrieval process was essentially a reverse of the above procedure. Incubation times varied from 3 to 11 hours, depending on dive schedules and the productivity anticipated.

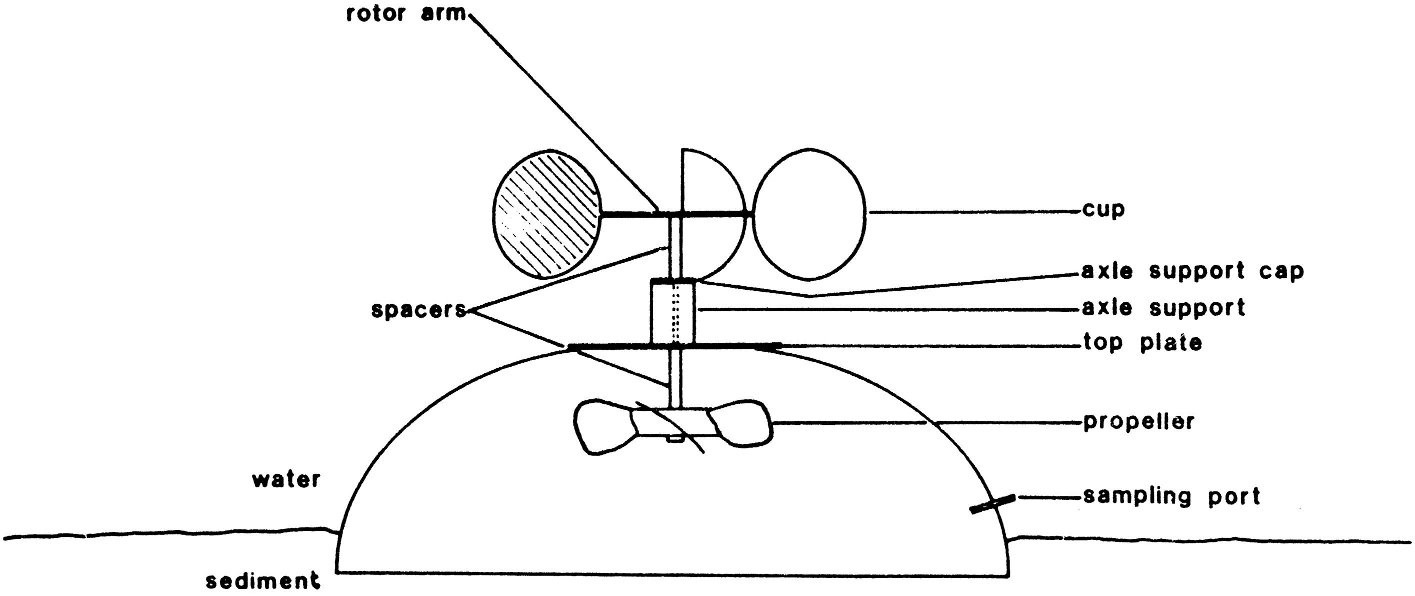

Figure 1. Diagram of a benthic chamber in place with whirling cup rotor stirring device attached. Chamber diameter is 30 cm.

Syringes containing water samples were returned to the ship for further handling and analysis. Water samples intended for oxygen analysis were fixed immediately after return to the surface by injection of manganous sulfate and alkaline iodide reagents directly into the sample syringes. Samples were then stored in the dark to prevent photooxidation of the resulting precipitate prior to further analysis. Oxygen samples were analyzed during the evening of each field day. Samples were acidified with sulfuric acid injected directly into sample syringes. Fifty ml were then dispensed into a clean flask and titrated against sodium thiosulfate solution, which had been standardized against potassium iodate, using starch indicator. Oxygen concentrations were calculated according to Strickland and Parson's (1972) equations for nonstandard sample volumes.

A potential source of error in the handling of oxygen samples might have arisen from degassing of oxygen during transport of the samples to the surface. Oxygen concentrations frequently exceeded the theoretical saturation level for atmospheric pressure, but never exceeded the saturation level for the depths at which the samples were taken. The short interval between sample withdrawal and fixation may have limited the problem. In any event, loss of oxygen from samples would most likely cause underestimates of gross production, since the greatest loss would occur in samples with the highest oxygen content, which would be those from the clear chambers at the end of an incubation.

Benthic primary production was estimated by comparing changes in oxygen concentration in clear and opaque chambers over the course of an incubation. Since the chambers integrated the oxygen flux effects of benthic microflora, benthic animals, bacteria, and chemical oxygen demand, calculations of net production (i.e., changes in clear chambers only during an incubation) would give misleadingly low values. Accordingly, gross production (i.e., differences between light and dark chambers at the end of an incubation) was calculated as a better estimator of actual benthic microalgal production. Oxygen concentration changes were converted to carbon flux assuming a photosynthetic quotient (PQ) of 1.2. PQ values below 1.2 would yield estimates of gross production lower than those reported here. Areal production rates were calculated using values for chamber volume and area of 3.5 liters and 0.14 m^2, respectively.

Primary production in the water column was measured simultaneously with benthic primary production on most dive missions. Since phytoplankton concentrations were usually very low, oxygen exchange methods were inappropriate, and the standard 14-carbon method was used instead (Parsons et al., 1984). All 14-carbon experiments were conducted in situ at four or five depths chosen to integrate the water column (surface and every five or ten meters to the bottom, including a near-bottom depth). Water incubated in these experiments was collected immediately before use from the corresponding sample depth with a Niskin or van Dorn bottle. Three clear and two opaque 300 ml bottles containing raw seawater were spiked with a known amount of 14-carbon labeled bicarbonate and suspended at each sample depth early in each working day and retrieved in late afternoon. All bottles were shaded immediately after retrieval and the contents fixed with a few drops of Lugol's iodine. The entire contents of each sample bottle were then filtered through a glass fiber filter (Gelman A/E), which was rinsed twice with fresh filtered seawater and placed in a scintillation vial containing 10 ml of Scintiverse II cocktail. Samples were counted on a Beckman LS-100 scintillation counter; sample counts were corrected for quench and counting efficiency using count data from internal and external standards. Primary production at each sample depth was calculated according to Parsons et al. (1984), using alkalinity data for each sample measured according to Parsons et al. (1984). Total water column primary production was calculated by integrating production estimates from each sample depth. Primary production estimates obtained by use of the 14-carbon method usually lie between actual net and gross production.

Light flux through the water column was measured with a LiCor 550B integrating quantum sensor equipped with a 4 pi collector during each productivity incubation. The sensor unit was placed within 1 m of the bottom during these measurements. This measurement technique was much preferred to use of a Secchi disc owing to the frequent occurrence of near-bottom turbidity, which would otherwise have caused overestimates of actual light flux to the bottom. Light flux measurements were made at or near solar noon of each working day; values from three one-minute integrations were averaged to yield an estimate of mean maximal light flux to the bottom.

The field sites chosen for this study were located in Onslow Bay off the central coast of North Carolina (Figure 2). Sites were chosen to give a range of depths and water types. The inshore sites were in or close to the nearshore turbid zone, and consequently had higher turbidity on average than the offshore sites.

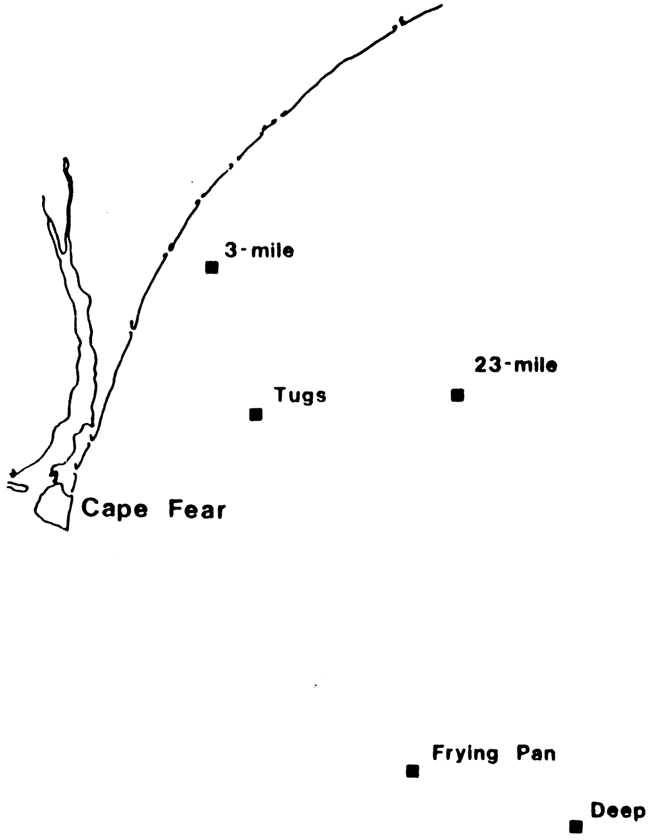

Figure 2. Map of the study area off the North Carolina coast, with individual study sites identified.

An effort was also made to sample during several seasons in the expectation that seasonality would be a major factor in controlling primary production. It should be noted that weather was an important factor that frequently limited dive operations. The work reported here was done in generally calm weather, although some sites were visited just after a major storm had passed.

RESULTS

Benthic microalgal production was measured 13 times during this study and averaged 16.7 mg C m^{-2} h^{-1}, with values ranging from those not significantly different from zero up to a high of 47.2 mg C m^{-2} h^{-1} (Table 2). The highest benthic microalgal production values occurred during the summer, but not all summer values were consistently high, indicating that some factor other than simple seasonality controls benthic production. Benthic production values were also highest at midshelf sites with depths around 30 m, but not all values at these sites were high, even in the summer. Comparisons of benthic production with maximal light flux to the bottom during each work day suggest that limited light availability at the bottom in the nearshore turbid zone and at the deepest site restrain benthic production in these locations. A regression of benthic production against maximal light flux to the bottom (including data from 1983 and 1984 not otherwise discussed here) yielded a positive significant regression coefficient (Figure 3). Thus light flux to the bottom drives/limits benthic primary production, although other factors must play a role.

Storm events strong enough to induce turbidity in the water column might be expected to cause reductions in benthic production, either by decreasing light flux to the bottom or by physical removal of benthic microalgae from the bottom. The data set presented for July 1985 at Frying Pan site illustrates the course of benthic production through time following Tropical Storm Bob, which passed this site on July 25, 1985. The data suggest that declining turbidity permitted increasing benthic production over the 4-6 day period following the storm. Visual observations of the bottom at the 23-mile site two weeks after Hurricane Diana, a much stronger storm, passed over that area in September 1984, revealed that the bottom had been thoroughly resuspended with virtually complete removal of benthic microalgae. Thus, storm events appear to play an important role in regulating benthic production by inducing turbidity and at least occasionally removing benthic microalgae.

Water column primary production was measured 12 times during this study and averaged 26.3 mg C m^{-2} h^{-1}, with values ranging from 2.9 to 71.0 mg C m^{-2} h^{-1} (Table 2). These integrated values showed no clear seasonal pattern, with the exception of markedly lower values throughout September 1985 compared to all other sample times.

Table 2. Comparisons of benthic microalgal and phytoplankton production at sites in Onslow Bay in 1985 and 1986. Locations as in Figure 2. BPP = gross benthic primary production (mg C m^{-2} h^{-1}); PP = integrated water column primary production (mg C m^{-2} h^{-1}).

Location	Date	Depth (m)	BPP	PP
23-mile	4/19/85	32	14.3*	24.4
Deep	4/21/85	41	4.0	71.0
3-mile	4/23/85	18	15.1*	47.9
Frying Pan	7/29/85	32	13.0	46.0
Frying Pan	7/30/85	34	46.3*	43.7
Frying Pan	7/31/85	30	47.2*	30.8
Frying Pan	9/6/85	32	32.8*	8.1
Frying Pan	9/7/85	31	9.4	6.6
Frying Pan	9/8/85	31	6.7*	2.9
Frying Pan	9/9/85	34	1.8	6.3
23-mile	9/25/85	34	14.1	6.3
3-mile	3/4/86	16	5.3*	21.6
Tugs	3/5/86	20	6.7	--

*Denotes significant differences ($P \leq 0.05$) in oxygen concentration changes between light and dark chambers during incubations (one-way ANOVA, Sokal and Rohlf, 1969).

Benthic production exceeded water column production only in the warm months, but this is only one way of viewing the importance of benthic production. If benthic production is assumed to be the activity occurring within the benthic chambers, with 8 cm vertical extent, then a given benthic production value represents a 187.5 fold concentration of the same amount of phytoplankton production occurring through a 15 m water column. Given that most of the production in a benthic chamber is likely to be concentrated at the sediment-water interface, benthic production is even more impressive.

DISCUSSION

Estimates of the primary productivity of North Carolina continental shelf waters, and the waters of continental shelves in general, have typically failed to consider the productivity attributable to benthic microalgae. At the times when productivity was measured in this study, benthic production ranged from a minimum of 5.6% of water column production up to a maximum of 40.5% of water column production. Thus, benthic

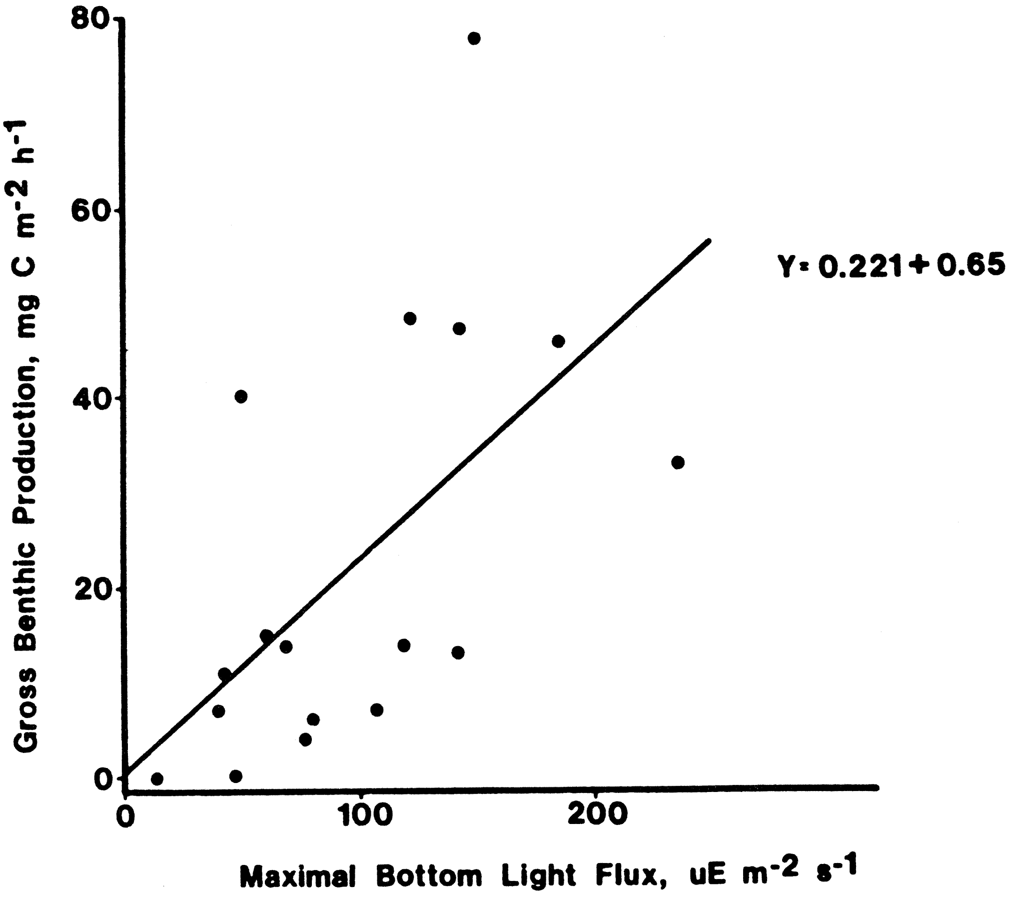

Figure 3. Regression of benthic primary production vs. light flux to the bottom. Regression line was fitted using Model I regression (Sokal and Rohlf, 1969).

microalgal production is a significant source of production in North Carolina continental shelf waters that has not been measured previously.

Benthic production measured in this study was particularly important in relative terms in the warm months and in the mid-shelf region. This may reflect the nature of the field sampling program, which was limited by weather and the availability of dive support. However, the apparent dependence of benthic production primarily on light flux to the bottom suggests that low light conditions, such as might be found in deeper, outer-shelf waters, in the nearshore turbid zone and after turbidity-inducing events, such as storms or strong plankton blooms, limits the relative importance of benthic production. A much more extensive field survey would be required to test these ideas and identify more conclusively the spatial and temporal maxima of benthic microalgal productivity in North Carolina waters. Nevertheless, there are times and places when benthic microalgal production are quite important in the North Carolina continental shelf ecosystem.

Generalizing from the case in North Carolina shelf waters leads to the prediction that benthic microalgal production could be significant in other shallow waters with high light flux to the bottom. Coral sand habitats are especially likely to be good habitats for benthic microalgae; measurements of microalgal production on coral sand in the Florida Keys (Cahoon, unpublished data) showed that significant production was occurring. In addition to shallow continental margins, marginal seas, such as the South China Sea and the Bering Sea, are areas of interest. Numerous investigators have, of course, reported benthic primary production data for estuarine waters, where conditions allow more frequently successful sampling, e.g., Cadee and Hegeman (1974, 1977).

If benthic microalgal production in North Carolina continental shelf waters is relatively important in comparison to phytoplankton production, then other processes that interact with primary production will be affected proportionately. For instance, if benthic microalgal production is roughly two-thirds of phytoplankton production, as the data presented here suggest, then nutrient uptake required to support total production must be two-thirds higher as well. Recent debates over the relative importance of nutrient sources for the South Atlantic Bight have used estimates of shelf production to calculate nutrient demand and the relative significance of particular nutrient sources. Dunstan and Atkinson (1976) have, for instance, determined that upwelling along the shelf break accounts for approximately 25% of the "new" nitrogen consumed in shelf waters. A revision of these figures with benthic microalgal nutrient demand factored in gives an estimate of about 15%. This suggests that sources of nutrients external to the shelf are less important than previously thought, while internal recycling is more important.

Benthic microalgae probably play an important role in nutrient recycling. A considerable fraction of total nutrient regeneration is likely to occur in or near the sediments (Rowe et al., 1975; Rowe and Smith, 1976). Benthic microalgae are ideally positioned to intercept regenerated nutrients. The techniques used to study benthic nutrient regeneration have not been used to detect microalgal effects on nutrient release from sediments. Furthermore, the apparent heterotrophic capabilities of at least some benthic microalgae (Lewin and Lewin, 1960; Lewin and Hellebust, 1976) raise the possibility that nitrogen, in particular, is recycled without necessarily being transformed into the inorganic compounds investigators commonly measure.

Benthic microalgae represent a productive, concentrated food source for benthic grazers and suspension feeders.

Comparisons of productivity data and biomass data (Cahoon, unpublished data) show that benthic microalgae can be as much as three orders of magnitude more concentrated than phytoplankton on a volume basis. Benthic microalgae should be immediately available to benthic meiofauna and other infaunal and epifaunal grazers and deposit feeders. Suspension of benthic microalgae by turbulence could make them available to suspension feeding organisms, including zooplankton. Thus, benthic microalgae are likely to play an important role in the continental shelf food web when and where conditions favor benthic production.

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A SURVEY OF THE RECENT FORAMINIFERA OF NORTH CAROLINA (ESTUARINE, SHELF, SLOPE, RISE, AND ABYSSAL PLAIN)

Joseph St. Jean
Department of Geology
University of North Carolina at Chapel Hill
Chapel Hill, North Carolina 27599-3315

ABSTRACT

Previously reported common to abundant modern Foraminifera of North Carolina are summarized. The region is divided into estuarine habitats, with salinities from 0.5^{o}/oo to >35^{o}/oo, and non-estuarine habitats from intertidal to abyssal plain.

The least saline estuarine environments are characterized by arenaceous lituolid, rzehakinid, and trochamminid Foraminifera with low species diversities. As estuarine environments grade to normal marine salinities, calcareous Foraminifera appear and increase in abundance accompanied by an increase in species diversity and a decrease in the numbers of arenaceous species. In littoral and shallow shelf environments, the same kinds of Foraminifera are found as occur in the estuarine habitats with normal marine salinities, except that planktic forms are usually more common. On the middle and outer shelf, planktic Foraminifera gradually increase in importance on the middle and outer shelf as calcareous benthic forms decrease. Planktic to benthic ratios on the continental slope remain similar to those on the outer shelf but there are changes in the generic composition of the faunas. Towards the abyssal plain, as carbonate dissolution depths are approached, calcareous Foraminifera give way to arenaceous ones. Unlike low saline estuarine environments, ammodiscid and different lituolidacid genera predominate. Benthic Foraminifera reach their greatest abundance and diversity on the shallow and middle shelf. Planktic Foraminifera are most abundant in the so-called "*Globigerina* oozes" in deeper waters of the shelf and continental slope above the carbonate compensation depth.

INTRODUCTION

Only common to abundant foraminiferal species are considered because they are the best indicators of well adapted elements of the faunas and reduce biases of accidentally injected species, aberrant foreign species, or recently evolved, but rare endemics (See introductory comments in Appendix I or Appendix II for usage of the terms, "common" and "abundant"). Foraminifera in the North Carolina area are like those found in similar habitats throughout the world. One would find no significant difference in the common to abundant genera from the same habitat in either the northern of southern hemispheres. Differences in benthic species do occur from region to region, but the North Carolina species are morphologically similar to those found in like habitats in other areas. North Carolina foraminiferal faunas are therefore typical and ecologically diagnostic.

Inland and off-shore waters of North Carolina are ideally suited for foraminiferal studies. Past investigations have been sparse compared to those along the Gulf Coast or Caribbean. For reviews of previous studies on the Foraminifera of North Carolina and related works, see especially Grossman (1967), Schnitker (1971), and LeFurgey (1976).

North Carolina foraminiferal faunas are considered under two major categories: estuarine and non-estuarine (i.e. littoral, neritic, and oceanic). Salinity is an important controlling physical factor with regard to Foraminifera in estuarine habitats. Foraminifera are influenced by temperature, depth, and current patterns in non-estuarine habitats.

Estuarine Environments

The term estuary is taken to mean that zone from the first detectable appearance of brackish water associated with fluvial systems to coastal areas bounded by tidal inlets and longshore bars (outer banks).

The North Carolina estuarine system is a complex of drowned river valleys that have been modified by sediment deposition and the consequent development of marginal swamps. Two areas into which the largest rivers discharge have produced sizable estuarine lagoons: Pamlico and Albemarle Sounds. Albemarle Sound is only slightly saline because of the absence of tidal inlets. Water in Albemarle Sound is flushed through Roanoke and Croatan Sounds and connects with the open ocean only through Oregon Inlet. No studies have been published on the Foraminifera of Albemarle Sound. Foraminifera are probably distributed sparsely over most of the Sound, increasing in abundance and diversification near the northern end of Croatan and Roanoke Sounds.

Estuarine habitats of North Carolina are divided into five categories:

1. Western fluvial estuaries: Neuse, Pamlico, and Pungo estuaries--the largest rivers draining into Pamlico Sound are the most remote from oceanic influences. The deepest water occurs in the estuarine channels.
2. Open sound: Pamlico sound--the largest estuarine water mass in the region.
3. Eastern estuaries and sounds: small linear sounds parallel to the coast, bounded to the east and north by marginal marine swamps and sluggish fluvial estuaries, and to the east and south, by the outer banks. Bogue, Core, and Roanoke Sounds are examples.

4. Tidal deltas: submerged, lagoonally directed deltas formed at tidal inlets through the outer banks. Foraminifera at Ocracoke, Beaufort, and Mason Inlets have been studied.
5. Tidal channels: Those areas, other than inlets, where strong tidal flow and current reversals are prominent. Foraminifera in tidal channels have been studied mostly in Bogue Sound and near Mason Inlet.

Mixing of shallow water open marine species with estuarine species occurs in the eastern portion of the open sound environment, as well as in the eastern estuaries and sounds, tidal deltas, and tidal channels. Only the estuaries south of Cape Hatteras have been studied, therefore comments on oceanic influences are restricted to the southern shallow shelf environment.

Western Fluvial Estuaries

Western fluvial estuaries are limited to the Neuse, Pamlico, and Pungo rivers. These estuaries have been studied by Grossman (1967) who sampled from 37 stations on both estuarine margins and in mid-channel. Depths range from mudflats to about 1 meter on estuarine margins to a maximum of 7.6 meters in mid-channel. Currents are moderate to weak, with a surface outflow of fresh water and a bottom inflow of salt water during high tides. Turbidity is moderately high, especially in mid-channel. Water stratification develops between denser bottom brackish water and less saline surface water. Ph tends to be slightly acid. Salinities range from $0.5^{o}/_{oo}$ upstream at New Bern, on the Neuse River, and at Washington, on the Pungo River, to $12^{o}/_{oo}$ at the river mouths. Salinities may be appreciably reduced during periods of heavy rainfall and elevated slightly during dry periods. The substrate ranges from clays with the consistency of axle-grease, when wet, to fine silts and sands. Fecal pellets are common in the fine silts. The Foraminifera diagnostic of the environment seem best adapted to salinities of $10^{o}/_{oo}$ to $15^{o}/_{oo}$.

Foraminiferal species diversity is especially low in the least saline facies and increases gradually to the most saline portion of the habitat.

All species characteristic of the western fluvial estuarine environment are arenaceous. (See Appendix I.) No Foraminifera were found in waters less saline than $1^{o}/_{oo}$. However, the testate thecamoebid Difflugia (a sarcodinid protozoan with an unilocular arenaceous test and lobose pseudopodia) seems to be common in salinities between $0.5^{o}/_{oo}$ and $2.0^{o}/_{oo}$. (See Grossman, 1967, p. 46.)

Open Sound

Pamlico Sound lies generally east of the western fluvial estuaries, with a bottom salinity gradient from $12^{o}/oo$ near river estuaries to $26^{o}/oo$ near tidal deltas. Bottom salinities fluctuate with wet and dry seasons. The average depth of Pamlico Sound is only 3.7 meters. The maximum depth is 6.7 meters, slightly less than in the deepest western fluvial channel. Currents tend to be weak although during hurricanes and storm surges, high energies can occur. Turbidity is usually high, water stratification is moderately to sporadically developed in the deeper areas. Water may be slightly to moderately acid, especially along the swampy landward margins. The substrate is mostly fine to medium sand with minor amounts of clay along leeward margins. The only published work dealing with the Recent Foraminifera of Pamlico Sound is by Grossman (1967) His 24 stations represent three north-south, and one northwest-southeast, transects across the Sound.

Species diversity is low in Pamlico Sound, but increases as salinity increases. Only three genera representing seven species occur commonly or abundantly. (See Appendix I.) These species are equally common in brackish-water fluvial environments and represent a transition to open lagoonal environments. Progressing eastward into the more saline waters of Pamlico Sound, calcareous hyaline species gradually become more dominant. In the most saline portions of the open lagoon, <u>Elphidium</u> represented by three common to abundant species is especially characteristic (Appendix I).

Eastern Estuaries and Sounds

These habitats consists of short fluvial estuaries of small creeks and rivers characterized by slow sluggish currents which drain lowland swamps and lakes as well as by small, narrow, linear sounds bounded on the landward side by low marginal marine swamps and on the oceanic side by longshore bars. The salinity transitions parallel those of the combined large western fluvial estuaries and open sounds environments, but the salinity gradient from fresh water to normal marine salinity is compressed to two kilometers or less in many cases as compared to more than 100 kilometers from Washington or New Bern to Ocracoke Inlet in the larger estuarine setting. No attempt is made to subdivide the eastern estuaries and sounds in the same fashion as in the western fluvial estuaries and open lagoons. Sampling densities in the comparable subdivisions are sparse and boundaries between subdivided habitats are less clearly defined. Even in the larger setting, boundaries are transitional. Because greater salinity gradients occur over shorter distances, a greater diversity of Foraminifera have been recorded. More students have studied the Foraminifera in these areas because a considerable diversity of habitats are easily accessible by small craft with a minimum of equipment.

The eastern estuaries and sounds are shallow, ranging from mudflats at water level to a meter or two deep in many places. Channels have been dredged up to 4 meters deep for the Intracoastal Waterway. Currents are weak, usually less than 2 km/hr, although locally, near tidal inlets, the currents may be stronger. Turbidity is low except when wind conditions are high. The water masses are too shallow to develop a good stratification so that there is little salinity gradient from bottom water to the surface. During dry seasons salinities can be high (up to $40^{\circ}/oo$) on marginal marshy environments and low during periods of heavy rain. Overall normal salinities vary from $0.5^{\circ}/oo$ in the upper reaches of tidal influence on the small creeks and rivers to $36^{\circ}/oo$ near tidal inlets. Spartina grass comprises an important part of the marsh biomass. Substrates consist mostly of fine silts and clays with considerable fecal pellet material. The substrate may be sandy near tidal inlets and channels.

This summary of the eastern estuaries and sounds is based on the works of LeFurgey (1976) for Croatan and Roanoke Sounds, Grossman (1967) for Core Sound, Akers (1971) and LeFurgey and St. Jean (1976) for eastern Bogue Sound, and Miller (1953) for Mason Inlet. LeFurgey (1976) gives an excellent synopsis of the ecological occurrence of most of the typical species listed in Appendix I (for the eastern estuaries and sounds). Although the majority of Miller's genera and species are typical, several that he reports are more characteristic of open ocean, middle to deep shelf environments. Possibly anomalous forms were introduced by coastal storms or perhaps specimens deposited during a higher sealevel stand have been reworked from nearby Holocene sediments and mixed with modern sediments.

As in the larger fluvial estuaries and sounds, arenaceous Foraminifera dominate the low salinity facies of small rivers and creeks, with a rapid transition to more calcareous forms and higher species diversity as salinity increases. These environments are considerably impacted by storms and abnormally high tides. Minor seasonal changes in foraminiferal populations have been noted by some of the above mentioned authors.

The lowest salinity facies are characterized by arenaceous Foraminifera, as in the case in the western fluvial and open lagoonal environments. However, in the eastern case, there is more generic and specific diversity (Appendix I). Akers (1971) reported a questionable Psammosphaera, but that genus is usually found in deep oceanic settings. The illustration is not typical for the genus. Textularia, represented only by T. palustris, is much more commonly associated with continental slope or shelf environments.

Miliolid Foraminifera are dominant in areas which approach normal marine salinities. Quinqueloculina is the dominant genus (Appendix I). Miller found two species of Quinqueloculina in low salinity environments along with several hyaline species typical of normal marine salinities. The estuary studied by Miller (1953) is located so close to normal marine and tidal influences that the milioloids may have been introduced by storms.

A modest diversity of hyaline Foraminifera is encountered in the eastern estuarine environments. Miller (1953) reported that two planktic genera (Globigerinella and Globigerinoides) were common in near normal marine facies although planktic foraminiferal tests are not usually prominent at depths of less than 20 meters on open shelf environments. However, they do occur in estuarine sediments on occasion.

Six benthic foraminiferal genera have been observed in the normal saline facies (Appendix I). Buliminella reported by both LeFurgey (1976) and Miller (1953), represents an anomalous genus for estuarine environments, all the rest are typical and specifically diverse. Included is Ammonia, which is somewhat unique amongst hyaline Foraminifera in that it has a wider salinity tolerance than most (0.05°/oo to 33°/oo). The best known species is the ubiquitous A. beccarii, which is found in most estuarine habitats and is well known in shallow shelf environments. Elphidium, Nonion, and Protelphidium are especially common in estuarine environments of moderate to normal marine salinities and are also found in tidal pools and in shallow shelf environments.

Tidal Delta

Tidal deltas on the North Carolina coast are generally small but dynamic environments transitional from estuarine to neritic habitats. They are fan-shaped deposits on the estuarine side of tidal inlets, breached by tidal channels characterized by strong reversing currents. Depths are shallow. Turbidity is moderate. Salinity ranges are moderate, from 24°/oo to about 30°/oo. The substrate is typically medium-grained sand with minor amounts of clay, especially on the delta flanks. Grossman (1967) did concentrated sampling on the tidal delta at Ocracoke Inlet (25 stations) and at Drum Inlet (6 stations). Miller (1953) studied the Foraminifera at one station on the Mason Inlet delta.

Species have a moderately high diversity and are those usually associated with near normal salinities. Miller reported low salinity arenaceous species to be common (Ammobaculites cassis) at the Mason Inlet delta, which is closer to low salinity environments than the other deltas. Grossman reported six milioloid species to be rare. They were most common at sites near the tidal channels at Ocracoke and Drum Inlet. Elphidium is the most typical genus. with five characteristic species (Appendix I). Grossman also found the marine species Cibicides lobautuls and Hanzawaia concentrica to be rare. Miller reported the common occurrence of an unidentified species of Nonion.

Tidal Channel

Tidal channels may extend from the tidal inlets to some distance into the estuarine environment, especially in the narrow estuaries parallel to the coast. Water depths are shallow and currents are strong. Turbidity is usually low. The habitat has nearly normal marine salinities, typically $31^{o}/oo$ to $33^{o}/oo$. The substrate consists mostly of fine to very fine sand with measurable amounts of silt and clay. This summary of tidal channel Foraminifera is based on four stations near Beaufort Inlet studied by Akers (1971), one station repeatedly sampled by LeFurgey and St. Jean (1976) (Foraminifera which passed through an intake pipe from near a tidal channel), and one station studied by Hadley (1936) from the deep channel in Beaufort Inlet proper. Two stations sampled by Miller (1953) are from near Mason Inlet.

Because tidal channels have nearly normal marine salinities, the associated Foraminifera display a moderate amount of generic and specific diversity.

Arenaceous Foraminifera are not as common as in less saline waters. However, a few species have been reported (Appendix I). The Miliolidae are more abundant and specifically diversified than in any other inland marine setting (Appendix I). In fact, one does not find them so abundant and diversified in neritic settings until waters reach about 9 meters deep. The species in the channels are the same as those in the neritic environment (Appendices I, II). *Quinqueloculina* is characteristic (Appendix I).

Planktic Foraminifera were reported as very abundant in the tidal channel at Mason Inlet by Miller (1953) (*Globigerinoides* cf. *G. ruber*) and common in moderately deep water at Beaufort Inlet by Hadley (1936) (*Globigerinoides* cf. *G. sacculifera*). Planktic Foraminifera do occur in shallow water settings, but there, presence in abundance is unusual. Akers (1971, p. 152) noted a considerable number of planktic Foraminifera and realized the incongruity of the sample. He suggested that they could be contaminants from samples dumped from the research vessel EASTWARD which was formerly berthed nearby.

Benthic Foraminifera are more abundant and diversified than others. *Elphidium* is the most characteristic (Appendix I). Akers (1971, p. 152) refers to *E. gentri*. As the species is not found in his faunal list (p. 162) but *E. gunteri* is included, and as there is no species *E. gentri* found in Ellis and Messina (1940 *et seq*.) *E. gentri* is here taken to be a misprint for *E. gunteri*. The closely related genus *Protelphidium*, represented by *P. tisburyense* are characteristic in Bogue Sound as are the rotaloid species *Ammonia beccarii* and *A. tepida*. All other noteworthy species are found in the deepest tidal channels at Beaufort Inlet and are commonly associated with open ocean shelf environments (Appendix I). Miller (1953) reported that Poroeponides repanda was common in the tidal channel at Mason Inlet, but the illustration strongly suggests the planktic species Globorotalia menardi, whose tests are more commonly associated with outer shelf and slope sediments.

Non-Estuarine Environments

Most studies concerning littoral, neritic, and oceanic Foraminifera have concentrated on their depth distributions, with some emphases on temperature and current controls, especially with respect to planktic species. Attention has been placed on current patterns off the North Carolina coast especially because of the contrasting faunas with Floridian and Caribbean affinities influenced by the Gulf Stream and the northern influences of the cooler water of the Labrador Current. The impingement of the two currents off of Cape Hatteras, where the continental shelf is unusually narrow and the continental slope is unusually steep, sets off a natural faunal boundary for continental shelf Foraminifera especially, as noted by Culver and Buzas (1981, p. 217). Not only does an important faunal change occur off Cape Hatteras, but a major change also occurs between continental shelf and continental slope faunas.

Some biases occur in published studies because there have been more studies and a higher sampling density south of Cape Hatteras than north of the Cape. More studies and greater numbers of sample localities have also been studied in the shallow water environments than in the deep water settings from outer shelf to the Hatteras Abyssal Plain. As with the summary of the estuarine Foraminifera, only those species which occur commonly or abundantly are considered. The fact that a species is not mentioned in a particular habitat does not mean that it does not occur.

The following non-estuarine foraminiferal habitats are considered:

1. Intertidal beach and surf. No stations north of Cape Hatteras have been reported.
2. Marine delta. A deltaic lobe on the ocean side of a tidal inlet (as opposed to the tidal delta on the estuarine side of the channel). No stations north of Cape Hatteras have been studied.
3. Shallow shelf north of Cape Hatteras. Low tide to 15 meters.
4. Shallow shelf south of Cape Hatteras.
5. Middle shelf north of Cape Hatteras. 15 to 60 meters.
6. Middle shelf south of Cape Hatteras.
7. Outer shelf north of Cape Hatteras. 60 to 200 meters.
8. Outer shelf south of Cape Hatteras.
9. Upper continental slope. 200 to 1000 meters.
10. Lower continental slope. 1000 to 3000 meters.

11. Continental rise. 3000 to 4000 meters.
12. Abyssal plain. 4000 to +5000 meters.

Culver and Buzas (1981) computed Jaccard coefficient clusters which distinguished northern and southern faunas for the continental slope environment. The boundary of their Analysis 1 is just to the south of North Carolina, though their Analysis 2 is set at about the Wilmington area. The data used in this summary is not sufficient to indicate a good faunal distinction for the slope and abyssal faunas, therefore the continental slope, continental rise, and abyssal plain habitats were not subdivided into a northern and southern zone.

The physical, chemical, and geologic setting of the continental margin of North Carolina have been reported in considerable detail by Newton and Pilkey (1971) and by Hine, Riggs, and others (1986).

Intertidal Beach and Surf

Foraminifera are not usually found in intertidal beach sands or in the surf. Hadley (1936) reports six species as common at Shackleford Beach. He gives no details as to the exact location of his material. It could be behind the point at the west end of Shackleford Bank. In any event, it must have been in a high energy beach environment. The other high energy environment is that reported by Miller (1953) in the surf, about 600 meters east-northeast of Mason Inlet. All but two of the species are identical with those reported from tidal channels (See Appendix I).

No arenaceous Foraminifera were reported. Three species were assigned to the milioloid genus _Quinqueloculina_ (Appendix II). The benthic hyaline species _Ammonia parkinsoniana_ and _Florilus_ aff. _F. auriculus_ were not reported from the tidal channels in the estuaries but the other benthic species, _Cibicides concentricus_, _Elphidium gunteri_, and _Elphidium poeyanum_ did occur in the channels. No planktic Foraminifera were reported. All of the Foraminifera Hadley and Miller found in intertidal beach sands and surf are typical of shallow neritic environments.

Marine Delta

Marine deltas are fan-shaped aprons of sediment located on the oceanic side of tidal inlets. Only one identified marine delta was studied. Grossman (1967) sampled 11 stations on the delta at Ocracoke Inlet. His samples extend to about 8 km offshore. He does not indicate water depths. A surf zone occurs on the margins of the deltas so that they represent high energy environments. The substrate is sand with minor amounts of shell material. Tidal currents are relatively strong.

Species diversity is moderate and few species are common at Ocracoke Inlet. Shallow water forms predominate. Arenaceous examples are absent. Milioloids are more numerous than in the sounds but only one species, *Quinqueloculina jugosa* is common. Although *Q. lamarckiana* is less usual, it was encountered at most stations. The planktic *Globigerina bulloides* was collected mostly on the southeast side of the delta, about 2.5 km offshore. The tests may have been brought in on prevailing southeast winds, for the species is not usual in nearshore environments (See Bock, 1982, p. 246). The rotaloid *Elphidium* is generally less abundant than in the sounds and only two species are prominent.

Shallow Shelf North of Cape Hatteras

Wilcoxin (1964, p. 20, 21) divided the shelf faunas into inner, middle, and outer shelf: at 1 to 15 meters, 15 to 61 meters, and 61 to 192 meters, on the basis of the occurrence of dominant species. McLean (1971, p. 20) compiled species depth range charts based on all species reported by Wilcoxin. He found what he thought were more significant breaks at 50 and 160 meters on the shelf. The inner shelf is here taken to range from 1 to 15 meters, following Wilcoxin, for only the common and abundant species are considered in this report and McLean's (1971, p. 36) charts indicate that some species are restricted to the shallowest shelf, in keeping with Wilcoxin's inner shelf zone.

Unlike the area South of Cape Hatteras, the shallow shelf to the north is bounded on the west by outer banks which form a broad, slightly sigmoid curve with only one tidal inlet, Oregon Inlet, near Roanoke Island. The area is dominated by the Labrador current, which is deflected under the Gulf Stream near Hatteras. However, within the 15 meter depths of the shallow shelf, the water temperatures do not vary greatly from those on the shallow shelf south of Cape Hatteras. The habitat is a high energy, wave dominated one.

Only one work (unpublished) has included inner shelf Foraminifera North of Cape Hatteras, that by Workman (1981). Two species occurred commonly to abundantly--*Elphidium clavatum* and *E. selseyense*. These occurred 9 meters deep, on a substrate of fine to medium sand which contained fine shell fragments. *E. clavatum* was a common to abundant species in the tidal channel in Bogue Sound and on estuarine tidal deltas as well as on the marine delta at Ocracoke Inlet. *E. selseyense* occurred commonly in the estuarine Roanoke Sound habitat which is located on the western side, 15 to 20 km south of the shallow shelf occurrence reported by Workman.

Shallow Shelf South of Cape Hatteras

More investigators have studied the shallow shelf Foraminifera south of Cape Hatteras than in any neritic habitat off the North Carolina coast. However, the numbers of stations are few (See Appendix II).

The western boundary is characterized by barrier islands formed into three large northerly and northwesterly concave arches shaped by eddie current gyres associated with the Gulf Stream. Bottom temperatures do not differ markedly from surface water temperatures due to the shallowness of the habitat. Waters are well mixed, aerated, and wave dominated. The environment can be substantially affected by storms. Schnitker (1971, Figure 2) shows the bottom substrates to consist of very fine to fine sand. A comparison of the northern and southern shallow shelf species diversity is not possible because of the little work done north of Cape Hatteras.

There is considerable species diversity south of Cape Hatteras, especially of the hyaline benthic species. Arenaceous species are uncommon. Schnitker reported that only *Placopsilina confusa* was abundant (22%) and that at just one station. Porcellaneous Foraminifera are represented entirely by *Quinqueloculina*, most of which commonly occur in the more saline estuarine habitats as well--except *Q. lata*. The genus is diverse with six common to abundant species (Appendix II). Planktic Foraminifera are rare except for a species of *Globigerinoides* compared to *G. sacculifera* by Hadley (1936). Hyaline benthic Foraminifera are by far the most diverse generically and specifically. At least 15 common to abundant species belonging to 7 genera have been reported. Of these, *Elphidium* is the most diverse, with 7 species. *E. clavatum* is the most abundant, but only at one locality. *E. clavatum* also commonly occurs in many estuarine as well as in deeper shelf habitats. *Ammonia* is represented by 2 species. *Ammonia beccarii* is also commonly found in estuarine environments. On the shallow shelf, *A. tepida* was reported from most of Workman's (1981) stations. All other genera with common to abundant species are represented by only one species each (See Appendix II). They are all typical of shallow open marine environments. A few of them are found in deeper shelf waters.

Middle Shelf North of Cape Hatteras

The middle shelf is the habitat *par excellence* for Foraminifera. Although not all Foraminifera are adapted to middle shelf habitats, more genera and species are found in the middle shelf depth ranges than any other ecologic setting. There are some biases in the foraminiferal record of the middle shelf north of Cape Hatteras. As with the shallow shelf, less work has been done here than to the south. The summarized information is based on studies by Cushman (1918-1931, 1 station), Murray (1969, 3 stations), Schnitker (1971, 22 stations), and Workman (1981, 7 stations). No real comparison can be made with the shallow shelf north of Cape Hatteras as so little work has been done there--only two species, belonging to Elphidium, are known to occur commonly. Another bias is that many more stations have been studied between 15 and 40 meters than between 40 and 60 meters so that changes between the middle and outer shelf may appear more marked and less transitional than is really the case. For comparisons of middle shelf faunas north and south of Cape Hatteras, see the following discussion on the middle shelf south of Cape Hatteras.

The northern middle shelf is significantly influenced by the southward flowing Labrador current which turns slightly eastward towards Cape Hatteras where its more dense cooler waters are forced under the north-northeasterly flowing warmer waters of the Gulf Stream.

The substrate varies from very fine to medium sands.

Arenaceous Foraminifera start to increase in importance in the middle shelf. As with the the less saline estuarine environments, the Lituolidaceae is the dominate group, but genera more characteristic of deeper shelf and ocean basin habitats, such as Eggerella, Liebusella, Placopsilina, Reophax, and Textularia, start to appear more commonly. There is little diversity, however, for each genus is represented by only one common species. All of these genera start to appear noticeably in shallow areas of the middle shelf (at about 20 meters).

Porcellaneous Foraminifera are much reduced over their abundance and diversification in the saline portions of the estuaries and on the shallow shelf south of Cape Hatteras. North of Cape Hatteras only Quinqueloculina seminula is common.

The planktonic Foraminifera begin to become much more important. There is a notable increase in skeletal occurrences in the sediment at about 20 meters depth and common to abundant occurrences at 60 meters. Globigerina bulloides is especially characteristic of the northern middle shelf and Globigerinoides ruber is also important.

As on the shallow shelf south of Cape Hatteras, the hyaline benthic forms are the most diverse and abundant. Elphidium continues to be represented by more common species (5 species) than any other genus, but it is not as diverse as in the shallow shelf south of Cape Hatteras (8+ species). The ubiquitous E. clavatum still remains the dominant species, extending through the whole depth range of the middle shelf. The salinity tolerant Ammonia tepida, found in estuaries and on the shallow shelf south of Hatteras, also occurs abundantly here, but it is the only species to do so. All the other examples are typical mid-shelf genera. Cibicides and Planulina are each represented by two species. Murray (1969) indicated that Rosalina consisted of more than one unassigned species. All other genera are represented by one species each (See Appendix II). Elphidium poeyanum, Elphidium selseyense, and Hanzawaia concentrica also occur on the shallow shelf south of Cape Hatteras. A species with affinities with Florilus auriculus is known as well from the surf zone near Mason Inlet, south of Cape Hatteras (Miller, 1953).

Middle Shelf South of Cape Hatteras

The middle shelf south of Cape Hatteras is dominated by the northward flowing Gulf Stream and its associated counter clockwise gyres. Differences in the foraminiferal faunas from those north of Cape Hatteras reflect an association of warm water species from the Gulf of Mexico and the Caribbean. Some nutrients may be brought northward through the Florida Straits which could have an influence on productivity as well (See Sen Gupta and Strickert, 1982).

More stations have been sampled for Foraminifera south of Cape Hatteras than to the north, but only by four investigators: Murray (1969), Schnitker (1971), Wilcoxin (1964) and Workman (1981). Murray, Schnitker, and Workman sampled most of the stations upon which the summary north of Cape Hatteras was presented above. By far the largest sample undertaking was that by Schnitker who collected from 39 of the 59 stations reported from the area. There is more faunal diversity amongst the common to abundant genera and species south of Cape Hatteras than to the north. Interestingly, all of the genera found to the north except Liebusella occur south of Cape Hatteras as well. However, Trochammina which does not occur to the north is prominent south of Hatteras. Trochammina is also characteristic in some estuarine habitats where certain species show a preference for increasing salinities while others have opposite preferences.

There is more diversification amongst the porcellaneous Foraminifera south of Cape Hatteras, with 9 species belonging to 4 genera, than to the north where only one species was found. Quinqueloculina is the dominant genus, represented by 5 species. Of these, Q. seminula, the only species found north of Hatteras, is the dominant species in the southern area. Quinqueloculina is more prominent on the shallower half of the middle shelf except for Q. seminula which ranges out to the upper continental slope. Peneroplis and the bizarre Calcituba are characteristic of warm water Mediterranean type environments, especially on carbonate platforms and banks. The miliolid Triloculina trigonula is found commonly in warm water environments as well.

Many more species of planktic Foraminifera occur south of Hatteras than to the north (10 species versus 2 species), but they are rare at depths less than 18 to 20 meters. Both Globigerina bulloides and Globigerinoides ruber, the only two species north of Hatteras, are both found in the southern faunas. However, G. bulloides is about three times more abundant to the north. G. ruber is commonly twice as abundant in the south. Tests of Globorotalia menardi found at about 40 meters deep in the southern area is usually a more dominant planktic test deposited in deeper waters on the continental slope, continental rise, and abyssal plain.

Amongst the benthic hyaline Foraminifera, Ammonia tepida, Cibicides bradyi, Cibicides concentricus, Elphidium clavatum, Hanzawaia concentrica, Planulina exorna, Planulina ornata and Stetsonia minuta are found both north and south of Cape Hatteras. Elphidium still remains the most dominant and diverse genus and E. clavatum a dominant species. Other than E. clavatum, however, all the remaining four southern species are distinct. The species of Elphidium north of Cape Hatteras have more in common with the shallow shelf and estuarine species south of Cape Hatteras. Elphidium subarcticum seems anomalous in the warm waters south of Cape Hatteras. Cibicides is the second most divers genus with three species. Two of them, C. bradyi and C. concentricus, are also found in the north. Hanzawaia concentrica occurs at more stations (27 stations) in the middle shelf area south of Cape Hatteras than any other species. It is also commonly encountered north of Cape Hatters. Bolivina, Cancris, Caribeanella, Cassidulina, and Trifarina are all encountered for the first time. The rotaloids (sensu stricto) are more diverse and more characteristically warm water species than in the north.

Outer Shelf North of Cape Hatteras

The outer shelf is here taken to be that zone from 60 to 200 meters deep. It is a zone where photopenetration declines markedly. The outer shelf north of Hatteras is still dominated by the colder waters of the Labrador Current.

The foraminiferal data may be somewhat biased in that few stations have been studied (a total of 8). There is an important gap in that no sampling has been reported between 140 and 200 meters.

The arenaceous Foraminifera are not as diverse as in the middle shelf north of Cape Hatteras, but they are typical deep water forms. Only two species were found to be common to abundant, Reophax atlanticus which also occurred commonly on the middle shelf north of Hatteras, and Tholosina vesicularis.

A noticeable change in the outer shelf is the lack of common to abundant porcellaneous species.

Another notable change is the increasing importance of planktic tests in bottom samples. Globigerina bulloides is the most abundant planktic species as it is in the northern middle shelf environment. Globigerina borealis [assigned by Schnitker to G. pachyderma (See Iaccarino 1985, p. 300)] is especially significant in that it is typically a cold water species.

The benthic species are much less diverse generically and specifically than on the middle shelf. Each of the six genera reported is represented by only one species. Most of them are cold water adapted species. Bulimina marginata and Islandiella subglobosa were found more widespread on the outer shelf than the other species.

Outer Shelf South of Cape Hatteras

Most of the generalities concerning the outer shelf north of Cape Hatteras apply equally to the south. Depths from 60 to 200 meters are transitional from the photic zone to a zone where light penetration is so low as to be of little use to photosynthetic organisms. The warmer waters of the Gulf Stream seem still to have some influence on both the benthic and planktic species. The planktic species show increasing diversity and the benthic ones a decrease in diversity. As with the collecting biases in the area north of Cape Hatteras, there are far fewer stations from which Foraminifera have been studied than is the case on the middle shelf. There are no reported stations between the depths of 159 and 200 meters.

Unlike the area to the north of Hatteras, no common or abundant arenaceous species were found.

Only one common or abundant porcellaneous species was found: Quinqueloculina seminula, which is more characteristic of shallower environments.

The planktic species are more diverse than they are on the outer shelf north of Hatteras. Three species are common to the northern area, Globigerina bulloides is very abundant in both areas, Neogloboquadrina dutertrei is about as common as it is to the north, and Globigerinoides ruber is much more abundant than to the north. Most of the species suggest moderately warm water.

Eight benthic genera represented by one species each characterizes the southern outer shelf. Islandiella subglobosa, found at one moderately deep station on the outer shelf, is the only species also found to the north. It is more commonly associated with cold water environments. On the other hand, Amphistegina lessoni, which occurred commonly at only one station on the shallow part of the outer shelf, is a well known warm water species. The common occurrence of these two species characteristic of diverse temperature tolerances at strikingly different depths suggests that some thermal water stratification occurs, or that tests of one or the other species have been transported from their normal habitat to the outer shelf south of Cape Hatteras. Elphidium clavatum is usually associated with more shallow environments, but occurs abundantly on the upper outer shelf here and commonly to depths of nearly 160 meters. Hanzawaia concentrica is still moderately common but not nearly as widespread as on the middle shelf. All of the other benthic species are typical of deeper middle to outer shelf and upper slope environments.

Upper Continental Slope

From the upper edge of the continental slope down to the Hatteras Abyssal Plain, the foraminiferal faunas are not set off into areas north and south of Cape Hatteras because so few collecting localities have been studied that comparisons would have little meaning. In addition, the deeper water is mostly cold so that upper water temperature distributions have less effect on the deeper benthic faunas. Planktic faunas start to become more important than the benthic faunas in terms of numbers of specimens for a given sample size. The planktic species are strongly influenced by upper water temperatures and current patterns (Bé, 1959, 1960, 1971). However, their tests can be transported considerable distances before final deposition and incorporation into bottom sediments, so that narrow ecologic boundaries such as between north and south of Cape Hatteras become fuzzy.

The upper continental slope is taken to be that zone from the break in slope at the edge of the continental shelf, at 200 meters, to a depth of 1000 meters. The lower limit is arbitrary.

As compared with shelf faunas, there are distinct differences in the arenaceous Foraminifera representative of the upper slope. Four species are common to abundant, each belonging to a different genus; Clavulina, Cyclammina, Psammosphaera, and Tholosina. The porcellaneous Foraminifera are greatly reduced in numbers. Only two common species occur, the ubiquitous Quinqueloculina seminula and the biloculine Pyrgo subsphaerica. Pyrgo is typical of slope environments. Quinqueloculina is more typical of shelf environments. The deposited tests of planktic Foraminifera are prominent in slope sediments. Many of the species encountered on the upper slope are the same as those found on the middle and upper shelf both north and south of Cape Hatteras, though there are some additional genera and species. Orbulina and Pulleniatina appear commonly to abundantly for the first time. Both cold and warm water species are common or abundant, which indicates the influence of both the Gulf Stream and the Labrador currents. Some species could possibly have been associated with the slowly circulating Sargasso Sea (See Bé, 1960). The warm water species seem to outnumber the cold water ones. Interestingly, no one has looked at coiling directions of some of the classic planktic species used for paleotemperature interpretations in other areas.

The benthic hyaline Foraminifera decline sharply. Most of the common to abundant genera are more characteristic of the middle to outer shelf. The lenticulinids are more prominent and the rotaliids (*sensu stricto*) less prominent than on the outer shelf.

Lower Continental Slope

The lower continental slope is taken to be that part of the slope which is between 1000 and 3000 meters deep. Very little previous work has been done off the North Carolina coast at these depths. The only detailed report of the Foraminifera is that by Cushman (1918-1931) which was based on the collections made by the U. S. Research Vessel "Albatross". Eight sites were reported on the North Carolina continental margin that had common to abundant species of Foraminifera. Depths are below the effective photic zone and bottom waters are cold. Most common to abundant species were collected above 2000 meters. Only *Astrorhiza angulosa* was listed as common in deeper water at one station.

Benthic faunas are dominated by arenaceous Foraminifera, especially such characterized deep water genera as *Astrorhiza*, *Bathysiphon*, *Reophax*, *Rhabdammina*, and *Saccammina*. No common to abundant porcellaneous species were reported. The planktic species are not as diverse as reported for the upper continental slope. However, in view of the fact that the major work was done before the great generic and specific splitting by modern students of planktic Foraminifera, the apparent reduced diversity may be an artifact of literature rather than a biological one. The bottom sediments are characterised by "*Globigerina* and pteropod" oozes.

Common and abundant benthic hyaline Foraminifera are much reduced generically and specifically. Though deep, depths are well above the carbonate dissolution zone. *Bulimina* is the dominant genus, represented by three species. *Bulimina marginata* occurs slightly deeper here than is typical to the north but *Uvigerina peregrina* is especially characteristic (See Streeter and Lavery, 1982).

Continental Rise

Only one station was reported to have common to abundant species on the continental rise, at 3739 meters (Appendix II). Only three species are arenaceous, all of the remaining 10 abundant species are planktic. Significantly, no hyaline nor porcellaneous benthic species were reported as common or abundant. Most of the abundant planktic species are the same that occurred abundantly on both the upper and lower continental slope. No typical cold water planktic species had settled in abundance on the continental rise at the sampled station.

Hatteras Abyssal Plain

Cushman (1918-1931) reported three stations from the Hatteras Abyssal Plain containing common to abundant species of Foraminifera. All but one of these are planktic. The depths should be near the carbonate dissolution line. Two species were previously reported from shallower sediments, the temperate water Globorotalia hirsuta and the tropical to subtropical Pulleniatina obliquiloculata. The absence of abundant or common benthic arenaceous species may seem anomalous. Though arenaceous species are characteristic of abyssal environments and they are usually the only Foraminifera recovered from below the carbonate compensation line, they usually do not occur abundantly in any one sample.

CONCLUSIONS

Estuarine Environments

The distribution of Foraminifera in estuarine environments is controlled by salinity. In low salinity areas, arenaceous forms dominate (Table 1). Miliammina is especially widespread because it tolerates wide salinity ranges. In the low salinity large western fluvial estuaries, Ammobaculites is the dominant genus whereas in areas of comparable salinities in the eastern estuaries Haplophragmoides and Trochammina are the dominant genera. In general, Ammobaculites and Haplophragmoides decrease in abundance with increasing salinities. In contrast, some species of Trochammina do the same but other species actually increase with increasing salinities (See eastern estuaries and sounds, Appendix I).

Salinities are not sharply set off in each environment, but rather grade from one to the other. Likewise there is a gradual change in the composition of the foraminiferal faunas from one habitat to another, so that transitional faunas are common. Therefore, as salinities gradually increase into open sound and lagoonal environments there is a gradual transition to more and more calcareous benthic Foraminifera (Table 4). Ammonia is one of the first calcareous Foraminifera to appear and persists on to normal marine salinities. Elphidium is especially characteristic after salinities reach about 20^{o}/oo and is found in large expanses of Pamlico Sound as well as in the smaller linear sounds adjacent to the outer banks. Porcellaneous forms are most striking in areas of near normal marine salinities, especially in well flushed tidal channels and on tidal deltas (Table 2). Channels near the mouths of tidal inlets and small inlets, such as Mason Inlet, which are especially subjected to periodic inundation of oceanic waters and sediments during severe storms are characterised by mixing of littoral and neritic species with the more normal inland water species, so that some anomalous species occur, though usually not abundantly so. Planktic species, which are normally associated with neritic and oceanic environments can be encountered in inland waters, but they are probably not indigenous (Table 3). Also, benthic species which are commonly associated with moderately deep shelf environments can be encountered. Where estuarine sounds are the most narrow, and where freshwater runoff from land surfaces are close by, transitions are rapid and greater foraminiferal diversities occur.

Non-Estuarine Environments

Most of the shallow shelf species also occur in the more saline environments in the estuaries, especially of *Ammonia*, *Elphidium*, and *Quinqueloculina* (Tables 2 and 4). Some characteristic benthic forms also become dominant such as species of *Cibicides*, *Discorbis*, *Guttulina*, *Hanzawaia*, and *Florilus*. A few planktic species begin to become common in the shallow water sediments (Table 3). Comparisons of shallow water faunas north and south of Cape Hatteras are not significant because of the little work which has been done to the north.

Likewise, for the middle shelf, less work has been done to the north. In the middle shelf, the planktic forms become prominent from about 20 meters deep (Table 3). Tests of open ocean arenaceous forms begin to appear commonly (Table 1), but the benthic hyaline species still dominate the sediment (Table 4). Both the porcellaneous and hyaline forms are at their optimum numbers and diversities (Tables 2 and 4). More benthic genera of greater species diversity occur on the middle shelf than in any other environment.

Many species continue from the middle to the outer shelf. Beyond about 150 meters depth, there is a striking lack of sampling which may cause the change from outer shelf to upper slope faunas to appear more prominent than is really the case. Planktic tests increase in importance, arenaceous tests should increase in the number of common species, but only two species were reported. The calcareous hyaline species also decrease in importance.

Tests of planktic Foraminifera dominate the slope faunas (Table 3). Most of them are warm water species, but a few are known to be cool to cold adapted forms, indicating that the Gulf Stream dominates the plankton of the North Carolina Coast. Because of slow settling rates and increasing water depth, many have been transported some distance northward from their normal adaptive latitudes. On the lower continental slope, arenaceous forms dominate the benthic foraminiferal faunas where *Astrorhiza*, *Bathysiphon*, *Cyclammina*, *Reophax*, and *Rhabdammina* are especially prominent, along with a number of other less common genera (Table 1). The hyaline benthic forms decrease strikingly on the lower continental slope.

Foraminifera on the continental rise and in the Hatteras Abyssal Plain have been inadequately studied (i.e. few collection sites). Only tests of planktic species from the upper water column occur in abundance (Table 3). Arenaceous species characteristically occur, but are sparse (Table 1). The calcareous benthic species should show increasing degrees of leaching due to carbonate dissolution.

Two recent works have analyzed foraminiferal populations over broad areas of the Atlantic continental margin in order to generalize about neritic and oceanic foraminiferal distributions (Culver and Buzas, 1981; Sen Gupta and Strickert, 1982). Both have used cluster analysis techniques. The faunal patterns and the diagnostic genera and species on the North Carolina continental margin appear to be compatible with the findings in both studies, though there are some differences in common and abundant species.

General Comments

The common and abundant Foraminifera reported in the estuaries and on the continental margin of North Carolina are typical of the environments they occupy and many of them are diagnostic, although there are some genera and species with wide ecological tolerances. Past studies, understandably, have concentrated on the most accessible collection sites which require the minimum equipment and support facilities. Nevertheless, there have been a number of important and extensive studies. All these data provide a sound base for future sampling of similar areas as well as for extension of studies into some of the least well studied regions, especially those at greater depths on the lower continental slope and the Hatteras Abyssal Plain. There have as yet been no studies conducted in the Hatteras Canyon. We also need a better look at the shelf and upper slope environments in the dynamic area off Cape Hatteras where there is the interesting interaction of the Labrador Current and Gulf Stream. There is also a surprising gap in faunal collection sites between about 150 and 200 meters on the outer shelf. A look at some of the more saline areas in Albemarle Sound could also prove to be of interest.

Previous studies on the Recent Foraminifera of North Carolina can serve as an important base for future monitoring of major ecological changes in the marine habitats in and around North Carolina, for many of the studies were undertaken at a time when pollution and other environmental impact factors had not yet developed to the present or probable future problem levels. Because of the sensitivity of Foraminifera to their environment, they can be important guides to environmental changes (See, for example, Sen Gupta, 1982).

Past research on the Recent Foraminifera of North Carolina serves as an important base for the interpretation of the paleoecologic and biostratigraphic interpretation of the Atlantic Coastal Plain and the marine geology off-shore.

The great diversity of Foraminifera in the inland waters and in the open ocean offer an abundance of material for purely biologic study of the Order Foraminifera in such areas as life-cycle studies, genetics, food-web relationships and cell biology; especially the symbiotic inter-relationship of chromatophores and mitochondria to the organism in the diverse habitats available for study in North Carolina waters (See Lee and Hallock, 1987).

ACKNOWLEDGEMENTS

The author is indebted to Professor Robert Y. George, without whose solicitation this paper would not have been written, to an anonymous reviewer for cogent and helpful comments which improved the presentation, and to Professor Paul Fullagar, former Chairman, Department of Geology at the University of North Carolina, Chapel Hill, for providing funds and facilities for illustrations. Appreciation goes to Ms. Laurel Kaczor for drafting.

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Table 1. **Recent Foraminifera of North Carolina**

Ecological Distribution of Common to Abundant ARENACEOUS genera

Habitat / Genera	ESTUARINE					NON-ESTUARINE											
	W FLUV ESTU	OPEN SOUNDS	E EST & SNDS	TIDAL DELTAS	TIDAL CHANN	BEACH & SURF	MARINE DELTA	SH SH N HATT	SH SH S HATT	MD SH N HATT	MD SH S HATT	OT SH N HATT	OT SH S HATT	UP CONT SLP	LOW CONT SLP	CONT RISE	ABYSSAL PLN
Ammobaculites	5	3	2	1	1												
Ammotium		1	4		1												
Ammoastuta			1														
Arenoparella			1														
Haplophragmoides			3												1		
Miliammina			2														
Psammosphaera			1														
Siphotrochammina			1														
Textularia			1							1	1						
Tiphotrocha			1														
Trochammina			5		1						3					2	
Placopsilina									1	1	1						
Eggerella										1	1						
Liebusella										1							
Rheophax										1	2	1			1		
Tholosina												1					
Clavulina														1			
Cyclammina														1	2		
Astrorhiza															2		
Bathysiphon															2		
Crithionina															1		
Discammina															1		
Martinottiella															1		
Proteonina															1		
Rhabdammina															1		
Rhizammina															1		
Saccammina															1		
Valvulina															1		
Hormosina																1	

NOTE: Arenaceous Foraminifera are dominate in the least saline portions of the estuarine environment and in the deepest oceanic environments, with a number of transitional genera of low species diversity. (Numbers refer to the number of common to abundant species in each genus.) W FLUV ESTU = western fluvial estuaries, E EST & SNDS = eastern estuaries and sounds, TIDAL CHANN = tidal channels, SH SH N HATTERAS = shallow shelf north of Cape Hatteras, SH SH S HATT = shallow shelf south of Cape Hatteras, MD SH N HATT = middle shelf north of Cape Hatteras, MD SH S HATT = middle shelf south of Cape Hatteras, OT SH N HATT = outer shelf north of Cape Hatteras, OT SH S HATT = outer shelf south of Cape Hatteras, UP CONT SLP = upper continental slope, LOW CONT SLP = lower continental slope, ABYSSAL PLN = abyssal plain.

Table 2. Recent Foraminifera of North Carolina

Ecological Distribution of Common to Abundant PORCELLANEOUS Genera

Genera \ Habitat	ESTUARINE					NON-ESTUARINE											
	W FLUV ESTU	OPEN SOUNDS	E EST & SNDS	TIDAL DELTAS	TIDAL CHAN	BEACH & SURF	MARINE DELTA	SH SH N HATT	SH SH S HATT	MD SH N HATT	MD SH S HATT	OT SH N HATT	OT SH S HATT	UP CONT SLP	LOW CONT SLP	CONT RISE	ABYSSAL PLN
Quinqueloculina			5		6	3	2		6	1	5		1	1			
Triloculina			1								1						
Calcituba											1						
Peneroplis											2						
Pyrgo														1			

NOTE: Quinqueloculina dominates the more saline parts of the estuaries and the shallow open ocean habitats out to the middle shelf. All the other genera show low species diversity. (Numbers refer to the number of common to abundant species in each genus). W FLUV ESTU = Western fluvial estuaries, E EST & SNDS = eastern estuaries and sounds, TIDAL CHAN = tidal channels, SH SH N HATTERAS = shallow shelf north of Cape Hatteras, SH SH SH S HATT = shallow shelf south of Cape Hatteras, MD SH N HATT = middle shelf north of Cape Hatteras, MD SH S HATT = middle shelf south of Cape Hatteras, OT SH N HATT = outer shelf north of Cape Hatteras, OT SH S HATT = outer shelf south of Cape Hatteras, UP CONT SLP = upper continental slope, LOW CONT SLP = lower continental slope, ABYSSAL PLN = abyssal plain.

Table 3. Recent Foraminifera of North Carolina

Ecological Distribution of Common to Abundant HYALINE PLANKTIC Genera

Habitat / Genera	ESTUARINE					NON-ESTUARINE											
	W FLUV ESTU	OPEN SOUNDS	E EST & SNDS	TIDAL DELTAS	TIDAL CHANN	BEACH & SURF	MARINE DELTA	SH SH N HATT	SH SH S HATT	MD SH N HATT	MD SH S HATT	OT SH N HATT	OT SH S HATT	UP CONT SLP	LOW CONT SLP	CONT RISE	ABYSSAL PLN
Globigerinella			1														
Globigerinoides			1		2				3	1	3	1	3	3	3		1
Globigerina							1			1	2	2	1	3	1	2	1
Globorotalia											2	1	1	3	3	4	4
Hastigerina											1			1			
Neogloboquadrina											1	1	1	1			
Pulleniatina											1			1			1
Globigerinita													1				
Orbulina														1	1	1	1

Note: Planktic Foraminifera are not found commonly or abundantly in estuarine environments. When they are found, they are usually restricted to areas of near normal marine salinity. In the open ocean, they are rarely found commonly or abundantly in bottom sediments at depths less than 20 meters. They occur in great abundance on the middle shelf to the continental slope, and decrease in the abyssal plain oozes below the carbonate compensation depth. (Numbers refer to the number of common to abundant species in each genus). W FLUV ESTU = western fluvial estuaries, E EST & SNDS = eastern estuaries and sounds, TIDAL CHANN = tidal channels, SH SH N HATTERAS = shallow shelf north of Cape Hatteras, SH SH S HATT = shallow shelf south of Cape Hatteras, MD SH N HATT = middle shelf north of Cape Hatteras, MD SH S HATT = middle shelf south of Cape Hatteras, OT SH N HATT = outer shelf north of Cape Hatteras, OT SH S HATT = outer shelf south of Cape Hatteras, UP CONT SLP = upper continental slope, LOW CONT SLP = lower continental slope, ABYSSAL PLN = abyssal plain.

Table 4. Recent Foraminifera of North Carolina

Ecological Distribution of Common to Abundant HYALINE BENTHIC Genera

Habitat / Genera	ESTUARINE					NON-ESTUARINE											
	W FLUV ESTU	OPEN SOUNDS	E EST & SNDS	TIDAL DELTAS	TIDAL CHANN	BEACH & SURF	MARINE DELTA	SH SH N HATT	SH SH S HATT	MD SH N HATT	MD SH S HATT	OT SH N HATT	OT SH S HATT	UP CONT SLP	LOW CONT SLP	CONT RISE	ABYSSAL PLN
Elphidium		2	5	4	3	2	2	2	8	4	4	1	1				
Ammonia			2		2	1			2	1	1						
Buliminella			1							1							
Elphidiella			1		1					1							
Nonion			1	1	1												
Poroeponides			1		1												
Protelphidium			1		1												
Cibicides					1	2			1	2	3	1		1	1		
Discorbis					1				1		2						
Guttulina					1				1	1							
Florilus						1			1	1	2						
Hanzawaia									1	1	1		1				
Asterigerinata										1							
Brizalina										1	1		1	1			
Fursenkoina										1	1						
Globobulimina										1					1		
Lagena										1							
Nonionella										1							
Planulina										1	2			1			
Reussella										1				1			
Rosalina										2	2		1				
Stetsonia										1	1						
Uvigerina										1				1	1		
Webbinella										1							
Asterigerina											1						
Bolivina											1						
Cancris											1	1					
Caribeanella											1						
Cassidulina											1		1	1			
Trifarina											1						
Bulimina												1		1	2		
Islandiella												1	1				
Robulus												1		2			
Amphistegina													1				
Angulogerina													1	1			
Marginulina														1			

Note: Hyaline benthic Foraminifera first appear in moderately low saline water in the estuaries and increase in abundance and diversification as salinites increase to normal. Foraminifera are especially prominent on all shelf environments of the open ocean reaching their ecological acme on the middle shelf. They continue to be prominent on the outer shelf and slope, but are overshadowed by the great abundance of planktic tests. Towards the lower shelf and abyssal plain, they are gradually replaced by arenaceous forms as the dominant benthic Foraminifera. (Numbers refer to the number of common to abundant species in each genus). W FLUV ESTU = western fluvial estuaries, E EST & SNDS = eastern estuaries and sounds, TIDAL CHANN = tidal channels, SH SH N HATTERAS = shallow shelf north of Cape Hatteras, SH SH S HATT = shallow shelf south of Cape Hatteras, MD SH N HATT = middle shelf north of Cape Hatteras, MD SH S HATT = middle shelf south of Cape Hatteras, OT SH N HATT = outer shelf north of Cape Hatteras, OT SH S HATT = outer shelf south of Cape Hatteras, UP CONT SLP = upper continental slope, LOW CONT SLP = lower continental slope, ABYSSAL PLN = abyssal plain.

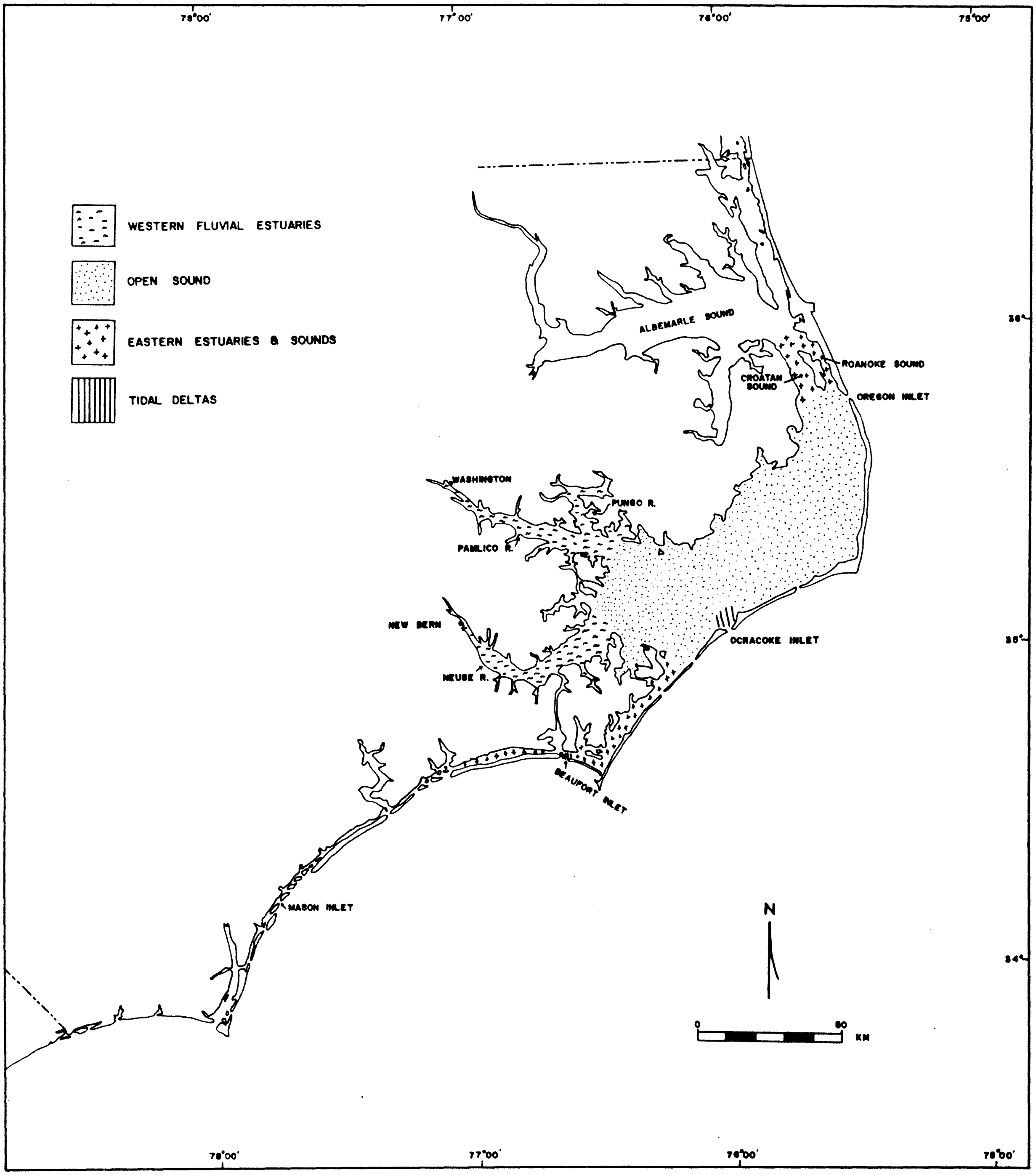

Figure 1. Index map of the principle foraminiferal estuarine habitat distributions of North Carolina.

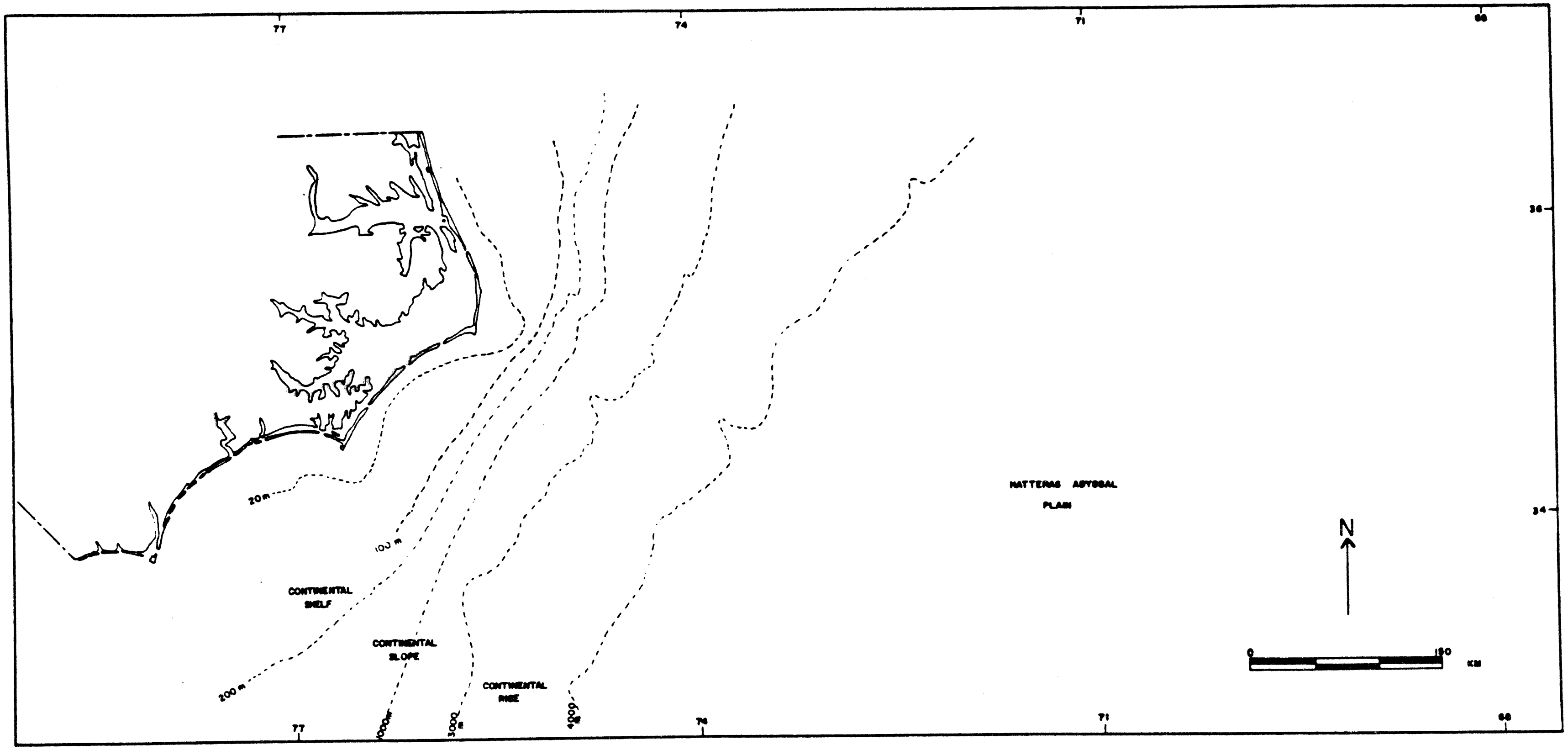

Figure 2. Chart off the North Carolina coast illustrating the position of the continental shelf, slope, rise and abyssal plain.

APPENDIX I--ESTUARINE FORAMINIFERA

The following faunal lists include only those species of Foraminifera which were reported as common to abundant by the indicated investigator. In cases where absolute numbers were presented, 10 or more specimens are included in the lists. Where percentages were given, abundances of 10% or greater are included. Notations are taken from the following indicated authors.

Symbols used:

- [A] = Akers (1971)
- [G] = Grossman (1967)
- [H] = Hadley (1936)
- [L] = living (based mostly on staining by rose Bengal)
- [LeF] = LeFurgey (1976)
- [LS] = LeFurgey and St. Jean (1976)
- [M] = Miller (1953)

Western Fluvial Estuaries

- Arenaceous
  - *Ammobaculites pamlicoensis* Grossman [G]--limited to western estuaries and western Pamlico Sound
  - *Ammobaculites crassus* Warren [G] [LeF]--western estuaries, western Pamlico Sound, Croatan Sound [L], Roanoke Sound [L], Stumpy Point Bay [L]
  - *Ammobaculites dilatatus* Cushman and Brönnimann [G]--limited western estuaries and western Pamlico Sound
  - *Ammobaculites exilis* Cushman and Brönnimann [G]--limited to western estuaries and western Pamlico Sound
  - *Ammobaculites neusensis* Grossman [G]--limited to western estuaries and western Pamlico Sound
- Porcellaneous--no common or abundant species
- Hyaline
  - Planktic--no common or abundant species
  - Benthic--no common or abundant species

Open Sound

- Arenaceous
  - *Ammobaculites pamlicoensis* Grossman [G]--low salinity facies, western Pamlico Sound
  - *Ammobaculites crassus* Warren [G]--low salinity facies, western Pamlico Sound
  - *Ammobaculites neusensis* Grossman [G]--low salinity facies, western Pamlico Sound
  - *Ammotium salsum* (Cushman and Brönnimann) [G]--low salinity facies, western Pamlico Sound
- Porcellaneous--no common or abundant species
- Hyaline
  - Planktic--no common or abundant species
  - Benthic
    - *Elphidium brooklynense* Shupack [G]--higher salinity facies, eastern Pamlico Sound

Elphidium incertum (Williamson) [G]--higher salinity facies, eastern Pamlico Sound

Eastern Estuaries and Sounds

Arenaceous

Ammoastuta inepta (Cushman and McCulloch) [A] [G]--Bogue Sound area, 1 meter; Core Sound

Ammobaculites crassus Warren [G] [LeF]--western estuaries, western Pamlico Sound, Croatan Sound [L], Roanoke Sound [L], Stumpy Point Bay [L]

Ammobaculites subcatenulatus Warren [A]--Bogue Sound area, 3-4 meters [L]

Ammotium fragile Warren [LeF]--Croatan Sound [L]

Ammotium palustris Warren [LeF]--Stumpy Point [L], Croatan Sound

Ammotium pseudocassis (Cushman and Brönnimann) [A]--Bogue Sound area, low tide [L]

Ammotium salsum (Cushman and Brönnimann) [A] [G] [LeF]--Bogue Sound area, 1-5 meters [L]; Core Sound, independent of salinity changes; Roanoke Sound, Croatan Sound

Arenoparella mexicana (Kornfeld) [A] [G]--Bogue Sound area, low tide to 1 meter [L]; Core Sound, decreases with increasing salinity

Haplophragmoides manilaensis Andersen [G]--Core Sound, decreases with increasing salinity

Haplophragmoides mexicanus Kornfeld [LeF]--Croatan Sound

Haplophragmoides wilberti Andersen [G] [A]--Bogue Sound area, low tide to 1 meter [L]; Core Sound, decreases with increasing salinity

Miliammina beaufortensis Akers [A]--Bogue Sound area, low tide [L]

Miliammina fusca Brady [A] [G] [LeF]--Bogue Sound area, low tide to 4 meters [L]; Core Sound, independent of salinity changes; Roanoke Sound [L], Croatan Sound [L], Stumpy Point Bay [L]

Psammosphaera sp. [A]--Bogue Sound area, low tide to one meter (Probably not *Psammosphaera*)

Siphotrochammina lobata Saunders [A]--Bogue Sound area, marsh, low tide

Textularia palustris Warren [A]--Bogue Sound area, low tide [L]

Tiphotrocha comprimata (Cushman and Brönnimann) [A]--Bogue Sound area, low tide to 1 meter [L]

Trochammina comprimata Cushman and Brönnimann [G]--Core Sound, decreases with increasing salinity

Trochammina inflata (Montagu) [G] [M]--Core Sound, increases with increasing salinity; Mason Inlet area

Trochammina irregularis Cushman and Brönnimann [A]--Bogue Sound area, low tide [L]

Trochammina laevigata Cushman and Brönnimann [A]--Bogue Sound area, low tide to 1 meter [L]

- *Trochammina macrescens* (Brady) [G]--decreases with increasing salinity

Porcellaneous
- *Quinqueloculina jugosa* Cushman [A] [M]--Bogue Sound area, 0.5 meters; Mason Inlet
- *Quinqueloculina lamarckiana* d'Orbigny [M]--Mason Inlet
- *Quinqueloculina poeyana* d'Orbigny [M]--Mason Inlet
- *Quinqueloculina seminula* (Linné) [A]--Bogue Sound area, 0.5 meters
- *Quinqueloculina* cf. *Q. seminula* (Linné) [A] [LeF] [M]--Bogue Sound area, 1-4 meters; Croatan Sound; Stumpy Point; Mason Inlet
- *Triloculina* cf. *T. brevidentata* Cushman [M] Mason Inlet

Hyaline
- Planktic
  - *Globigerinella* sp. [M]--Mason Inlet (More typical of an open ocean setting)
  - *Globigerinoides* cf. *G. ruber* (d'Orbigny) [M]--Mason Inlet (More typical of an open ocean setting)

Benthic
- *Ammonia beccarii* (Linné) [A] [G] [L] [M]--Bogue Sound area, low tide to 5 meters [L]; Core Sound; Roanoke Sound; Mason Inlet
- *Ammonia limbatobeccari* (McLean) [G]--Bogue Sound area, occurs independent of salinity changes
- *Buliminella elegantissima* (d'Orbigny) [M]--Mason Inlet (More typical of a middle to deep shelf setting)
- *Elphidiella mexicana* (Kornfeld) [M]--Mason Inlet
- *Elphidium excavatum* (Terquem) [LeF]--Roanoke Sound
- *Elphidium gunteri* Cole [A]--Bogue Sound Area, 0.5 to 2 meters [L]
- *Elphidium incertum* (Williamson) [A] [M]--Bogue Sound area, 1 to 5 meters [L]; Mason Inlet
- *Elphidium selseyense* (Heron-Allen and Earland) [LeF]--Roanoke Sound [L]
- *Elphidium* sp. [A]--Bogue Sound area, 2 meters [L]
- *Nonion* sp. [M]--Mason Inlet
- *Poroeponides repanda* (Fichtel and Moll) [M]--Mason Inlet [May be the planktic species *Globorotalia menardi* (Parker, Jones, and Brady)]
- *Protelphidium tisburyense* (Butcher) [G]--Bogue Sound area

Tidal Deltas (Ocracoke, Drum, and Mason Inlets)

Arenaceous
- "*Ammobaculites*" *A. cassis* (Parker) [M]--Mason Inlet

Porcellaneous--no common or abundant species

Hyaline
- Planktic--no common or abundant species
- Benthic
  - *Elphidium brooklynense* Shupack [G]--important, but less common than in the open sound biofacies

Elphidium clavatum Cushman [G]--important, but less common than in the open sound biofacies

Elphidium galvestonensis Kornfeld [M]--Mason Inlet

Elphidium incertum (Williamson) [G]--important, but less common than in the open sound biofacies

Nonion sp. [M]--Mason Inlet

Tidal Channel

Arenaceous

Ammobaculites cf. *A. dilatatus* Cushman and Brönnimann [A]--Bogue Sound, 4 meters

Ammotium salsum (Cushman and Brönnimann) [LS]--Bogue Sound

Trochammina inflata (Montagu) [M]--Mason Inlet

Porcellaneous

Quinqueloculina cf. *Q. flexuosa* d'Orbigny [H]--Bogue Sound, 12 meters

Quinqueloculina jugosa Cushman [M]--Mason Inlet

Quinqueloculina lamarckiana d'Orbigny [H]--Bogue Sound, 12 meters

Quinqueloculina poeyana d'Orbigny [H] [M]--Bogue Sound, 12 meters; Mason Inlet

Quinqueloculina seminula (Linné) [A]--Bogue Sound, 4 meters

Quinqueloculina cf. *Q. seminula* (Linné) [H] [M]--Bogue Sound, 12 meters; Mason Inlet

Hyaline

Planktic

Globigerinoides cf. *G. ruber* (d'Orbigny) [M]--Mason inlet (more commonly associated with open ocean environments)

Globigerinoides cf. *G. sacculifera* (Brady) [H]--Bogue Sound, 12 meters

Miscellaneous plankton (*Globigerinoides conglobatus*, *Globigerinoides ruber*, *Globigerinoides sacculifera*, *Globoquadrina dutertrei*, *Globorotalia menardi*, *Globorotalia truncatulinoides*, *Pulleniatina obliquiloculata*--probably dumped from the research vessel Eastward after an open ocean voyage, as noted by Akers, 1971, p. 152)

Benthic

Ammonia beccarii (Linné) [A] [LS] [M]--Bogue Sound, low tide; Mason Inlet

Ammonia tepida (Cushman) [H]--Bogue Sound, 12 meters

Cibicides concentricus (Cushman) [H]--Bogue Sound, 12 meters

Discorbis subaraucana Cushman [H]--Bogue Sound, 12 meters

Guttulina australis (d'Orbigny) [H]--Bogue Sound, 12 meters

Elphidiella mexicana (Kornfeld) [M]--Mason Inlet

Elphidium clavatum Cushman [LS]--Bogue Sound [LS]

Elphidium gunteri Cole [A] [H]--Bogue Sound, low tie to 12 meters. NOTE--Akers, 1971, p. 152, refers to "*E. gentri*". This may be a misprint as there is no *E. gentri* in the Catalogue of Foraminifera (Ellis and Messina, 1940 *et seq.*)

Elphidium poeyanum (d'Orbigny) [H]--Bogue Sound, 12 meters

Nonion grateloupi (d'Orbigny) [H]--Bogue Sound, 12 meters

Protelphidium tisburyense (Butcher) [LS]--Bogue Sound

Poroeponides repanda (Fichtel and Moll) [M]--Mason Inlet

APPENDIX II--NON-ESTUARINE FORAMINIFERA

The following faunal lists include only those species of Foraminifera which were reported as common to abundant by the indicated investigator. In cases where absolute numbers were presented, 10 or more specimens are included in the lists. Where percentages are given, abundances of 10% or greater are included. Notations are taken from the following indicated authors.

Symbols used:

- [A] = Akers (1971)
- [C] = Cushman (1918-1931)
- [G] = Grossman (1967)
- [H] = Hadley (1936)
- [L] = some specimens living
- [Mi] = Miller (1953)
- [Mu] = Murray (1969)
- [S] = Schnitker (1971)
- [Wi] = Wilcoxin (1964)
- [Wo] = Workman (1981)

Intertidal Beach and Surf

- Arenaceous--no common or abundant species reported
- Porcellaneous
  - *Quinqueloculina* cf. *Q. flexuosa* d'Orbigny [H]--beach
  - *Quinqueloculina jugosa* Cushman [Mi]--surf
  - *Quinqueloculina* cf. *Q. seminula* (Linné) [H]--beach
- Hyaline
  - Planktic--no common or abundant species reported
  - Benthic
    - *Ammonia parkinsoniana* (d'Orbigny) [H]--beach
    - *Cibicides concentricus* (Cushman) [H]--beach
    - *Cibicides* cf. *C. concentricus* (Cushman) [Mi]--surf
    - *Elphidium gunteri* Cole [H]--beach
    - *Elphidium poeyanum* (d'Orbigny) [H]--beach
    - *Florilus* aff. *F. auriculus* (Heron-Allen and Earland) [Mi]--surf (Note: Miller referred the species to *Nonionella*)

Marine Delta

- Arenaceous--no common or abundant species reported
- Porcellaneous
  - *Quinqueloculina jugosa* Cushman [G]
  - *Quinqueloculina lamarckiana* d'Orbigny [G] (encountered at most stations, but not very common)
- Hyaline
  - Planktic
    - *Globigerina bulloides* d'Orbigny [G] (rare, except at one station on the southeast side of Ocracoke delta)

Benthic
    Elphidium brooklynense Shupack [G]
    Elphidium clavatum Cushman [G]

Shallow Shelf North of Cape Hatteras

Arenaceous--no common or abundant species reported
Porcellaneous--no common or abundant species reported
Hyaline
    Planktic--no common or abundant species reported
    Benthic
        Elphidium clavatum Cushman [Wo]--9 meters
        Elphidium selseyense (Heron-Allen and Earland) [Wo]--9 meters

Shallow Shelf South of Cape Hatteras

Note: Murray (1969) did not give depth data. Depths are estimated based on Schnitker's (1971) depth data at nearby stations and rounded off to the nearest 5 meters.

Arenaceous
    Placopsilina confusa Cushman [S]--15 meters
Porcellaneous
    Quinqueloculina cf. *Q. flexuosa* d'Orbigny [H]--9 meters
    Quinqueloculina jugosa Cushman [Wo]--9 meters
    Quinqueloculina lamarckiana d'Orbigny [H] [Mu] [Wo]--9 to 15 meters [L]
    Quinqueloculina lata Terquem [Mu]--10 meters [L]
    Quinqueloculina poeyana d'Orbigny [H]--9 meters
    Quinqueloculina seminula (Linné) [A] [Wi]--11 to 15 meters
Hyaline
    Planktic
        Globigerinoides ruber (d'Orbigny) [Wi]--15 meters
        Globigerinoides sacculifera (Brady) [Wi]--15 meters
        Globigerinoides cf. *G. sacculifera* (Brady) [H]--9 meters
    Benthic
        Ammonia beccarii (Linné) [A] [Mu] [S]--10 to 12 meters [L]
        Ammonia tepida Cushman [H] [Wi] [Wo]--7 to 15 meters
        Cibicides concentricus (Cushman) [H] [Mu]--9 to 15 meters
        Discorbis subaraucana Cushman [H]--9 meters
        Elphidium clavatum Cushman [S]--12 meters
        Elphidium galvestonense Kornfeld [Wi]--11 to 15 meters
        Elphidium gunteri Cole [A] [H] [Wo]--7 to 11 meters [L]
        Elphidium incertum (Williamson) [H]--9 meters
        Elphidium limatulum Copeland [Wo]--7 to 13 meters [L]
        Elphidium poeyanum (d'Orbigny) [H] [Mu]--9 to 15 meters
        Elphidium selseyense (Heron-Allen and Earland) [Wo]--7 to 13 meters
        Elphidium spp. [Mu]--15 meters [L]
        Florilus grateloupi (d'Orbigny) [H] [Mu]--9 to 15 meters [L]
        Guttulina australis (d'Orbigny) [H]--9 meters

- Hanzawaia concentrica (Cushman) [A]--11 meters

Middle Shelf North of Cape Hatteras

Note: Murray (1969) did not give depth data. Depths are estimated based on Schnitker's (1971) depth data at nearby stations and rounded off to the nearest 5 meters.

- Arenaceous
  - Eggerella advena (Cushman) [Mu] [Wo]--19 to 40 meters [L]
  - Liebusella sp. [Wo]--23 meters
  - Placopsilina confusa Cushman [S]--20 meters
  - Reophax atlanticus (Cushman) [S]--20 to 50 meters [L]
  - Textularia sp. [Wo]--17 meters
- Porcellaneous
  - Quinqueloculina seminula (Linné) [S]--20 to 38 meters [L]
- Hyaline
  - Planktic
    - Globigerina bulloides d'Orbigny [S]--60 meters
    - Globigerinoides ruber (d'Orbigny) [S]--60 meters
  - Benthic
    - Ammonia tepida (Cushman) [Wo]--17 meters [L]
    - Asterigerinata pulchella (Parker) [S]--26 meters [L]
    - Brizalina sp. [Mu]--35 to 40 meters [L]
    - Buliminella elegantissima (d'Orbigny) [Mu]--40 meters [L]
    - Cibicides bradyi (Trauth) [S]--20 to 50 meters
    - Cibicides concentricus (Cushman) [C] [Mu]--29 to 40 meters
    - Elphidiella mexicana (Kornfeld) [S]--38 meters
    - Elphidium advenum (Cushman) [Wo]--18 meters
    - Elphidium clavatum Cushman [Mu] [S] [Wo]--18 to 60 meters [L]
    - Elphidium poeyanum (d'Orbigny) [Mu]--30 meters
    - Elphidium selseyense (Heron-Allen and Earland) [Wo]--17 to 23 meters
    - Florilus auriculus (Heron-Allen and Earland) [S]--20 meters
    - Fursenkoina fusiformis (Williamson) [S]--50 meters [L]
    - Globobulimina spinescens (Brady) [C]--29 meters
    - Guttulina lactea (Walker and Jacob) [S]--26 meters [L]
    - Hanzawaia concentrica (Cushman) [S]--19 to 38 meters [L]
    - Lagena distoma Parker and Jones [C]--29 meters
    - Nonionella sp. [Mu]--35 to 50 meters [L]
    - Planulina exorna Phleger and Parker [S]--38 meters
    - Planulina ornata (d'orbigny) [S]--22 to 32 meters
    - Reussella atlantica Cushman [S]--32 meters
    - Rosalina spp. [Mu]--40 meters
    - Stetsonia minuta Parker [Mu]--35 meters [L]
    - Uvigerina peregrina Cushman [C]--29 meters
    - Webbinella concava (Williamson) [S]--22 to 23 meters

Middle Shelf South of Cape Hatteras

Note: Murray (1969) did not give depth data. Depths are estimated based on Schnitker's (1971) depth data at nearby stations and rounded off to the nearest 5 meters.

- Arenaceous
    - *Eggerella advena* (Cushman) [Mu]--30 to 45 meters [L]
    - *Placopsilina confusa* Cushman [S]--20 to 28 meters
    - *Reophax atlanticus* (Cushman) [S]--20 meters
    - *Reophax scorpiurus* Montfort [S]--25 to 30 meters
    - *Textularia secanensis* Lalicker and McCulloch [Wi]--18 to 41 meters
    - *Trochammina compacta* Parker [Mu]--45 meters [L]
    - *Trochammina ochracea* (Williamson) [MU]--20 meters [L]
    - *Trochammina pacifica* Cushman [Wi]--30 meters
- Porcellaneous
    - *Calcituba decorata* (Heron-Allen and Earland) [S]--23 to 28 meters
    - *Peneroplis carinatus* d'Orbigny [Mu]--35 meters
    - *Peneroplis proteus* d'Orbigny [S] [Wi]--22 to 44 meters
    - *Quinqueloculina akneriana* d'Orbigny [Wi]--24 meters
    - *Quinqueloculina compacta* Cushman [Wi]--26 meters
    - *Quinqueloculina compta* Cushman [S]--17 meters
    - *Quinqueloculina lamarckiana* d'Orbigny [S] [Wi] [Wo]--16 to 41 meters
    - *Quinqueloculina seminula* (Linné) [S] [W]i--17 to 57 meters
    - *Triloculina trigonula* (Lamarck) [Wi]--30 meters
- Hyaline
    - Planktic
        - *Globigerina bulloides* d'Orbigny [S] [Wi]--18 to 55 meters
        - *Globigerina eggeri* Rhumbler [Wi]--20 to 41 meters
        - *Globigerinoides ruber* (d'Orbigny) [S] [Wi]--18 to 55 meters
        - *Globigerinoides sacculifera* (Brady) [Wi]--18 to 41 meters
        - *Globigerinoides trilobus* (Reuss) [S]--33 to 55 meters
        - *Globorotalia menardi* (d'Orbigny) [Wi]--40 to 41 meters
        - *Globorotalia truncatulinoides* (d'Orbigny) [Wi]--20 meters
        - *Hastigerina aequilateralis* (Brady) [Wi]--26 to 41 meters
        - *Neogloboquadrina dutertrei* (d'Orbigny) [S]--55 meters (assigned by Schnitker to *Globigerina*)
        - *Pulleniatina obliquiloculata* (Parker and Jones) [Wi]--20 meters
    - Benthic
        - *Ammonia tepida* (Cushman) [Wi] [Wo]--16 to 26 meters
        - *Asterigerina carinata* d'Orbigny [S] [Wi]--22 to 36 meters
        - *Bolivina pulchella* (d'Orbigny) [Wi]--30 meters
        - *Brizalina paula* (Cushman and Cahill) [Wi]--20 meters (placed in *Bolivina* by Wilcoxin)
        - *Brizalina* sp. [Mu]--20 to 30 meters [L]

- *Cancris auricula* (Fichtel and Moll) [Mu]--45 meters [L]
- *Caribeanella polystoma* Bermudez [S]--26 meters
- *Cassidulina subglobosa* Brady [Wi]--40 meters
- *Cibicides bradyi* (Trauth) [S]--42 meters
- *Cibicides concentricus* (Cushman) [M]--20 to 45 meters [L]
- *Cibicides mollis* Phleger and Parker [Wi]--18 to 41 meters
- *Discorbis floridanus* Cushman [Wi]--18 meters
- *Discorbis lomaensis* (Bandy) [Wi]--22 meters (referred by Wilcoxin to *Rotorbinella*)
- *Elphidium clavatum* Cushman [Mu] [S]--16 to 57 meters
- *Elphidium discoidale* (d'Orbigny) [Wi]--18 to 41 meters
- *Elphidium limatulum* Copeland [Wo]--16 to 17 meters
- *Elphidium rugulosum* Cushman and Wickenden [Wi]--30 meters
- *Elphidium subarcticum* Cushman [Wi]--18 to 30 meters
- *Florilus grateloupi* (d'Orbigny) [Mu]--30 meters [L]
- *Florilus atlanticus* (Cushman) [Wi]--24 to 26 meters (assigned to *Nonionella* by Wilcoxin)
- *Fursenkoina* sp. [Mu]--30 to 45 meters [L]
- *Hanzawaia concentrica* (Cushman) [S] [Wi]--18 to 33 meters
- *Planulina exorna* Phleger and Parker [Wi]--40 to 41 meters
- *Planulina ornata* (d'orbigny) [S]--29 to 42 meters
- *Rosalina* spp. [Mu]--20 to 35 meters [L]
- *Stetsonia minuta* Parker [Mu]--30 to 35 meters [L]
- *Trifarina angulosa* (Williamson) [Mu]--20 to 45 meters [L]
- *Trifarina bradyi* Cushman [Wi]--30 meters

Outer Shelf North of Cape Hatteras

- Arenaceous
  - *Reophax atlanticus* (Cushman) [S]--70 to 90 meters [L]
  - *Tholosina vesicularis* (Brady) [C]--122 meters
- Porcellaneous--no common to abundant species reported
- Hyaline
  - Planktic
    - *Globigerina borealis* (Brady) [S]--70 to 140 meters (assigned by Schnitker to *G. pachyderma*. See Iaccarino, 1985, p. 300)
    - *Globigerina bulloides* d'Orbigny [S]--70 to 140 meters
    - *Globigerinoides ruber* (d'Orbigny) [S]--70 to 120 meters
    - *Globorotalia inflata* (d'Orbigny) [S]--70 to 140 meters (assigned to *Globigerina* by Schnitker)
    - *Neogloboquadrina dutertrei* (d'Orbigny) [S]--120 meters (assigned to *Globigerina* by Schnitker)
  - Benthic
    - *Bulimina marginata* d'Orbigny [S]--70 to 140 meters
    - *Cancris sagra* (d'Orbigny) [S]--90 meters

- *Cibicides pseudoungerianus* (Cushman)--70 meters
- *Elphidium clavatum* Cushman [S]--70 to 140 meters
- *Islandiella subglobosa* (Brady) [S]--70 to 140 meters
- *Robulus orbicularis* d'Orbigny [S]--70 to 120 meters (assigned to *Lenticulina* by Schnitker)

Outer Shelf South of Cape Hatteras

- Arenaceous--no common or abundant species reported
- Porcellaneous
  - *Quinqueloculina seminula* (Linné) [S]--70 to 122 meters
- Hyaline
  - Planktic
    - *Globigerina bulloides* d'Orbigny [S]--75 to 159 meters
    - *Globigerinoides ruber* (d'Orbigny) [S] [Wi]--65 to 159 meters
    - *Globigerinoides sacculifera* (Brady) [Wi]--145 meters
    - *Globigerinoides trilobus* (Reuss) [S]--75 to 125 meters
    - *Globigerinita glutinata* (Egger) [S]--75 meters
    - *Globorotalia menardi* (d'Orbigny) [S] [Wi]--140 to 145 meters
    - *Neogloboquadrina dutertrei* (d'Orbigny) [S] [Wi]--65 to 122 meters (Schnitker put the species in *Globigerina*. See Iaccarino, 1985. Wilcoxin recognized the synonym *Globigerina eggeri* Rhumbler. See Bolli and Saunders, 1985, p. 211)
  - Benthic
    - *Amphistegina lessoni* d'Orbigny [S]--70 meters
    - *Angulogerina angulosa* (Williamson) [Wi]--145 meters
    - *Brizalina paula* (Cushman and Cahill) [Wi]--145 meters (placed in *Bolivina* by Wilcoxin)
    - *Cassidulina subglobosa* Brady [Wi]--145 meters
    - *Elphidium clavatum* Cushman [S]--65 to 159 meters
    - *Hanzawaia concentrica* (Cushman) [S]--65 to 122 meters
    - *Islandiella subglobosa* (Brady) [S]--155 meters
    - *Rosalina globularis* d'Orbigny [S]--125 meters

Upper Continental Slope

- Arenaceous
  - *Clavulina flintia* Cushman [C]--218 meters
  - *Cyclammina compressa* Cushman [C]--943 meters
  - *Psammosphaera fusca* Schultze [C]--305 meters
  - *Tholosina vesicularis* (Brady) [C]--260 meters
- Porcellaneous
  - *Pyrgo subsphaerica* (d'Orbigny) [Wi]--483 meters
  - *Quinqueloculina seminula* (Linné) [Wi--338 to 669 meters
- Hyaline
  - Planktic
    - *Globigerina borealis* (Brady) [Wi]--338 meters (Placed by Wilcoxin in *G. pachyderma*. See Iaccarino, 1985, p. 300)
    - *Globigerina bulloides* d'Orbigny [Wi]--669 to 793 meters
    - *Globigerina dubia* Egger [C]--260 meters

- *Globigerinoides conglobatus* (Brady) [C]--260 meters (Cushman put the species in *Globigerina*)
- *Globigerinoides ruber* (d'Orbigny) [C] [Wi]--260 to 793 meters
- *Globigerinoides sacculifera* (Brady) [C] [Wi]--260 to 793 meters
- *Globorotalia inflata* (d'orbigny) [C]--260 to 943 meters (Cushman put the species in *Globigerina*)
- *Globorotalia menardi* (d'Orbigny) [C] [Wi]--307 to 752 meters
- *Globorotalia truncatulinoides* (d'Orbigny) [Wi]--483 meters
- *Hastigerina aequilateralis* (Brady) [C] [Wi]--307 to 752 meters
- *Neogloboquadrina dutertrei* (d'Orbigny) [Wi]--338 to 752 meters (Wilcoxin put the species in *Globigerina* and also recognized the synonym *Globigerina eggeri* Rhumbler. See Bolli and Saunders, 1985, p. 211)
- *Orbulina universa* d'Orbigny [C]--260 to 307 meters
- *Pulleniatina obliquiloculata* (Parker and Jones) [C] Wi]--307 to 752 meters

Benthic

- *Angulogerina angulosa* (Williamson) [Wi]--338 to 752 meters
- *Brizalina paula* (Cushman and Cahill) [Wi]--483 to 793 meters (put in *Bolivina* by Wilcoxin)
- *Bulimina marginata* d'Orbigny [Wi]--752 meters
- *Cassidulina subglobosa* Brady [Wi]--483 to 793 meters
- *Cibicides mollis* Phleger and Parker [Wi]--338 meters
- *Marginulina bachei* Bailey [C]--218 meters
- *Planulina ariminensis* d'Orbigny [Wi]--338 to 752 meters
- *Reussella atlantica* Cushman [Wi]--752 meters
- *Robulus lucidus* (Cushman) [C]--218 meters (assigned to *Cristellaria* by Cushman)
- *Robulus occidentalis* (Cushman) [Wi]--338 meters
- *Uvigerina hispidocostata* Cushman and Todd [Wi]--752 to 793 meters

Lower Continental Slope

Arenaceous

- *Astrorhiza angulosa* Brady [C]--2982 meters
- *Astrorhiza arenarea* Norman [C]--1241 to 1428 meters
- *Bathysiphon discreta* (Brady) [C]--1241 meters (placed in *Rhabdammina* by Cushman)
- *Bathysiphon filiformis* Sars [C]--1241 to 1428 meters
- *Crithionina pisa* Goës [C]--1241 to 1428 meters
- *Cyclammina compressa* Cushman [C]--1541 to 1715 meters
- *Cyclammina pauciloculata* Cushman [C]--1172 to 1441 meters
- *Discammina compressa* (Goës) [C]--1172 meters (Cushman identified this species as *Haplophragmoides emaciatum* (Brady). See Barker, 1960, p. 68)

  - *Haplophragmoides subglobulosum* Sars [C]--1172 meters
  - *Martinottiella communis* (d'Orbigny) [C]--1172 meters (Cushman placed the species in *Clavulina*)
  - *Proteonina difflugiformis* (Brady) [C]--1715 meters
  - *Reophax dentilinaformis* Brady [C]--1172 meters
  - *Rhabdammina cornuta* (Brady) [C]--1541 meters
  - *Rhizammina indivisa* Brady [C]--1431 meters
  - *Saccammina sphaerica* Sars [C]--1172 meters
  - *Valvulina conica* (Parker and Jones) [C]--1172 to 1541 meters
- Porcellaneous--no common or abundant species reported
- Hyaline
  - Planktic
    - *Globigerina dubia* Egger [C]--1172 to 1715 meters
    - *Globigerinoides conglobatus* (Brady) [C]--1172 to 1715 meters (Cushman put the species in *Globigerina*)
    - *Globigerinoides ruber* (d'Orbigny) [C]--1715 meters
    - *Globigerinoides sacculifera* (Brady) [C]--1715 meters (Cushman put the species in *Globigerina*)
    - *Globorotalia inflata* (d'Orbigny) [C]--1172 to 1715 meters
    - *Globorotalia menardi* (d'Orbigny) [C]--1441 meters
    - *Globorotalia tumida* (Brady) [C]--1441 meters
    - *Orbulina universa* d'orbigny [C]--1172 to 1715 meters
  - Benthic
    - *Bulimina inflata* Seguenza [C]--1441 meters
    - *Bulimina marginata* d'Orbigny [C]--1172 meters
    - *Globobulimina pyrula* (d'Orbigny) [C]--1715 meters (Cushman put the species in *Bulimina*)
    - *Cibicides pseudoungerianus* (Cushman) [C]--1441 meters
    - *Uvigerina peregrina* Cushman [C]--1441 to 1715 meters

Continental Rise

- Arenaceous
  - *Hormosina globulifera* Brady [C]--3739 meters
  - *Trochammina globulosa* Cushman [C]--3739 meters
  - *Trochammina subturbinata* Cushman [C]--3739 meters
- Porcellaneous--no common or abundant species reported
- Hyaline
  - Planktic
    - *Globigerina bulloides* d'Orbigny [C]--3739 meters
    - *Globigerina dubia* Egger [C]--3739 meters
    - *Globigerinoides conglobatus* (Brady) [C]--3739 meters (Cushman put the species in *Globigerina*)
    - *Globigerinoides ruber* (d'Orbigny) [C]--3739 meters
    - *Globigerinoides sacculifera* (Brady) [C]--3739 meters (Cushman put the species in *Globigerina*)
    - *Globorotalia inflata* (d'Orbigny) [C]--3739 meters
    - *Globorotalia menardi* (d'Orbigny) [C]--3739 meters
    - *Globorotalia truncatulinoides* (d'Orbigny) [C]--3739 meters
    - *Globorotalia tumida* (Brady) [C]--3739 meters
    - *Orbulina universa* d'orbigny [C]--3739 meters

Benthic--no common or abundant species reported

Hatteras Abyssal Plain
Arenaceous--no common or abundant species reported
Porcellaneous--no common or abundant species reported
Hyaline
- Planktic
    - *Globigerina dubia* Egger [C]--4592 to 5391 meters
    - *Globigerinoides sacculifera* (Brady) [C]--4592 to 4706 meters (Cushman put the species in *Globigerina*)
    - *Globorotalia hirsuta* (d'Orbigny) [C]--4706 meters
    - *Globorotalia menardi* (d'Orbigny) [C]--4592 to 4706 meters
    - *Globorotalia truncatulinoides* (d'Orbigny) [C]--3739 meters
    - *Globorotalia tumida* (Brady) [C]--3739 meters
    - *Orbulina universa* d'orbigny [C]--3739 meters
    - *Pulleniatina obliquiloculata* (Parker and Jones) [C]--5391 meters
- Benthic--no common or abundant species reported

CONTINENTAL SHELF MOLLUSCAN ZOOGEOGRAPHY OF NORTH AND SOUTH CAROLINA

Hugh J. Porter
Institute of Marine Sciences
University of North Carolina
Morehead City, North Carolina 28557

ABSTRACT

The marine molluscan fauna of North and South Carolina is re-examined in relation to recent collections and zoogeographic literature on Middle Atlantic Bight fauna. Its mollusca are described belonging to the Arctic-Boreal, Boreal, Transhatteran, Carolinian, Caribbean, Bathyal, and Abyssal provinces. Of these the fauna of the Carolinian, Caribbean, and Boreal in these waters is imperfectly known.

About 1550 different kinds of mollusca are known from marine and estuarine waters of North and South Carolina. Recent common mollusca are listed by province. Molluscan habitat and feeding types frequently found within each province are discussed.

The Transhatteran province in North and South Carolina waters is characterized by and found along a southern flowing nearshore current. Offshore of these same waters, the Caribbean province is found along the northward flowing Gulf Stream. The Carolinian province occurs between these currents over the mid-shelf area. There the waters move in an on-shore off-shore counterclockwise direction. Flushing time of these waters is believed sufficient to permit larvae spawned there to metamorphosis in the same waters and thus perpetuate the local Carolinian province fauna. Where both currents and associated provinces interact with the Carolinian mid-shelf fauna, considerable overlapping of province faunas takes place.

INTRODUCTION

Recent molluscan papers by Franz and Merrill (1980a and 1980b) effectively redefined the zoogeography of the continental shelf area north of Cape Hatteras using the following faunal groupings: Arctic-Boreal, Boreal, and Transhatteran. These were based on minimum and maximum depth ranges, geographical ranges, and geological origin. They further discussed the relationship of these regions to the Boreal, Carolinian, Transatlantic, and Virginian regions of Coomans (1962) and Johnson (1934). The latter authors had Cape Hatteras as a southern boundary of the Virginian region and the northern boundary of the Carolinian region. The Transatlantic region of Franz and Merrill (1980a and 1980b) was now designated to include species, not having the cape as its northern or southern boundary, but including species occurring from New England waters south into Florida and New Mexico waters. Differences between Transhatteran, Carolinian, and the Caribbean provinces were not examined by Franz and Merrill (1980a and 1980b).

Cerame-Vivas and Gray (1966) divided the North Carolina marine area into three biogeographic provinces: Virginian, Carolinian, and Tropical [Caribbean]. Relative areas covered by these faunal provinces were additionally illustrated by Abbott (1968). Cerame-Vivas and Gray recognized that Cape Hatteras was more a barrier between the Virginian and Tropical provinces than it was between the Virginian and Carolinian. The barrier was described in terms of water temperature differences, coastal current circulation, and the temperature-current interrelationships of larval-adult survival, reproduction, and larval drift patterns. Intrusions of Virginian or Florida currents over this barrier caused species to overlap into provinces north or south of their viable ranges. The Carolinian and Tropical provinces were thought to be separable and existing as distinct areas. However, statistical analysis of samples, taken along a transect just south of Cape Hatteras (near Cape Lookout) from 0-200 m depth by Day et al. (1971), was unable to confirm a separation between the Carolinian and Tropical (Caribbean) provinces of Cerame-Vivas and Gray. Johnson (1934) and later Rehder (1954) pointed out that the area of transition between the Carolinian and Caribbean provinces was mainly speculative.

This paper attempts to: redefine or separate the Transhatteran, Carolinian, and Caribbean faunal provinces off the coast of the Carolinas, to identify their major molluscan elements in those waters, and discuss faunal interrelationships within them.

Menzies et al., 1973 is followed in use of the terms "faunal province" and "faunal zone"; faunal province is defined as a major division of a realm and faunal zone as a subdivision of a province.

METHODS

North Carolinian molluscan records in the UNC-IMS mollusk collection that resulted from efforts aboard the R/V's ADVANCE II, CAPE HATTERAS, DAN MOORE, EASTWARD, ENSIGN, MACHAPUNGA, OREGON, CAPRICORN, etc. plus a number of offshore commercial trawlers from dredge, trawl, scuba, echinoderm stomach samples, etc. are the initial data base (Porter, 1947b). Added to that data base are North and South Carolina records published since 1974 or not previously included, such as: Abbott, 1974; Emerson and Jacobson, 1976; Eyster, 1980; Merrill and Petit, 1965; Mikkelsen and Mikkelsen, 1984; Porter, 1974a; Porter and Safrit, 1981; Porter and Schwartz, 1981; Rehder, 1981; Rios, 1975; Scheltema, 1985; Schwartz and Porter, 1976; Shoemaker et al., 1978. A 1987 summarization of North and South Carolina mollusks housed in the UNC-IMS collection, along with approximate numbers of collections per species; minimum and maximum collection depths of each live-collected and non-live collected material for each species, geographical range, and North and South Carolina published depths are included. The latter follow Abbott, 1974; Emerson and Jacobson, 1976; Franz and Merrill, 1980a; Merrill et al., 1978; Porter, 1974b; Rehder, 1981 plus specific citations as noted in Tables 1, 3-6.

Taxonomic order follows Vaught (1989). Genus and species generally follow Turgeon et al. (1989).

Depth zone categories - <0-10 (m); 11-45; 46-80; 81-100; 101-246; 247-445; 446-940; >940 (note Tables 1,3-6) - were modified from those used by Franz and Merrill (1980a) and Menzies et al. (1973). General habitat and feeding type was included where possible for each species.

Molluscan density records of species found in the Carolina coastal region are not available from the UNC-IMS collection. As an alternative density each species was assigned a given rating equal to the product of the number of its occurrences in the UNC-IMS collection and estimated number of original published records in North or South Carolina for it. The latter was based on the number of original citations per species in Porter, 1974b and recorded since then.

All species were assigned to one of four density categories, based on the density rating of each. Density values and their category were: <3 non-recent = "vr" [very rare]; 3-5 (2-5 if recent live collection or publication) = "s" [scarce]; 6-20 = "c" [common]; >20 = "a" [abundant]. Density values were set so that each zoogeographic fauna would contain some of each density and that density categories would reflect this author's knowledge of the molluscan fauna in the Carolinas.

Each species was assigned to one or more of the following faunal provinces:

Arctic-Boreal

The Arctic-Boreal province occurs north of Newfoundland, its southern limits are near Cape Cod, although about 25% of the fauna occurs farther south in deeper waters. It contains amphiatlantic and North Pacific species arising during late Pliocene to early Pleistocene (Franz and Merrill, 1980b) and contains a large proportion of species of deep-water capabilities (7.7% <101 m maximum depth and 76.9% having maximum depths >200 m - data, Franz and Merrill, 1980a).

Boreal

The Boreal province, Cape Cod to Cape Hatteras, contains transarctic migrants from the Pliocene, amphiatlantic species, and endemic species from the Miocene (Franz and Merrill, 1980b). Most species occupy 100-200 m depths (25.0% <101 m maximum depth and 28.6% with maximum depths over 200 m - data, Franz and Merrill, 1980a). Assignment of a species to either the Arctic-Boreal or Boreal provinces was difficult when its northern boundary was north of Cape Cod, its southern boundary was near Cape Hatteras, and when paleontological history was not known.

Transhatteran

Molluscan members of this province range north to the Gulf of St. Lawrence and south of Cape Hatteras. No Pacific or amphiatlantic species are present. Geologically, these species are closely related with or derived from warm-temperate American Miocene species (Franz and Merrill, 1980b). Populations are maintained in thermally unstable, shallow waters north and south of Cape Hatteras (Franz and Merrill, 1980a). Depth data (Franz and Merrill, 1980a) indicates that the Transhatteran province occupies almost equally all depth categories: <10 m, 8.8%; 10-50 m, 19.1%; 51-100 m, 29.4%; 101-200 m, 16.2%; >200 m, 26.9%. Franz and Merrill (1980a) further divided the Transhatteran into two subgroups: #2 had northern limits north of Cape Cod and frequently was from shallow waters; #1 had its northern limits south of Cape Cod and generally was found at depths deeper than at #2.

Carolinian

The northern limit of this province is Cape Hatteras. Its range extends southward to near Palm Beach or St. Lucie Inlet near Stuart, Florida and then reappears north and west of Tampa or Cedar Keys in the Gulf of Mexico (Work, 1969). Initially, mollusks south of Cape Hatteras, found inshore of the Lithothamnion reef (80-100 m depth, Menzies et al., 1973) and not Transhatteran, were characterized here as Carolinian. Later, this outer depth boundary was moved inshore to a 62 m depth, approaching the 50 m depth Carolina Capes shelf break (Pietrafesa et al., 1985).

Caribbean

The Caribbean province lies south of Cape Hatteras over a 80-100 m depth Lithothamnion reef influenced by the Gulf Stream. Its fauna was considered by Menzies et al. (1966) to be a submerged tropical shelf faunal zone. Inshore and offshore depth boundaries are 62 and 246 m. The area offshore of the reef to about a 246 m depth, is called the "outer shelf" (Menzies et al., 1973) and species therein are believed to be Caribbean. Lyons and Collard (1947) believed one of the major differences separating the Carolina and Caribbean faunas was that the Carolinian is mainly a soft substrate inhabiting group, whereas, the Caribbean is a hard substrate fauna.

Bathyal

Inshore and offshore boundaries of the Bathyal faunal province are designated as 247 and 940 m depths. Quinn (1979) lists an Upper Bathyal zone at 180-1000 m depth. A somewhat similar area at 445-940 m depths off the Carolinas is called an "Archibenthal zone of Transition" (Menzies et al., 1973). Quinn's (1979) designation is used here in preference to the "zone of transition" of Menzies et al. zone of transition. Species in this province have, I believe, a northern boundary near Cape Hatteras.

Abyssal

The Abyssal province includes all species reported from depths >940 m. Menzies et al. (1973) considered this depth as the beginning of the "Upper Abyssal" province off the Carolinas. Some species reported from almost all depths, designated here as Abyssal, may be questioned. This and the Bathyal provinces were represented by few collections in the UNC-IMS collection.

Endemic

Species labeled endemic were known from few specimens and from waters only off the Carolinas; as such, this distribution generally precluded assignment of them of a faunal province.

RESULTS

A total of about 1550 different marine mollusca (in 220 families) are known from the waters off the Carolinas. Species recorded from live collections having densities "a" and "c", unless otherwise noted, are listed in Tables 1, 3-5 (420 species). Species listed as "Characteristic" of their province, are species considered most common and not of questionable status in their province. Species having a "s" density or "a" and "c" densities but not collected alive are listed at the addendum at the end of this paper - this includes an additional 515 species. An additional 600+ species having a "vr" density can not be listed because of space limitations of this paper.

Percent species by faunal province is indicated in Table 7. Substantial overlap of depth-zonal fauna into neighboring depth zones >247 m depth is indicated (Figures 1-3). Depth data south of Cape Hatteras was restructured to have a break at 62-63 m instead of at 80-81 m so as to provide a better separation point between the Carolinian and Caribbean provinces than was present at the 80-81 m depth. Restructured bivalve data of 63-100 and 101-246 m depth zones was similar but different from the 11-62 m data. Gastropod data had a closer relationship between the 63-100 and 101-246 m depth zones than between the 11-62 and 63-100 m zones (Figure 3).

The percentage of total species in each density category is: "vr" = 46%; "s" = 33%; "c" = 12%; and "a" = 10% (Table 8). Density percentage values are different when only live-collected species are considered [live-collected = species that have been collected alive at least once from Carolina waters]. There, percentages for "s", "c", and "a" are nearly equal and the value for "vr" is considerably less than the other three. This value is expected, for, generally if a species has been collected alive, it has sufficient density points to raise it above the "vr" density category.

Arctic-Boreal and Boreal Provinces

There were not enough Arctic-Boreal species from Carolina waters to show a depth habitat difference from Boreal species also from the Carolina waters (Table 1). Boreal gastropods were spread throughout the depth range with most occurring in depths <81 m. The Bivalvia may occur in deeper depths than the gastropods (Table 1). The few characteristic Arctic-Boreal species are: BUCCINIDAE: *Colus pubescens*; YOLDIIDAE: *Yoldia sapotilla*; and MYTILIDAE: *Modiolus modiolus*.

Characteristic Boreal species are: BUCCINIDAE: *Colus stimpsoni*; HAMINEIDAE: *Haminoea solitaria*; YOLDIIDAE: *Yoldia limatula*; MYTILIDAE: *Mytilus edulis*; TELLINIDAE: *Macoma balthica*; VENERIDAE: *Pitar morrhuanaus*; MYIDAE: *Mya arenaria*; and LYONSIIDAE: *Lyonsia hyalina*.

Transhatteran Province

Transhatteran species occupy primarily depths <101 m, with highest numbers <11 m depth (Table 3). This differed from Franz and Merrill (1980a) data where the species were found equally throughout all depths. Franz and Merrill also recorded that their Transhattern #1 species were generally found in deeper depths than were those of Transhatteran #2. There does not seem to be any depth differences between the Carolina Transhatteran #1 or #2 species (Table 3). Differences between the data of Franz and Merrill and the data presented in this paper may be partly a function of sampling differences.

Characteristic live-collected Transhatteran faunal species (densities: "a", "c") listed on Table 3 include: Transhatteran #1 - ISCHNOCHITONIDAE: *Chaetopleura apiculata*; FISSURELLIDAE: *Diodora cayenensis*; LITTORINIDAE: *Littorina irrorata*; CREPIDULIDAE: *Crepidula fornicata*, *C. plana*; NATICIDAE: *Polinices* (*Neverita*) *duplicatus*; CERITHIOPSIDAE: *Seila adamsi*; MURICIDAE: *Eupleura caudata*; COLUMBELLIDAE: *Anachis* (*Constanachis*) *avara*, *Mitrella lunata*; MELONGENIDAE: *Busycon carica*, *B. sinistrum*, *Busycon* (*Busycotypus*) *canaliculata*; PYRAMIDELLIDAE: *Odostomia* (*Boonea*) *impressa*; ACTEONIDAE: *Rictaxis punctostriatus*; OCTOPODIDAE: *Octopus vulgarus*; NUCULANIDAE: *Nuculana acuta*; ARCIDAE: *Anadora ovalis*;

MYTILIDAE: *Ischadium recurvum*; PECTINIDAE: *Chlamys* (*Argopecten*) *irradians concentricus*; CARDIIDAE: *Laevicardium mortoni*; TELLINIDAE: *Macoma tenta*; SEMELIDAE: *Abra lioica*; PSAMMOBIIDAE: *Tagalus divisus*; DONACIDAE: *Donax roemeri protracta*; and CORBULIDAE: *Corbula contracta*.

Transhatteran #2 - CERITHIIDAE: *Bittium varium*; NATICIDAE: *Natica pusilla*; MURICIDAE: *Urosalpinx cinerea*; COLUMBELLIDAE: *Anachis* (*Costanachis*) *lafresnayi*; NASSARIIDAE: *Ilyanassa obsoleta*; PYRAMIDELLIDAE: *Odostomia* (*Boonea*) *seminuda*; LOLIGINIDAE: *Loligo pealeii*; SOLEMYIDAE: *Solemya velum*; NUCULIDAE: *Nucula proxima*; MYTILIDAE: *Geukensia demissa*; OSTREIDAE: *Crassostrea virginica*; MACTRIDAE: *Mulinia lateralis*; CULTELLIDAE: *Ensis directus*; VENERIDAE: *Gemma gemma*, *Mercenaria mercenaria*; and PETRICOLIDAE: *Petricola pholadiformis*.

Carolinian and Caribbean Provinces

Characteristic Carolinian live-collected species (densities: "a", "c") from off the Carolinas (Table 4) include- TROCHIDAE: *Calliostoma pulchrum*; TURBINIDAE: *Turbo castanea*; PHASIANELLIDAE: *Tricolia thalassicola*; CERITHIIDAE: *Obtortio adamsi*; EULIMIDAE: *Melanella conoidea*, *Niso aeglees*, *Strombiformis auricinctus*; STROMBIDAE: *Strombus alatus*; TRIVIIDAE: *Trivia maltbiana*; TONNIDAE: *Tonna galea*; MURICIDAE: *Chicoreus florifer dilectus*, *C.* (*Phyllonotus*) *pomum*, *Hexaplex* (*Muricanthus*) *fulvescens*, *Murexiella levicula*; BUCCINIDAE: *Pisania tincta*; FASCIOLARIIDAE: *Fasciolaria lilium hunteria*; OLIVIDAE: *Oliva sayana*; MARGINELLIDAE: *Marginella aureocinctus*; TEREBRIDAE: *Terebra concava*; TURRIDAE: *Cerodrillia simpsoni*, *Cryoturris citronella*, *Kurtziella rubella*, *Nanodiella oxia*; ARCIDAE: *Anadara floridana*, *Arca zebra*, *Barbatia candida*, *B. domingensis*; MYTILIDAE: *Brachidontes exustus*, *Lithophaga aristata*, *L. bisulcata*, *Modiolus americanus*, *Musculus lateralis*; PTERIIDAE: *Pteria colymbus*; CHAMIDAE: *Arcinella cornuta*; CARDIIDAE: *Laevicardium laevigatum*, *Trachycardium egmontianum*; MACTRIDAE: *Spisula raveneli*; TELLINIDAE: *Tellina aequistriata*, *T. sybaritica*; SEMELIDAE: *Semele proficua*; VENERIDAE: *Callista* (*Macrocallista*) *nimbosa*; and PHOLADIDAE: *Martesia cuneiformis*.

Caribbean - TROCHIDAE: *Microgaza rotella inornata*; CERITHIIDAE: *Litiopa melanostoma*; CYPRAEIDAE: *Cypraea spurca acicularis*; NATICIDAE: *Polinices lacteus*; RANELLIDAE; *Distorsio constricta mcgintyi*; OLIVIDAE: *Olivella watermani*; PECTINIDAE: *Chlamys benedicti*; TELLINIDAE: *Tellina americana*; VENERIDAE: *Callista eucymata*, *Chione cancellata mazycki*, *C. litilirata*, *Pitar fulminatus*; and DENTALIIDAE: *Dentalium laqueatum*.

Bathyal and Abyssal Provinces

Characteristic live-collected Bathyal and Abyssal faunal species (densities: "a", "c", and "s"; Table 5 include ["s" and several "vr" densities included as provinces represented less than 1% of all samples in UNC-IMS collection]: Bathyal RISSOIDAE: ?Alvania syngenes [density = vr]; CASSIDAE: Oocorys sulcata; BUCCINIDAE: Mohnia carolinensis? [density = vr]; TURRIDAE: Drillia cf. oleacina; PYRAMIDELLIDAE: Pyramidella lissa; and CUSPIDARIIDAE: Cardiomya costellata?.

Abyssal - TROCHIDAE: Solariella infundibulum, SKENEIDAE: Ganesa proxima?; BUCCINIDAE: Colus obesus, ?Mohnia caelatulus; TURRIDAE: Gymnobela agassizii, Oenopota subvitreus, Pleurotomella atypha, P. bairdii; LIMACINIDAE: Limacina inflata, L. lesueurii; CAVOLINIIDAE: Clio recurva, Creseis acicula, C. virgula, Diacria quadridentata, D. trispinosa, Hyalocylix striata; PERACLIDAE: Peracle reticulata, P. triacantha; ARGONAUTIDAE: Argonauta argo; MALLETIIDAE: Malletia obtusa; SEMELIDAE: Abra longicallis americana; and DENTALIIDAE: Dentalium meridionale verrilli.

Endemic and Other Faunas

There are 17 endemic live-collected species known from Carolinian marine waters, see Table 6 for listing of them. The total number of endemic species from Carolinian province waters is 63 if mollusks known from dead shell are included.

At least 110 species (including three live-collected forms) could not be assigned to any faunal province. There were also 44 pelagic species of world-wide distribution which could not be assigned to any faunal province. Most of these and all of the unknown fauna species were of "s" or "vr" densities.

Range Extensions

One Arctic-Boreal and three Boreal province species (Table 1) were recorded with new southern ranges: MYTILIDAE: Modiolus modiolus; PYRAMIDELLIDAE: Odostomia (Boonea) bisuturalis, O. (Fargoa) gibbosa; and NUCULIDAE: Nucula delphinodonta.

Nine Carolinian and Caribbean province species (Table 4) with new northern ranges are: EULIMIDAE: Melanella conoidea; BUCCINIDAE: Engina corinnae; OLIVIDAE: Olivella pusilla, O. watermani, MITRIDAE: Mitra fulgurita?; TURRIDAE: Cryoturris fargoi, Mangelia (Glyphoturris) rugirima; PYRAMIDELLIDAE: Odostomia emeryi; and PECTINIDAE: Chlamys benedicti.

Another possible 14 range extensions are within the "s" density species listed in the Addendum.

Overlapping Provinces

Total species occurrences (2121), number of species per faunal group, and density per faunal group are recorded in Table

8. As mentioned earlier, 1548 different species are recorded off North and South Carolina waters. The difference is caused by species with dual faunal province affinities (=overlap). Of known species collected alive, the Carolinian province has the highest density (39%) of total species collected alive (Table 8). The combined Transhatteran fauna has the second highest density followed closely by the Caribbean fauna. Of the total known fauna, the Caribbean has the highest density (29%) followed closely by the Carolinian, Abyssal, and then the Transhatteran faunas. The Arctic-Boreal and Bathyal faunas had the lowest density of living and total faunal species.

Little change was present in the above density order if the species were considered by their faunal or overlapping faunal provinces (Table 7). The "Carolinian + Caribbean" group however was third and fourth highest in density when live collected and total species were considered. Twenty-six percent of both live-collected and total species groups were in overlapping faunal provinces.

Molluscan species present in Carolina waters north of Cape Hatteras are composed of: Arctic-Boreal - 5%, Boreal - 14%, Transhatteran - 30%, Abyssal - 40%, and Endemic - 4%. An additional 8% (5% Carolinian and 3% Caribbean) are representatives north of their expected range. Species south of Cape Hatteras are: Transhatteran - 16%, Carolinian - 22%, Caribbean - 29%, Bathyal - 6%, Abyssal - 21%, and again Endemic - 4%; 3% (1% Arctic-Boreal and 2% Boreal) are species south of their geographic range (Table 9). Of total Carolinian Arctic-Boreal and Boreal species, 27 and 38% were south of Cape Hatteras (83 and 75% of live-collected, "a" and "c" density species). Only 14% of the Carolinian and 6% of the Caribbean species ranged north of Cape Hatteras (23 and 22% of live-collected, "a" and "c" density species).

Habitat and Feeding Types

Percent habitat and feeding types by faunal province for the Gastropoda and the Bivalvia, where known, are listed on Tables 10 and 11. Similar data on Polyplacophora, Scaphopoda, and Cephlopoda are not included as North and South Carolina representatives have few living species of each.

DISCUSSION

Separation of Arctic-Boreal, Boreal, and Transhatteran Provinces

What distinguishes the Carolina molluscan provinces from each other so that they can be considered having unique, perpetuating, but overlapping faunas?

The barrier affect of Cape Hatteras separating the cold water provinces (Arctic-Boreal) of the Middle Atlantic Bight from the more southern provinces (Carolinian and Caribbean) of the South Atlantic Bight has been thoroughly discussed by many including: Cerame-Vivas and Gray, 1966; Day et al., 1971; Franz and Merrill, 1980b; Stefansson et al., 1971. Their discussions document the role Cape Hatteras may play in effectively deflecting the southern-flowing Labrador or Virginian Current seaward, confining most Arctic-Boreal and Boreal species and their larvae in waters to the north of Cape Hatteras.

Depth separable characteristics of Arctic-Boreal, Boreal, and Transhatteran mollusca of the Middle Atlantic Bight (Franz and Merrill, 1980b) were generally not repeated in the molluscan fauna of the Carolinas. Bivalves of Arctic-Boreal and bivalves and gastropods of Transhatteran provinces had a greater proportion of species in depths shallower than those given by Franz and Merrill (1980a) for similar provinces (Tables 1, 3). Franz and Merrill (1980a) listed most Boreal mollusks from 100-200 m depths; however, most Carolina Boreal species were from waters <101 m depths. Carolina Transhatteran species were restricted to more shallow waters than Carolina Arctic-Boreal or Boreal and Transhatteran species of Franz and Merrill.

Separation of Carolinian and Caribbean Provinces

North of the Carolinas, Carolinian species are recorded at 26-156 m depths (Merrill et al., 1978). The fauna has been characterized as temperate, eurytolerant, and having few hard substrate species (Lyons and Collard, 1974). Porter and Safrit (1981) delineated it to nearshore estuarine waters and containing species not dependent upon larval drift from Caribbean waters for population recruitment. Separation of the Caribbean and "Gulf-Atlantic shelf [Carolinian]" provinces from each other occurred during the early Paleocene (Givens, pers. comm.). Separation continued thru the middle Eocene and was affected by marine transgressions attributed to rising and falling of sea level and the more turbid, cooler, slightly less saline waters present above the "Florida-Georgia cut" than in the Caribbean waters south of the cut. This separation has continued through succeeding periods. The Gulf-Atlantic shelf province of Givens may include elements of the Transhatteran province.

Carolinian and Caribbean province molluscan faunas can not be separated precisely by depth characteristics using the data presented here. Forty-one percent of species with depth faunas characterized as Carolinian overlapped depths faunas of species characterized as Caribbean (living molluscan species only); 66% of the species with Caribbean depth faunal affinities overlapped mollusks with Carolinian depth faunal affinities (data developed from Table 7).

The Caribbean fauna occurred slightly offshore of the Carolinian (Figure 1). Depth zones faunas, <0-10 and 11-62 m, while different from each other, were also different or separated from faunas of >63 m depth (Figure 3). Depth zone faunas >62 m depth were not clearly separable from each other (Figure 3). While Day et al. (1971) were unable to show a difference between the Carolinian and Tropical provinces of Cerame-Vivas and Gray (1966), they found faunal differences between their depth zone groupings of 3-20, 40-120, and 120->200.

The Carolinian fauna has been stated by Work (1969) to extend southward to near Stuart, Florida and then reappear north of Tampa in the Gulf of Mexico. Few published listings exist for Carolinian Atlantic Coast molluscan species south of South Carolina. A comparison is made here of the Gulf of Mexico and Caribbean molluscan species to that of the Carolinas (Table 12). The Gulf of Mexico faunal listings closely resemble Transhatteran and Carolinian province lists in North and south Carolina waters. More than 70% of the Gulf of Mexico species could be categorized into either Transhatteran and Carolinian faunal species, with less than 25% from the Carolinian + Caribbean, Caribbean, and Bathyal areas. Further, over 46% of the Gulf of Mexico species were also common or abundant ("a" or "c" densities) in North and South Carolina waters.

A comparison was made of Caribbean mollusk species collected from the Caribbean (Table 12). The percent of Caribbean collected species occurring in the Carolinian+Caribbean, Caribbean, and Bathyal provinces [off Carolina coast] was considerably higher than the percent of Gulf of Mexico species found in our Carolinian+Caribbean, Caribbean, and Bathyal provinces (>38 vs. <25%) (Table 12). A smaller percentage of mollusks from the Caribbean were found in the Transhatteran and Carolinian provinces (Table 12) than were found in the Gulf of Mexico lists. Only 10-56% of the species from the Caribbean were recorded as common or abundant in North and South Carolina waters whereas 46-81% of the Gulf of Mexico species were recorded ("a" - "c" densities) in waters of the Carolinas. If most of the Caribbean collected mollusks, not reported in waters off North and South Carolina (20[?], 42-74% of total), are considered Caribbean, and if about half of those that reach the Carolina waters might be considered of Carolinian or Transhatteran faunal origin, then less than 25% of the species reported in the Caribbean faunal lists overlap the Transhatteran and Carolinian provinces of North and South Carolina. A comparison of the Carolinian+Caribbean zone species groupings with published lists of Gulf of Mexico - Carolinian species and UNC-IMS collection data, confirmed that many species in the Carolinian+Caribbean list are not Caribbean but Carolinian.

Relationship of Circulation Within South Atlantic Bight to Perpetuation of Molluscan Provinces

Any continuance of the faunal separation between provinces is greatly dependent upon the ability of species within each being able to perpetuate their existence within each province. This is not a problem of molluscan species having non-pelagic larval development, such mollusca include: Buccinidae, and the genus Busycon (Robertson, 1974); Fasciolaridae, Prunum apicinum (D'Asaro, 1970); and most of the Muriciadae (Radwin and D'Atillio, 1976) - all represented by less than 4% of total recorded species from Carolinian waters. Most mollusca, however, reproduce through planktonic larval development lasting, for some bivalve larvae, as short as one to two weeks (Loosanoff and Davis, 1963; Castagna and Duggen, 1971) or longer than three months for some gastropod larvae (Scheltema, 1971). Continuance within a zoogeographic province of species populations having planktonic development depends on where oceanic currents have placed the larvae of these populations when metamorphosis or setting of their larvae begins.

Scheltema (1971) demonstrated that gastropod larvae are transported past the Carolinas by the Gulf Stream. Gulf Stream water is of Caribbean origin with little contribution from other sources (Stefansson et al., 1971). Gulf Stream water containing larvae from spawnings of mollusca in the Caribbean are probably the only means of continuance of the offshore Carolina Capes Caribbean fauna. Spawn from Caribbean province mollusca off the coast of the Carolinas are probably carried out to sea by the Gulf Stream where few if any can undergo metamorphosis. If the molluscan fauna from the shelf of the Carolinas is dependent on the Gulf Stream for continuance of its existence, then this fauna should be primarily Caribbean. It will be shown, however, that the fauna present on the shelf within the Carolina Capes is a fauna including many species not found in Caribbean waters, a fauna here called the Carolinian. It has also been stated (Givens, pers. comm.), that the very turbid waters of the Gulf-Atlantic shelf province may have been a barrier to larvae from clear Caribbean waters.

It is postulated here that within the boundaries of the shelf of the Carolina Capes, recirculating currents exist that enable molluscan larvae to complete larval development within the same waters that were they spawned. These waters over the Carolina Capes shelf contain the Carolinian province.

Waters to the south of Cape Hatteras, commonly referred to as the South Atlantic Bight, can be divided into three geographic subdivisions or flow areas (Lee et al., 1985): nearshore-intertidal, continental shelf, and shelf break. At the shelf break, eastern boundary of the South Atlantic Bight and western boundary of the Gulf Stream, water depth is about 10-20 m near the Florida Keys (Atkinson and Menzel, 1985), to 50 m (Peitrafesa et al., 1985) or, 80-100 m depth (Menzes et al., 1973) off the Carolinas.

The nearshore and intertidal area is an area of high physical variability. Temperatures and salinities are affected by drainage from estuaries, eddies from the Gulf Stream, and augmented by Labrador Current or Virginia Coastal waters escaping over the Cape Hatteras barrier (Gray and Cerame-Vivas, 1963; Cerame-Vivas and Gray, 1966). Stefansson et al. (1971) documenting penetrations by the latter, in February, March, and September, 1966 and April, 1967, believe that a surge into Raleigh Bay by the latter may be of greater influence to the nearshore waters south of Cape Hatteras than runoff from adjacent estuaries. direction of flow by this nearshore current is wind related and generally to the south or southwest (Gray and Cerame-Vivas, 1963; Stefansson et al., 1971; Blumberg and Mellor, 1983). This nearshore area is where the Transhatteran species are most abundant in Carolinian waters (Table 3). As Transhatteran species occur both north and south of Cape Hatteras in the nearshore waters, gene flow between northern and southern populations may be continued by way of runoff of the Labrador Current integrating northern population larvae into the nearshore current south of Cape Hatteras.

The shelf area is the habitat of the Carolinian province. It is an area where waters are dominated by winds and influenced more by the Gulf Stream then by nearshore estuarine waters (Atkinson and Menzel, 1985). This Carolina Capes shelf water has a higher salinity than shelf waters from the Middle Atlantic Bight to the north and the Georgia Bight to the south because of relatively low runoff from its neighboring estuaries (Pietrafesa et al., 1985). Circulation is wind related and possibly of at least two types - counter clockwise and inshore-offshore. Gray and Cerame-Vivas (1963) suggested a counter-clockwise circulation pattern existing in the Raleigh Bay area of the shelf. Stefansson et al. (1971) noted that while a similar pattern was not always the case in Raleigh Bay, in Onslow Bay there was always an indication of such an eddy. The numerical simulations of circulation in the South Atlantic Bight by Blumberg and Mellor (1983) were predictive of this counter-clockwise circulation over the shelf area of the South Atlantic Bight. To the south of Onslow Bay in the South Atlantic Bight, a counter-clockwise circulation or gyre occurs on the shelf in what is called the "Charleston Trough." This gyre is believed caused by the offshore deflection of the Gulf Stream as it passes over the "Charleston Bump", just south of the trough (Pietrafesa et al., 1985).

Circulation over the Carolina Capes shelf has also been described as having an inshore and offshore pattern. Miller et al, (1984) divided circulation on the shelf into three periods-winter, spring/summer, and fall. A surface layer 2-5 m thick and a thin bottom layer moves waters offshore in the winter while a large interior layer, occupying up to 70% of the water column, moves it in an onshore direction. The spring/summer period has an offshore flow on a surface layer 2-7 m thick; an onshore bottom flow occurs as a layer 1-3 m thick. Nearshore flow is in a northeast direction parallel to the coastline. The fall circulation has surface waters being blown onshore; nearshore or coastal waters are driven southward and the bottom layer moves offshore. It is probable that a complex interaction of the counter-clockwise and the inshore-offshore types of circulation enable many Carolinian province larvae to remain through metamorphosis within the shelf waters.

Circulation over the shelf is also affected by subsurface Gulf Stream meanders, filaments, and eddies forming along the western edge of the Gulf Stream (Pietrafesa et al., 1985). About 35 may occur each year at a frequency of one every five to ten days; they seem to grow in intensity north of the Charleston Bump (Blanton et al., 1981). Downstream of the Carolina Capes they induce upwelling of Gulf Stream waters (Blanton et al., 1981) into the shelf waters. These intrusions not only intrude Gulf Stream water into the shelf water but also contribute to flushing of the Carolina Bays. Estimates of flushing time in Onslow Bay range from one to two weeks (Stefansson et al., 1971) to about three months (Atkinson and Pietrafesa, 1980). While the Stefansson et al. flushing estimate is sufficient period for some larval bivalves to metamorphosis, the more recent figure of Atkinson and Pietrafesa (1980), three months, is long enough for setting of most Carolinian mollusks to be completed before being flushed out of the shelf area into the Gulf Stream.

Overlap of Provinces

Franz and Merrill (1980b) discuss at length overlapping between Arctic-Boreal, Boreal, and Transhatteran provinces north of Cape Hatteras. Their data from south of Cape Hatteras also contains records of overlap by Carolinian and Caribbean species (Franz and Merrill, 1980a).

The data of Coomans (1962) have overlaps within the Carolina faunal provinces south of Cape Hatteras. His Virginian fauna overlaps by 72% the Arctic-Boreal and Boreal faunas; his Carolinian fauna is overlapped 56% by his Caribbean faunal species [Porter calculations}. While many of the Virginian species of Coomans are Boreal according to Franz and Merrill (1980a and 1980b) data, overlapping of species in provinces north of Cape Hatteras is still present after this data adjustment. Unfortunately, most of his Carolinian and Caribbean faunal species are Transhatteran. Franz and Merrill (1980b) show that this documented overlapping of provinces is contrary to the beliefs by some who suggest that zoogeographic provinces support faunas of relatively consistent taxonomic composition and are thus non-overlapping.

Overlapping of species within the provinces off the Carolinas was listed earlier (note Tables 7, 12). The Transhatteran province of the South Atlantic Bight may be characterized by its nearshore southern flowing current and the Caribbean province by the northward flowing Gulf Stream. Both of the currents are highly variable. Where these currents and their associated provinces interact with the shelf fauna, overlapping of provinces will take place.

Neighboring zoogeographic provinces can overlap if each is occupied by an unique fauna distinguished by a distinctive characteristic (Franz and Merrill, 1980b). I suggest that the distinctive characteristics of the North and South Carolina zoogeographiic provinces are: 1. Carolinian province separated from Caribbean province starting in the Paleocene. 2. Carolina province larvae are constrained within the Carolinian province by recirculation of waters within the South Atlantic Bight for a sufficient period for many to metamorphos within these same waters.

Province Habitat and Feeding Relationships

Most molluscan species in all provinces, occurred on soft substrates (Tables 10 and 11). Hard substrate preference was highest in the Caribbean province, followed closely by the Carolinian; lower percentages were of Transhatteran, Bathyal, and Arctic-Boreal or Boreal province mollusks. Lyons and Collard (1974) believed one of the major differences between the two provinces was that the Caribbean fauna was one of hard substrates whereas the Carolinian was one of soft substrates. The significance of the difference between the percentage hard substrate preference in the two provinces in my data is questionable. Menzies et al. (1973) and described the habitat of the Carolina slope as generally smooth and of coarse sand and shell hash. Many of the Carolinian province UNC-IMS collections were made where shell hash (frequently Chlamys gibbus) was common. Such hash is hard substrate for many mollusks. This shell hash also contained slabs of Castle Hayne marl (Porter and Wolfe, 1972). Thus, unexpectedly high values were obtained for hard substrate preference mollusks in the Carolinian province. Dredge samples in the Caribbean province over the Lithothamnion reefs on the shelf break frequently did not include only reef material but also included soft substrate and shell hash from between the reefs.

Highest sessile habitat percentages were the Transhatteran followed by the Caribbean, and Carolinian provinces. Highest percent commensal habitat was among the species believed endemic to the Carolina Cusp region (Tables 10 and 11).

All provinces possessed a greater percent of carnivorous gastropods than of any other type. Other types, in descending percentage, were grazers, herbivorous, parasitic, scavengers, and planktonic and/or deposit feeders (Table 10). Boreal species were represented by an unusually high percentage of parasitic and scavenger feeding types. Endemic species also were highly composed of parasitic gastropods. Herbivorous and grazer feeding types were more numerous in the Bathyal province while planktonic feeders were most numerous in the Abyssal province.

Bivalves, in all provinces, were mainly plankton feeders (Table 11). Highest percentages of deposit feeders were found in provinces having the deepest depths: Abyssal, Bathyal, and Arctic-Boreal. Percent of bivalve deposit feeders was nearly equal in the remaining provinces.

ACKNOWLEDGEMENTS

Comments attributed to Dr. C. R. Givens, Department of Earth Science, Nicholls State University, Thibodaux, LA were from a paper, "North American Paleogene molluscan biogeography: an overview." presented by him at the 1987 American Malacological Union meetings. Dr. Harry G. Lee of Jacksonville, FL is thanked for identification in 1988 of several common molluscan species not previously recognized existing in the UNC-IMS collections. I wish to thank H.K. Page and his late wife Valarie for preparation of figures; and B. Bright, J. Garner, and my wife Dorothy P. Porter for table preparation. Appreciation is given to Drs. R. Luettich for software help and to F. J. Schwartz for many ideas during the data preparation, for review of this paper, and for the series of mollusks from the trawled deep-water stations off Capes Hatteras and Lookout that prompted this examination of the zoogeographical provinces off the coasts of North and South Carolina.

ADDENDUM

ALL "s" DENSITY and NON-LIVE-COLLECTED MOLLUSKS of "a" and "c" DENSITIES.

Abyssal species:

NATICIDAE: Polinices pallida *!(AB); TURRIDAE: Cerodrillia (Cymatosyrinx) centimata, Leucosyrinx subgrundifera, Oenopota (=Propebela) rathbuni, O. subturgida (EN), Pleurotomella chariessa phalera (EN*); NUCULANIDAE: Nuculana bushiana; PECTINIDAE: Hyalopecten eucymatus; THYASIRIDAE: Thyasira ferruginea (AB); T. grandis; Thyasira ovoidea (EN); MONTACUTIDAE: Mysella tumidula; DENTALIIDAE: Graptacme perlongum; ENTALINIDAE: Heteroschismoides callithrix; PULSELLIDAE: Pulsellum lobatum (AB); SIPHONODENTALIIDAE: Polyschides grandis.

Abyssal, Bathyal, etc Species

ATLANTIDAE: _Atlanta inclinata_ !(CB); EPITONIIDAE: _Epitonium babylonium_ (CB); MURICIDAE: _Urosalpinx macra_? (CB); TURRIDAE: _Drillia lithocolleta_; _Leucosyrinx verrillii_; SPORTELLIDAE: _Basterotia quadrata_ (CB); ASTARTIDAE: _Astarte smithii_(CB); VERTICORDIIDAE: _Verticordia acuticostata_; _Verticordia sequenzae_.

Artic-Boreal Species

LITTORINIDAE: _Littorina_ cf. _obtusata_!, _Littorina saxatilis_*!; MYTILIDAE: _Musculus corrugatus_, _M. niger_; ASTARTIDAE: _Tridonta borealis_*; MACTRIDAE: _Mactromeris polynyma_.

Boreal Species

RISSOIDAE: _Boreocingula castanea_!; NATICIDAE: _Euspira heros_ !(c), _E. triseriata_!; BUCCINIDAE: _Colus caelatulus_*!; _C. pygmaeus_*, TURRIDAE: _Suavodrillia tanneri_*; PYRAMIDELLIDAE: _Odostomia hendersoni_, _Sayella chesapeakea_ *(?T1), _Turbonilla aequalis_, _T. nivea_, _T. toyatani_ (?T1); APLYSIIDAE: _Aplysia brasiliana perviridis_*; OCTOPODIDAE: _Octopus bairdii_*; SOLEMYIDAE: _Solemya borealis_; MALLETIIDAE: _Neilonella (=Saturnia) subovata_ (A); MYTILIDAE: _Crenella fragilis_ (?T1); LUCINIDAE: _Lucinoma blakeanum_*!; THYASIRIDAE: _Axinopsida cordata_, _Thyasira gouldii_ (A), _T. tortuosa_ *(A); KELLIIDAE: _Aligena elevata_*; MONTACUTIDAE: _Montacuta percompressa_*; CARDITIDAE: _Cyclocardia borealis_*; ASTARTIDAE: _Astarte Castenea_*, _A. undata_*!; CULTELLIDAE: _Siliqua costata_; DONACIDAE: _Donax fossor_*; PHOLADIDAE: _Zirphaea crispata_*!; THRACIIDAE: _Thracia conradi_!; PERIPLOMATIDAE: _Periploma leanum_!; PULSELLIDAE: _Pulsellum occidentale_ (?A), _P. verrilli_ (A); SIPHONODENTALIIDAE: _Polyschides_(?) _atlanticus_ (A).

Bathyal Species

FISSURELLIDAE: _Puncturella erecta_; TROCHIDAE: _Calliostoma benedicti_, _C._, _psyche_, _C. sayanum_; TURBINIDAE: _Homalopoma indutum_; MURICIDAE: _Murexiella hidalgoi_; VOLUTIDAE: _Scaphella gouldiana_; TURRIDAE: _Leucosyrinx tenoceras_, _Pleurotomella extensa_; PYRAMIDELLIDAE: _Odostomia tornata_; PECTINIDAE: _Palliolum leptaleus_; VENERIDAE: _Gemma gemma manhattanensis_.

Caribbean and Bathyal Species

FISSURELLIDAE: _Emarginula phrixodes_*; TROCHIDAE: _Calliostoma jujubinum_, _Dentistyla asperrima_*; VITRINELLIDAE: _Teinostoma multistriatum_; NATICIDAE: _Polinices (Sigatica) carolinensis_; MURICIDAE: _Pterynotus phaneus_; COLUMBELLIDAE: _Mitrella raveneli_; VOLUTIDAE: _Scaphella dubia_*; MITRIDAE: _Mitra swainsonii antillensis_; TURRIDAE: _Daphnella morra_;

NUCINELLIDAE: _Nucinella serrei_; ARCIDAE: _Bathyarca glomerula_; GRYPHAEIDAE: _Neopycnodonte cochlear_?, _Parahyotissa macgintyi_; DENTALIIDAE: _Antalis circumcinctum_; SIPHONODENTALIIDAE: _Polyschides agassizii_.

Carolinian and Bathyal Species

XENOPHORIDAE: _Xenophora longleyi_ (CB); LUCINIDAE: _Lucina nassula_ !(CB)(c); SPORTELLIDAE: _Basterotia quadrata_ (A,CB); TELLINIDAE: _Tellina gouldii_ (CB), _T. probrina_ (CB); DENTALIIDAE: _Antalis taphrium_ *(CB).

Transhatteran Species

FISSURELLIDAE: _Diodora tanneri_?; TROCHIDAE: _Calliostoma bairdii_*; SKENEOPSIDAE: _Skeneopsis planorbis_; VITRINELLIDAE: _Teinostoma cryptospira_ (c); TONNIDAE: _Eudolium crosseanum_*; EPITONIIDAE: _Epitonium dallianum_, _Opalia leeana_; NASSARIIDAE: _Nassarius acutus_; MARGINELLIDAE: _Dentimargo eburneolus_, _Volvarina veliei_; TURRIDAE: _Inodrillia dalli_*, _Kurtziella cernia_ (c); PYRAMIDELLIDAE: _Odostomia cancellata_, _Turbonilla reticulata_ (CR); STILIGERIDAE: _Hermaea_ (_Placida_) _dendritica_*; ELYSIIDAE: _Elysia chlorotica_*; APLYSIIDAE: _Aplysia morio_; CORAMBIDAE: _Doridella obscura_*; DENDRODORIDIDAE: _Doriopsilla pharpa_*; FACELINIDAE: _Cratena pilata_*; ELLOBIIDAE: _Detracia floridana_*; NUCULANIDAE: _Nuculana aspecta_*; ARCIDAE: _Arca holmesii_; LIMOPSIDAE: _Limopsis sulcata_ (c); MYTILIDAE: _Amygdalum papyrium_; PECTINIDAE: _Aequipecten glyptus_, _A. phrygium_; LUCINIDAE: _Linga amiantus_; THYASIRIDAE: _Thyasira trisinuata_; UNGULINIDAE: _Diplodonta verrilli_; MONTACUTIDAE: _Pythenella cuneata_*; ASTARTIDAE: _Astarte crenata subequilatera_*; TELLINIDAE: _Tellina tenella_; VENERIDAE: _Cyclinella tenuis_*, _Gemma gemma purpurea_*; OMMASTREPHIDAE: _Illex illecebrosus_*.

Transhatteran and Abyssal Species

CASSIDAE: _Oocorys abyssorum_*; TURRIDAE: _Gymnobela agassizii_*; SCAPHANDRIDAE: _Cylichna alba_, _Scaphander punctostriatus_*; LIMOPSIDAE: _Limopsis cristata_; MYTILIDAE: _Amygdalum politum_; PECTENIDAE: _Cyclopecten thalassinus_; THYASIRIDAE: _Thyasira flexuosa_; SEMELIDAE: _Abra longicallis americana_*; CUSPIDARIIDAE: _Cuspidaria rostrata_; DENTALIIDAE: _Antalis entale stimpsoni_*.

Carolinian Species

CAECIDAE: _Caecum carolinianum_ (c); VITRINELLIDAE: _Parviturboides interruptus_ (c), _Teinostoma cocolitoris_ (c); TORNIDAE: _Cochliolepis striata_ (c); CASSIDAE: _Cassis madagascariensis_*; TRIPHORIDAE: _Metaxia metaxae taeniolata_ (EN); MALONGENIDAE: _Busycon carica eliceans_*; OLIVIDAE:

Olivella adelae*; PYRAMIDELLIDAE: Odostomia emeryi (c); PLEUROBRANCHIDAE: Pleurobranchus hedgepethi*!; GONIODORIDIDAE: Ancula evelinae*, OKENIIDAE: Okenia impexa*; POLYCERATIDAE: Polycera hummi*; CHROMODORIDIDAE: Chromodoris aila* ?EN; DORIDIDAE: Doris verrucosa*; DISCODORIDIDAE: Discordoris pusae*; DENDRODORIDIDAE: Dendrodoris warta*, Doriopsilla leia* (EN); TRITONIIDAE: Tritonia bayeri*, T. wellsi*; DOTOIDAE: Doto chica*, Miesea evelinae*; ARMINIDAE: Armina tigrina*!; TERGIPEDIDAE: Cuthona tina*; FACELINIDAE: Cratena kaoruae*, Dondice occidentalis*, Facelina (=Learchis) poica*; SPURILLIDAE: Burghia verrucicornis*; ELLOBIIDAE: Detracia clarki*; ARCIDAE: Anadara notabilis*; LUCINIDAE: Codakia costata, Divaricella dentata!, Linga pennsylvanica*, Lucina pectinata; UNGULINIDAE: Diplodonta sp.; LASAEIDAE: Erycina linella; MONTACUTIDAE: Neaeromya floridana*; MACTRIDAE: Raeta plicatella(c); TELLINIDAE: Macoma brevifrons, M. constricta (c), M. limula, Strigilla carnaria*, Tellidora cristata*, Tellina fausta, T. laevigata, T. magna, T. texana (c); PSAMMOBIIDAE: Solecurtus sanctaemarthae; TRAPEZIIDAE: Coralliophaga coralliophaga*; VENERIDAE: Anomalocardia auberiana, Transennella conradiana, Ventricolaria rigida; COOPERELLIDAE: Cooperella atlantica*; GASTROCHAENIDAE: Gastrochaena ovata*, G. stimpsoni, G. (Spengleria) rostrata*; PHOLADIDAE: Pholas campechiensis (c); THRACIIDAE: Asthenothaerus hemphilli*, Cyathodonta cruziana.

Caribbean species

ISCHNOCHITONIDAE: Chaetopleura staphylophera*; SCISSURELLIDAE: Anatoma crispata (c); HALIOTIDIDAE: Haliotis pourtalesii; FISSURELLIDAE: Diodora aquayoi, D. fluviana (c), D. sayi*, Rimula frenulata; ACMAEIDAE: Lottia (=Collisella) cf. leucopleura; COCCULINIDAE: Cocculina sp.; TROCHIDAE: Mirachelus corbis, Tegula fasciata (c); TRICOLIIDAE: Tricolia bella; TRUNCATELLIDAE: Truncatella caribaeensis, T. pulchella; CAECIDAE: Caecum bipartitum, C. heladum, C. insularum; VITRINELLIDAE: Anticlimax cf. pilsbryi, Teinostoma goniogyrus; TORNIDAE: Macromphalina palmalitoris; MODULIDAE: Modulus carchedonius; CERITHIIDAE: Cerithium litteratum; FOSSARIIDAE: Fossarus compactus; TURRITELLIDAE: Turritella variegata; STROMBIDAE: Strombus pugilis, S. raninus; HIPPONICIDAE: Cheilea equestris (c); VANIKOROIDAE: Vanikoro oxychone; CREPIDULIDAE: Crucibulum auricula(c); CAPULIDAE: Capulus (Hyalorisia) sp., C. incurvatus, C. inornatus*; TRICHOTROPIDAE: Trichotropis migrans*; XENOPHORIDAE: Xenophora caribaea; CYPRAEIDAE: Cypraea cinerea*; OVULIDAE: Phenacovqlva piragua, Pseudocyphoma intermedium; TRIVIIDAE: Trivia candidula (c), T. pediculus*; LAMELLARIIDAE: Lamellaria perspicua*; NATICIDAE: Natica livida, N. marochiensis; CASSIDAE: Cassis tuberosa, Cypraecassis testiculus*, Phalium coronadoi coronadoi*; RANELLIDAE: Cymatium cingulatum*, C. corrugatum krebsii*, C. labiosum*, C. martinianum; BURSIDAE: Bursa rhodostoma thomae*; CERITHIOPSIDAE: Cerithiopsis fusiformis, C. iota, C. latum, C. pupa; TRIPHORIDAE: Metaxia metaxae, Triphora compsa, T.

dupliniana, *T. melanura* (c), *T. triserialis*; EPITONIIDAE: *Depressiscala nitidella*, *Epitonium* cf. *fractum*, *E. echinaticostum*, *E. foliaceicostum*, *freilei*, *E. krebsii* (c), *E. lamellosum*, *Opalia burryi**, *O. pumilio*, *O. p. morchiana*, *Sthenorytis pernobilis*; EULIMIDAE: *Eulimostraca subcarinata*, *Melanella arcuata*, *Niso hendersoni*; ACLIDIDAE: *Henrya morrisoni*; MURICIDAE: *Murex cabritii*, *Pteropurpura bequaerti*, *Trachypollia nodulosa*; CORALLIPHILIDAE: *Coralliophila abbreviata*, *C. scalariformis**; COLUMBELLIDAE: *Aesopus stearnsii* (c), *Cosmioconcha calliglypta*; VOLUTIDAE: *Scaphella junonia**; OLIVIDAE: *Jaspidella jaspidea*, *Olivella bullula* (c), *O. nivea*; MARGINELLIDAE: *Marginella amabilis*, *M. guttata*, *Volvarina avena*; MITRIDAE: *Mitra nodulosa* (c), *M. straminea*; COSTELLARIIDAE: *Vexillum arestum*, *V. hendersoni* (c), *V. histrio*, *V. styria*; CANCELLARIIDAE: *Agatrix agassizii*; CONIDAE: *Conus daucus*, *C. juliae**, *C. stimpsoni**; TURRIDAE: *Cerodrillia thea*, *Cochlespira radiata*, *Crassispira digitalis*, *C. tampaensis*, *Daphnella corbicula*, *D. lymneiformis*, *Drillia actinocycla*, *Drillia canna*, *Drillia ebur*, *Drillia enae*, *Hindsiclava alesidota**, *Inodrillia miamia*, *Ithycythara cymella*, *I. lanceolata*, *I. parkeri*, *Lioglyphostoma* (=*Glyphostomops*) *hendersoni**, *Mangelia* (*Saccharoturris*) *monocingulata*, *Pyrgocythara candidissima*, *P.* cf. *densestriata*, *P. dubia*, *Pyrgospira ostrearum**, *Splendrillia fucata*; *S.* (*Fenimorea*) *halidorema**, *S.* (*F.*) *janetae*; TEREBRIDAE: *Hastula* cf. *hastula*, *Terebra onslowensis*; ARCHITECTONICIDAE: *Discotectonica discus* (=*Architectonica peracuta*)*, *Spirolaxis centrifuga*; MATHILDIDAE: *Mathilda barbadensis*, *M. scitula* *(EN), *M. yucatecana*; PYRAMIDELLIDAE: *Odostomia engonia**!, *Peristichia agria*, *P. toreta* (c), *Sayella crosseana*, ?*Striopyrgus hybridus*(?f), *Triptychus pliocena*(?f), *Turbonilla curta*, *T. dalli*, *T. exilis*, *T. hemphilli*, *T. obeliscus*, *T. portoricana*, *T. punicea*, *T. virga*; ACTEONIDAE: *Acteon* cf. *danaida*; RINGICULIDAE: *Ringicula semistriata*; HYDATINIDAE: *Micromelo undatus*; SCAPHANDRIDAE: *Acteocina eburnea*, *Cylichna verrillii* (c); HAMINEIDAE: *Atys caribaeus*; RETUSIDAE: *Volvulella paupercula*; UMBRACULIDAE: *Umbraculum rushii*; TYLODINIDAE: *Tylodina americana**; SIPHONARIIDAE: *Siphonaria alternata*; SOLEMYIDAE: *Solemya* cf. *occidentalis*; NUCULIDAE: *Nucula tenuis**; NUCULANIDAE: *Nuculana carpenteri*; ARCIDAE: *Barbatia cancellaria*; LIMIDAE: *Lima scabra* forma *tenera**; GRYPHAEIDAE: *Hyotissa thomasi*; PECTINIDAE: *Pecten chazaliei**; TEREDINIDAE: *Bankia fosteri**; CUSPIDARIIDAE: *Cardiomya ornatissima**!; DENTALIIDAE: *Dentalium bartletti*, *Graptacme calamus* (c).

Carolinian and Caribbean Species

ACANTHOCHITONIDAE: *Acanthochitona pygmaea*?*; TROCHIDAE: *Calliostoma marionae* (c); SKENEIDAE: *Cyclostremiscus beauii*; TURBINIDAE: *Lithopoma americanum**; RISSOIDAE: *Alvania auberiana* (c); CAECIDAE: *Caecum imbricatum* (c); VITRINELLIDAE: *Aorotrema cistronium* (EN)(c), *Circulus supressus*, *Didianema pauli**, *Teinostoma* cf. *parvicallum*, *T. obtectum*, *Vitrinella* *diaphana**, *V. floridana*, *V. helicoidea* (c); TORNIDAE: *Macromphalina floridana**; MODULIDAE: *Modulus modulus**; CERITHIIDAE: *Cerithium flavum**; STROMBIDAE: *Strombus costatus**; OVALIDAE: *Cyphoma gibbosum*!; NATICIDAE: *Polinices uberinus**, *P.* (*Sigatica*) *semisulcata*; RANELLIDAE: *Charonia tritonis variegata**, *Cymatium moritinctum caribbaeum**; BURSIDAE: *Bufonaria bufo**; CERITHIOPSIDAE: *Cerithiopsis abrupta* (c); TRIPHORIDAE: *Triphora decorata*, *T. ornata*, *T. pulchella* (c), *T. turristhomae* !?(c); EPITONIIDAE: *Epitonium albidum**, *E. candeanum*?*; MURICIDAE: *Trachypollia didyma**; BUCCINIDAE: *Cantharus cancellarius*; COLUMBELLIDAE: *Columbella mercatoria*; MELONGENIDAE: *Busycon spiratum pyruloides**; FASCIOLARIIDAE: *Colubraria obscura*; MARGINELLIDAE: *Marginella lavelleeana**; COSTELLARIIDAE: *Vexillum albocinctum**; CONIDAE: *Conus floridensis**; TURRIDAE: *Agathotoma* (*Vitricythara*) *elata**; *Cerodrillia bealiana* (c), *C.* (*Viridrillia*) *cervina**, *Compsodrilla eucosmia*, *Drillia cydia**, *Glyphostoma gabbii*, *Pilsbryspira* cf. *albomaculata*; TEREBRIDAE: *Hastula salleana*; PYRAMIDELLIDAE: *Odostomia canaliculata**, *O. laevigata**, *Pyramidella candida**; ACTEONIDAE: *Acteon candens*; BULLIDAE: *Bulla striata**; RETUSIDAE: *Volvulella recta*!; SIPHONARIIDAE: *Williamia krebsii**; NOETIIDAE: *Arcopsis conradiana**; GLYCYMERIDIDAE: *Glycymeris spectralis**, *G. undata**; MYTILIDAE: *Lithophaga antillarum**; PTERIIDAE: *Pinctada imbricata**; MALLEIDAE: *Malleus candeanus**; ISOGNOMONIDAE: *Isognomon bicolor**; LIMIDAE: *Lima scabra**; OSTREIDAE: *Dendostrea frons**; PECTINIDAE: *Chlamys sentis**; SPONDYLIDAE: *Spondylus americanus**; LUCINIDAE: *Anodontia alba* (c), *A. philippiana*, *Codakia orbicularis**, *C. orbiculata**, *Lucina radians*; MONTACUTIDAE: *Mysella triquetra* (c); CARDIIDAE: *Laevicardium sybariticum**; VENERIDAE: *Chione pygmaea*; PHOLADIDAE: *Jouannetia quillingi**; TEREDINIDAE: *Nototeredo knoxi**; *Teredo bartschi**; CUSPIDARIIDAE: *Cardiomya glypta*, *Plectodon granulatus*; VERTICORDIIDAE: *Verticordia fischeriana**.

Pelagic and Worldwide Species

Histioteuthidae: *Histioteuthis meleagroteuthis**, *H. reversa**; OMMASTREPHIDAE: *Ommastrephes bartrami**; AGRONAUTIDAE: *Argonauta agro**; JANTHINIDAE: *Janthina globosa* *(CB); *J. janthina*; LIMACINIDAE: *Limacina bulimoides*, *Limacina retroversa*; CAVOLINIIDAE: *Cavolinia inflexa* *!(CB), *Clio pyramidata*, *Creseis acicula clava*, *C. acicula conica*, *Cuvierina columnella*, *Styliola subula*; PERACLIDAE: *Peracle apicifulva*, *P. bispinosa**.

Endemic Species

CAECIDAE: *Caecum tortile*; VITRINELLIDAE: *Aorotrema cistronium* (CR.CB)(c), *Teinostoma minusculum*, *Vitrinella carinata*: NATICIDAE: *Polinices mamillaris*?*; TRIPHORIDAE: *Metaxia taeniolata* (CR); ACLIDIDAE: *Aclis carolinensis*; TURRIDAE: *Eubela calyx* (A), *Oenopota* (=*Propebela*) *subturgida*

(A), *Pluerotomella chariessa phalera**(A); MATHILDIDAE: *Mathilda scitula* *(CB); PYRAMIDELLIDAE: *Odostomia disparilis* (BTH); HAMINEIDAE: *Atys mandrewii*?; CHROMODORIDIDAE: *Chromodoris aila**(CR); DENDRODORIDIDAE: *Doriopsilla leia* *(CR); THYASIRIDAE: *Thyasira ovoidea* (A); KELLIDAE: *Bornia longipes*; LASAEIDAE: *Erycina emmonsi*; MONTACUTIDAE: *Montacuta minuscula*, *Mysella casta*, *M. striatula*; SPORTELLIDAE: *Ensitellops protexta*; VENERIDAE: *Pitar zonatus*; HIATELLIDAE: *Panopea americana**; THRACIIDAE: *Thracia morrisoni*; DENTALIIDAE: *Dentalium gouldii*; GADILIDAE: *Cadulus minusculus*.

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Table 1. Arctic-Boreal and Boreal marine mollusks of North and South Carolina water. Only live collected species having densities "a" and "c" are included. Published NC-SC or UNC-IMS collection living depths are indicated by an "X". Unpublished southern range extensions into North/South Carolina waters indicated by a "#". Explanation for abbreviations are found in Table 2.

	DEPTHS (m)										
	0-10	11-45	46-80	81-100	101-246	247-445	446-940	940	Faunal Group	Published Range	Dens.
CAECIDAE											
Caecum johnsoni		X							B!	MA - SC	c
EPITONIIDAE											
Epitonium championi		X							B!	MA - SC	a
BUCCINIDAE											
Colus pubescens			X	X	X	X	X	X	AB!A!	ASea - Sc	c
Colus stimpsoni			X	X	X	X	X	X	B!	Lab - NC	c
MARGINELLIDAE											
Marginella roscida	X	X	X	X	X				?T1 ?B	MA - SC	a
PYRAMIDELLIDAE											
Boonea bisuturalis		#							B!	GSL - DE	c
Fargoa dianthophila	X	X							B!	MA - NC	c
Fargoa gibbosa		X							T1	ME - Y	c
HAMINEIDAE											
Haminoea solitaria	X								B!	CC - NC	c
NUCULIDAE											
Nucula delphinodonta					#				B A	Lab - ME	c
YOLDIIDAE											
Yoldia limatula		X	X						B!	NS - NC	c
Yoldia sapotilla					X				AB!	ASea NC	c
MYTILIDAE											
Crenella glandula		X	X						B!	Lab - NC	a
Modiolus modiolus		#	#	# 1					AB!	ASea - NJ 2	c
Mytilus edulis	X	X							B!	ASea - SC	a
PECTINIDAE											
Placopecten magellanicus		X	X	X	X				B	Lab - NC-CH	c
AMONIIDAE											
Anomia squamula	X	X							B!	Lab - NC	c
CARDIIDAE											
Cerastoderma pinnulatum		X							B!	Lab - NC	c
MACTRIDAE											
Spisula solidissima	X	X							B!	NS - NC 1	a
TELLINIDAE											
Macoma balthica	X								B! ?T2	ASea - GA	a
Tellina agilis	X	X	X	X					AB! ?T2	GSL - GA	a
ARCTICIDAE											
Arctica islandica		X	X						B	NFD - NC	c
VENERIDAE											
Pitar morrhuanaus		X		X	X				B!	GSL - NC	a
MYIDAE											
Mya arenaria	X								B!	Lab - NC	a
LYONSIIDAE											
Lyonsia hyalina	X	X	X						B!	NC - SC	a
DENTALIIDAE											
Dentalium meridionale verrilli								X	B A	MA - NC	c

1 Bedauperthuy, 1967
2 Franz and Merrill, 1980b

Table 2. Abbreviations of Tables and Text.

Abbreviation	=
!	NC-SC record is N or S of faunal boundary
?	Questionable Fauna or Species
*	Live-Collected Species
a	Abundant (density [approx. value = >20])
A	Abyssal Fauna
AB	Arctic-Boreal Fauna
AL	Alabama
AR	Argentina
ASea	Arctic Sea
AT	Atlantic
B	Beaufort (published ranges only)
B	Boreal Fauna
Bah	Bahamas
Barb	Barbados
BCan	Canarie Islands Basin
BCb	Caribbean Basin
Ber	Bermuda
BGM	Gulf of Mexico Basin
BNAm	North American Basin
BNCan	North Canadian Basin
BR	Brazil
BTH	Bathyal Fauna
C	Common (density approx. value = 6 - 20])
Cb	Caribbean
CB	Caribbean Fauna
CC	Cape Cod
CC-S	South of Cape Cod
CH	Cape Hatteras
ChB	Chesapeake Bay
ChB-N	North of Chesapeake Bay
CN	Canada
CR	Carolinian Fauna
CT	Connecticut
CU	Cuba
DB	Delaware Bay
DE-InR	Indian River, Delaware Bay
DI	Drum Inlet, NC
EN	Endemic (NC-SC) Species
FL	Florida
FL-CC	Cape Canaveral, FL
FL-E	East of Florida
FL-FR	Fernadina, FL
FL-KW	Key West, FL
FL-KY	Florida Keys
FL-Mi	Miami, FL
FL-N	North of Florida
FL-NE	Northeast of Florida
FL-S	South of Florida
FL-SA	St. Augustine, FL
FL-TB	Tampa Bay, FL
GA	Georgia
GB	Georges Bank
GM	Gulf of Mexico
GR	Greenland
GSL	Gulf of St. Lawrence
LA	Louisiana
LAB	Labrador
LAnt	Lesser Antilles
MA	Massachusetts
MA-CC	Cape Cod, MA
MD	Maryland
ME	Maine
MV	Martha's Vineyard
MX	Mexico
MX-E	East of Mexico
N-AT	North Atlantic
NC	North Carolina
NC-CF	Cape Fear, NC
NC-CH	Cape Hatteras, NC
NC-CL	Cape Lookout, NC
NC-CurBh	Currituck Beach, NC
NE	Northeast
NFD	Newfoundland
NJ	New Jersey
NJ-HerIn	Hereford Inlet, NJ
NJ-S	South of New Jersey
NS	Nova Scotia
NY	New York
Pel	Pelagic
PR	Puerto Rico
Q-S	South of Quebec
RI	Rhode Island
s	Scarce (density [approx. value = 3 - 5 or 1 - 2 if recent collection or publication])
S	South
SC	South Carolina
T1	Transhatteran Faunal Group #1
T2	Transhatteran Faunal Group #2
TX	Texas
TX-S	South of Texas
UNC-IMS	Univ. of North Carolina, Inst. of Marine Sci.
UR	Uruguay
VA	Virginia
VA-CCrl	Cape Charles, VA
VA-CHN	Cape Henry, VA
VA-Wach	Wachapreague, VA
vr	Very Rare (density [approx. value = <3 non-recent])
WI	West Indies
WW	Worldwide
Y	Yucatan

Table 3. Transhatteran marine mollusks of North and South Carolina waters. Only live-collected species of densities "a" and "c" are included; published NC-SC or UNC-IMS collection living depths are indicated by an "X". Note Table 2 for additional abbreviations.

	DEPTHS (m)										
	0-10	11-45	46-80	81-100	101-246	247-445	446-940	940	Faunal Group	Published Range	Dens.
ISCHNOCHITONIDAE											
Chaetopleura apiculata	X	X			X				T1	CC - FL	a
FISSURELLIDAE											
Diodora cayenensis	X	X							?T1	MD - FL Br	a
TROCHIDAE											
Solariella lacunella			X						?T1	VA - FL-S	c
LITTORINIDAE											
Littorina irrorata	X								T1	NY - FL TX	a
CAECIDAE											
Caecum cooperi		X							T1	CC-S - FL-W TX	a
Caecum pulchellum		X	X						T1	ME - Br 1	a
TURRITELLIDAE											
Turritella (*Torcula*) *exoleta*		X	X	X	X				?T1	VA - WL Br	a
CERITHIIDAE											
Bittium varium	X								T2	GSL - FL TX Br	a
Finella dubia		X	X						T1	CN - FL Br	a
CREPIDULIDAE											
Crepidula convexa	X	X							T1	MA - FL TX WL	a
Crepidula fornicata	X	X	X	X					T1	CN - FL TX	a
Crepidula plana	X	X	X						T1	Cn - TX Br	a
Crucibulum striatum			X	X					T2	NS - FL	c
OVULIDAE											
Simnialena uniplicata	X	X	X	X	X				?T1	VA - FL Br	a
NATICIDAE											
Natica pusilla	X	X	X	X	X				T2	ME - FL GM Br	a
Polinices (*Neverita*) *duplicatus*	X	X							T1	MA - FL GM	a
Sinum perspectivum	X	X	X						?T1	NJ - FL TX WL Br	a
CERITHIOPSIDAE											
Cerithiopsis emersonii		X							T1	MA - WL Br	a
Cerithiopsis greeni	X	X	X	X					T1	CC - FL Br	c
Seila adamsi	X	X							T1	MA - FL TX Br	a
TRIPHORIDAE											
Triphora nigrocincta	X	X	X	X					T1	MA - FL TX Br	a
EPITONIIDAE											
Epitonium angulatum	X								T1	NY - FL TX	a
Epitonium humphreysii	X								T1	CC - FL TX	c
Epitonium multistriatum		X							T1	MA - TX FL	c
Epitonium novangliae		X	X						?T1	VA - TX Br	c
Epitonium rupicola	X		X						T1	CC - FL TX	c
EULIMIDAE											
Melanella intermedia	X	X	X						?T1	NJ - Br	a
MURICIDAE											
Eupleura caudata	X	X							T1	S of CC - FL-S	a
Urosalpinx cinerea	X								T2	NS - FL -NE	a
CORALLIPHILIDAE											
Coralliophila aberrans		X							T1	MA - GM Cb Br	c
COLUMBELLIDAE											
Anachis (*Costoanachis*) *avara*	X	X	X	X	X				T1	MA - FL-E TX	a
Anachis (*Costoanachis*) *lafresnayi*	X	X	X						T2	ME - FL-E Y	a
Anachis (*Parvanachis*) *obessa*		X	X						?T1	VA - FL TX UR	a
Mitrella lunata	X	X	X	X					T1	MA - FL TX Br	a
NASSARIIDAE											
Ilyanassa obsoleta	X								T2	GSL - FL-NE	a
Ilyanassa trivattata		X	X	X					T2	NFD - FL-NE	a
Nassarius vibex	X	X							T1	CC - FL TX WI Br	a
MELONGENIDAE											
Busycon carica	X	X							T1	CC - FL-CC	a
Busycon sinistrum	X	X							T1	NJ - FL GM	a
Busycon (*Busycotypus*) *canaliculata*	X	X							T1	CC - FL-SA	a
OLIVIDAE											
Olivella mutica	X	X	X	X					?T1	NJ - HerIn - FL	a
MARGINELLIDAE											
Granulina ovuliformis		X				X	X		?T1	VA - Wach - FL WI	a
Marginella roscida	X	X	X	X	X				?T1 ?B	MA - SC	a
TEREBRIDAE											
Terebra dislocata	X								?T1	MD - FL WI TX Br	a
TURRIDAE											
Pyrgocythara plicosa	X								T1	MA - TX	c

Table 3 (continued)

	DEPTHS (m)										
	0-10	11-45	46-80	81-100	101-246	247-445	446-940	940	Faunal Group	Published Range	Dens.
PYRAMIDELLIDAE											
Odostomia (*Boonea*) *impressa*	X								T1	MA - GM	a
Odostomia (*Boonea*) *seminuda*	X	X	X						T2	NS - FL TX	a
Odostomia (*Fargoa*) *bushiana*	X	X	X	X	X				T1	CC - RI TX	c
Turbonilla interrupta		X							T2	GSL - WI Br	a
ACTEONIDAE											
Rictaxis punctostriatus	X		X						T1	CC - FL-FK TX AR	a
SCAPHANDRIDAE											
Acteocina canaliculata 2	X								?T2	ME - FL GM TX	a?
APLYSIIDAE											
Aplysia brasiliana	X	X							T1	CC - FL TX WI	a
SCYLLAEIDA											
Scyllaea pelagica	X								T1	MA - WI	c
ELLOBIIDAE											
Melampus bidentus	X								T2	Q-S TX WI	c
LOLIGINIDAE											
Loligo pealeii		X							T2	NS - FL TX VN	a
Lolliguncula brevis	X	X	X	X	X	X	X		?T1	MD - TX Br	a
OCTOPODIDAE											
Octopus vulgaris	X	X	X	X	X	X			T1	CT - FL WI	a
SOLEMYIDAE											
Solemya velum	X	X							T2	NS - FL-N	c
NUCULIDAE											
Nucula proxima	X	X	X						T2	NS - FL TX	a
NUCULANIDAE											
Nuculana acuta		X	X	X	X				T1	MA-CC - TX WL Br	a
ARCIDAE											
Anadara ovalis	X								T1	CC - TX WI Br	a
Anadara transversa	X	X							T1	CC-S - FL TX	a
NOETIIDAE											
Noetia ponderosa	X								?T1	VA - FL TX	a
LIMOPSIDAE											
Limopsis sulcata				X	X				T1	MA-CC - FL GM WI	c
MYTILIDAE											
Crenella decussata		?X	?X						T2 A	Gr - NC BGM BCb	3c
Geukensia demissa	X								T2	GSL - FL-NE	a
Ischadium recurvum	X								T1	CC - WI	a
LIMIDAE											
Limatula subauriculata			X	X	X				T2 A	Gr - PR	c
OSTREIDAE											
Crassostrea virginica	X								T2	GSL - GM WI Br	a
Ostreola equestris	X	X							?T1	VA - TX WL Br AR	a
PECTINIDAE											
Chlamys (*Argopecten*) *gibbus*	X	X	X	X	X				?T!	MD - FL TX-S Br	a
Chlamys (*Argopecten*) *irradians concentricus*	X								?T1	NJ - FL-TB LA	a
Cyclopecten nanus		X	X	X					?T1	DE-InR - TX PR	c
Pecten raveneli		X	X	X					?T1	VA-CCrl - WI GM	c
ANOMIIDAE											
Anomia simplex	X	X							T1	MA-CC - FL TX Br	a
LUCINIDAE											
Divaricella quadrisulcata	X								T1	MA - FL-S WL Br	a
Lucinoma filosum					X				T2	NFD FL-N GM	c
Lucina (*Parvilucina*) *multilineata*	X	X	X	X					?T1	VA - FL Br	a
MONTACUTIDAE											
Mysella planulata		X	X	X					T2	NS - TX WI	c
CARDITIDAE											
Pleuromeris tridentata	X	X	X	X	X				?T1	Va-Ch - FL	a
CRASSATELLIDAE											
Crassinella lunulata	X	X	X						T1	MA - FL TX Br	a
CARDIIDAE											
Laevicardium mortoni	X								T1	MA-CC - FL TX	a
Laevicardium pictum		X	X	X	X				?T1	VA-CHn FL-SE Br	4a
Laevicardium (*Dinocardium*) *robustum*	X	X							?T1	VA - FL-N TX MX	a
Nemocardium peramabile			X	X	X				T1	RI - GM Br	c
MACTRIDAE											
Mulinia lateralis	X								T2	ME - FL-N TX	a
Rangia cuneata	X	X							?T1	ChB-N - TX	a

Table 3 (continued)

	DEPTHS (m)										
	0- 10	11- 45	46- 80	81- 100	101- 246	247- 445	446- 940	940	Faunal Group	Published Range	Dens.
SOLENIDAE											
Solen viridis	X								T1	RI - FL-N GM	c
CULTELLIDAE											
Ensis directus	X	X							T2	Lab - SC FL?	a
Ensis minor	X	X							?T1	NJ - FL TX	c
TELLINIDAE											
Macoma balthica	X								B ?T2	ASEa - GA	a
Macoma mitchelli	X								?T1	VA - FL-TB TX	a
Macoma tenta	X	X							T1	CC - FL-S Br	a
Tellina agilis	X	X	X	X					AB ?T2	GSL - GA	a
Tellina versicolor	X	X	X						T1	RI - FL-KW TX WI	a
SEMELIDAE											
Abra lioica		X	X	X	X				T1	CC - FL-S WI	a
Cumingia tellinoides	X	X							T2	NS - FL-SA	a
PSAMMOBIIDAE											
Tagelus divisus	X								T1	CC - FL-S TX Br	a
Tagelus plebeius	X								T1	CC - FL TX WI Br	a
DONACIDAE											
Donax roemeri protracta 5	X	X							T1	NY - FL-S TX	a
DREISSENIDAE											
Mytilopsis leucophaeata	X								T1	NY - FL TX MX	c
CORBICULIDAE											
Polymesoda caroliniana	X								?T1	VA - FL-N TX	c
VENERIDAE											
Dosinia discus	X								?T1	VA - FL TX Bah	6a
Gemma gemma	X								T2	NS - FL TX Bah	a
Mercenaria campechiensis	X	X							?T1	NJ-S - FL TX	a
Mercenaria mercenaria	X								T2	GSL - FL GM	a
PETRICOLIDAE											
Petricola pholadiformis	X	X							T2	GSL - TX - UR	a
MYIDAE											
Paramya subovata	X								?T1	DE - FL TX	c
CORBULIDAE											
Corbula contracta	X	X							T1	CC - FL TX WL	a
Corbula swiftiana	X	X	X	X					T1 A	MA - FL TX WI	a
Corbula (Varicorbula) operculata		X	X	X	X				?T1	VA-CHm FL TX 4	a
HIATELLIDAE											
Hiatella arctica		X	X						T2	ASea - WI	a
PHOLADIDAE											
Barnea truncata		X							T1	MA - TX Br	a
Cyrtopleura costata	X								T1	MA-S TX Br	c ?
Diplothyra smithii	X								T1	MA - TX	c
TEREDINIDAE											
Bankia gouldi	X	X							?T1	NJ - FL TX Br	c
PANDORIDAE											
Pandora inflata		X	X	X	X				?T1	NJ - FL	a
Pandora trilineata	X	X							?T1	VA - FL TX 6	a
POROMYIDAE											
Poromya granulata		X			X				T2 A	ASea - WI	c
VERTICORDIIDAE											
Verticordia ornata		X	X	X	X				T1	MA - FL WI Br	a
SIPHONODENTALIIDAE											
Polyschides carolinensis		X							?T1	Va-Wach - FL TX	a

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1 Rehder, 1981
2 redescription by Mikkelsen and Mikkelsen, 1984
3 Clarke, 1962
4 Merrill, et al., 1978
5 =Donax variabilis Say
6 Franz and Merrill, 1980a

Table 4. Carolinian and Carribean marine mollusks of North and South Carolina waters. Only live-collected species having densities "a" and "c" are included; published NC-SC or UNC-IMS collection living depths indicated by an "X". Unpublished northern range extensions into North/South Carolina waters are indicated by a "#". "*" here indicates species added after 1987; their data has not been included in Tables 7-12. Note Table 2 for additional abbreviations.

	Depths (m)									
	0-10	11-62	63-100	101-246	247-445	446-940	940	Faunal Group	Published Range	Dens.
ISCHNOCHITONIDAE										
Ischnochiton striolatus	X							CR	NC - FL TX Br 5	c
TROCHIDAE										
Calliostoma euglyptum	X	X						CR	NC - FL TX MX	c
Calliostoma pulchrum	X	X	X					CR	NC - FL GM WI	c
Calliostoma yucatecanum		X	X					CR	NC - TX MX Y	c
Microgaza rotella inornata				X				CB	NC - FL Mi	c
Solariella lamellosa				X				CB	NC - FL Barb	c
SKENEIDAE										
Cyclostremiscus pentagonus		X						CR	NC - FL TX WL	c
TURBINIDAE										
Arene bairdii			X					CB	NC - FL-KW	a
Arene tricarinata		X	X					CR	NC - FL-S Br	a
Arene variabilis				X				CB	NC - FL WL Br	c
Astralium phoebium		X						CR	NC - FL WL Br	c
Turbo castanea	X	X						CR	NC - FL TX WL Br	a
PHASIANELLIDAE										
Tricolia thalassicola		X						CR	NC - FL Br	a
VITRINELLIDAE										
Vitrinella terminalis		X						CR	NC - FL-NW	c
CAECIDAE										
Caecum cubitatum		X						CR	NC - TX Br	c
Caecum floridanum		X						CR	NC - Br	c
RISSOIDAE										
Rissoina decussata		X						CR	NC - TX WI	c
Schwartziella catesbyana		X						CR	NC - TX Br	c
Zebina browniana		X						CR	NC - FL TX Br	c
TURRITELLIDAE										
Turitella (Torcula) acropora		X						CR	NC - FL TX WI	a
Vermicularia knorrii		X	X	X				CR CB?	NC - FL GM	c
SILIQUARIIDAE										
Siliquaria squamata				X				CB	NC - WI Br 1	c
CERITHIIDAE										
Cerithium atratum	X	X						CR	NC - FL-S TX Br	c
Lithopa melanostoma	X							CB	Pel NC - FL Br	c
Obtortio adamsi (=*Finella adamsi*)		X	X					CR	NC - FL Cb	a
EULIMIDAE										
Melanella conoidea		#						CR	FL WI	a
Niso aeglees		X	X	X				CR!	NC - TX WI Br	a
Strombiformis auricinctus		X						CR	NC - FL WI	a
Strombiformis bilineatus		X						CR	NC - WI	c
CREPIDULIDAE										
Calyptraea centralis		X	X					CR	NC - TX WI Br	a
Crepidula aculeata	X	X	X					CR	NC - FL TX Br	a
XENOPHORIDAE										
Xenophora conchyliophora		X	X					CR	NC - WI Br	a
STROMBIDAE										
Strombus alatus		X						CR	NC - FL TX	a
TRIVIIDAE										
Erato maugeriae	X	X						CR	NC - FL Br	c
Trivia antillarum			X					CR CB?	NC - FL-SE Br	c
Trivia maltbiana		X						CR	NC - FL Cb	c
CYPRAEIDAE										
Cypraea cervus		X						CR	NC - FL CU	c
Cypraea spurca acicularis		X	X	X				CB	NC - Y WI Br	c
OVULIDAE										
Cyphoma mcgintyi		X						CB	NC - FL Bah TX	c
NATICIDAE										
Natica canrena		X	X					CR	NC - FL WL Br	a
Polinices lacteus		X	X	X				CB	NC - FL Br	a
Sinum maculatum		X	X					CR	NC - FL WI	c
TONNIDAE										
Tonna galea		X	X					CR	NC - TX WI Br	a
FICIDAE										
Ficus communis		X						CR	NC - GM	c
CASSIDAE										
Cassis madagascariensis spinella		X						CR	NC - FL WI	c
Phalium granulatum granulatum		X	X					CR	NC-CurBh - TX Br	c

Table 4 (continued)

	Depths (m)									
	0- 10	11- 62	63- 100	101- 246	247- 445	446- 940	940	Faunal Group	Published Range	Dens.
RANELLIDAE										
Cymatium parthenopeum		X	X					CR	NC - TX Br	c
Distorsio clatharata		X	X	X				CR CB	NC - TX Br	c
Distorsio constricta mcgintyi		X	X					CR CB	NC - FL Br	c
EPITONIIDAE										
Amaea retifera		X	X					CR? CB	NC - FL Br	c
Cirsotrema dalli		X	X					CR CB?	NC FL Br	c
Depressiscala nautlae		X						CR!	NC - FL MX	c
Epitonium apiculatum	X	X						CR	NC PR	c
MURICIDAE										
Chicoreus florifer dilectus		X	X					CR	CH - FL-S GM	a
Chicoreus (*Phyllonotus*) *pomum*		X	X					CR	CH - FL Br	a
Favartia cellulosa		X						CR	NC - GM Br	c
Hexaplex (*Muricanthus*) *fulvenscens*		X	X					CR	NC-CH - FL TX	a
Murex rubidus		X	X					CR? CB	NC - FL Ba	c
Murexiella levicula		X	X					CR	NC - FL-W	a
Thais haemastoma floridana	X	X						CR	NC - FL Cb Br	c ?
CORALLIPHILIDAE										
Coralliophila caribaea		X	X					CB	SC - FL Br	c
BUCCINIDAE										
Antillophos candei			X					CB	NC - FL WI Br	c
Cantharus multangulus		X						CR	NC - Y CU	c
Engina corinnae		#	#					CR CB	SE of FL	c
Pisania tincta	X	X	X					CR!	NC - FL TX WL Br	a
COLUMBELLIDAE										
Anachis (*Costoanachis*) *floridana**	X							CR	NC - FL-SE TX	c
Nassarina glypta		X	X					CR! CB!	NC - GM	c
Nassarina (*Steironepion*) *minor*		X	X					CR CB	NC - FL-W WL	a
Suturoglypta iontha		X	X					CR	NC - FL-KW - TX 2	c
FASCIOLARIIDAE										
Columbraria lanceolata		X	X					CR? CB	NC - FL Br	c
Fasciolaria lilium hunteria	X	X	X					CR!	NC - AL	a
Fasciolaria tulipa		X	X					CR	NC - FL-S TX WI Br	c
Pleuroploca gigantea		X	X					CR	NC - FL TX Y	c
NASSARIIDAE										
Nassarius albus		X	X					CR CB?	NC - FL TX WL Br	c
OLIVIDAE										
*Oliva bifasciata bellingi**			X					CB	NC! FL-Mi WI	c
Oliva sayana		X						CR	NC - FL GM Br	a
Olivella bullula				X				CB	NC - FL-SE Cb	c
Olivella floralia	X	X	X					CR	NC-CurBh - FL WL Br	a
Olivella pusilla		#						CR	FL	c
Olivella watermani			#	#				CB	FL-FK GM Br	a
MITRIDAE										
Mitra fulgruita 3		#	#					CB	FL CU Br	c
COSTELLARIIDAE										
Vexillum wandoense		X						CR? CB	NC - FL-Y GM	a
MARGINELLIDAE										
Dentimargo aureocinctus		X	X					CR!CB!	NC - FL WL Br	a
Marginella apicina		X	X					CR	NC - FL GM WI	c
Marginella bella		X	X					CR	NC - FL-KW	c ?
Marginella limatula		X	X					CB!		c
Marginella virginiana		X	X					CR	NC FL-W Y	a
CANCELLARIIDAE										
Axelella smithii		X	X					CR ?	NC Y	c
Cancellaria reticulata		X						CR	NC - FL TX Cb - Br	c
CONIDAE										
Conus delessertii		X	X					CR CB	SC - FL-KM GM	a
Conus floridanus		X	X					CR CB	NC - FL	c
TEREBRIDAE										
Terebra concava		X						CR	NC-CurBh - FL TX Br	a
Terebra protexta			X					CR! CB!	NC - FL TX Br	c
TURRIDAE										
Bellaspira pentagonalis		X	X					CR CB?	NC - FL LAnt	c ?
Cerodrilla simpsoni		X						CR	NC - GM	a
Cryoturris cerinella	X							CR	NC - FL TX 1	c
Cryoturris citronella		X						CR	NC - FL	a
Cryoturris fargoi		#						CR	FL-W	c
Inodrilla aepynota		X	X					CR? CB	NC - FL-SE	a

Table 4 (continued)

	Depths (m)									
	0-10	11-62	63-100	101-246	247-445	446-940	940	Faunal Group	Published Range	Dens.
Ithycythara psila		X	X					CR! CB!	NC - PR	c
Kurtziella atrostyla		X						CR! CB!	NC - FL TX WI	a
Kurtziella limonitella		X	X					CR CB?	NC - FL	a
Kutziella rubella		X	X					CR	NC - FL-SE TX	a
Mangelia (Brachycythara) barbarae		X						CR	NC-CF - FL	a
Mangelia (Brachycythara) biconica		X						CR CB?	NC - WI GM Y	c
Mangelia (Glyphoturris) rugirima		#	#					CR CB?	FL-S	c
Nannodiella oxia		X						CR!	NC - FL GM Y	a
Nannodiella vespuciana		X						CR! CB!	NC FL TX WI	c
Pyrgocythara metria		X						CR	NC - GM TX	c
Splendrillia moseri		X						CR	NC - GM Bar	a
ARCHITECTONICIDAE										
Architectonica nobilis		X	X					CR CB?	NC - TX Br	c
Heliacus bisulcus		X						CR CB?	NC - TX Br	c
Philippi krebsii			X					CB	NC - FL-SE Br	c
RETUSIDAE										
Retusa (Pyrunculus) caelatus		X						CR CB?	NC - FL-SE TX	a
Retusa sulcata		X						CR	NC - FL-SE WI	a
Volvulella persimilis		X						CR! CB!	NC - FL-SE TX Br	a
HAMINEIDAE										
Atys sandersoni		X	X					CR	NC - FL-SE WL Br	c
SCAPHANDRIDAE										
Acteocina candei	X	X						CR!	NC-CH - FL - AR	a
Cylichnella bidentata		X	X					CR! CB!	NC - FL - Br TX	a
Scaphander watsoni		X	X	X				CR? CB	NC-CH - FL Bar VN	c
PHILINIDAE										
Philine sagra		X						CR! CB!	NC - FL Br	a
PYRAMIDELLIDAE										
Cyclostremella humilis		X						CR	NC-CH - TX Lant	c
Odostomia emeryi		#						CR ?f	FL-SP	c
Odostomia teres	X							EN CR!	NC SC	c
Pyramidella crenulata		X	X					CR! CB!	NC - TX WI 1	c
APLYSIIDAE										
Bursatella leachii pleii	X							CR	NC - FL WL Br	c
OCTOPODIDAE										
Octopus briareus				X				CB	NC - FL WI	c ?
NUCULIDAE										
Nucula crenulata				X				CB	SC - FL TX BR	c
ARCIDAE										
Anadara brasiliana	X							CR	NC - FL-W TX Br	c
Anadara floridana		X	X					CR	NC - TX FL GAnt	a
Arca imbricata	X	X						CR	NC - TX WL Br	a
Arca zebra	X	X	X	X				CR	NC - FL TX-S Br	a
Arcopsis adamsi		X	X					CR	NC - FL-W TX Br	a
Barbatia candida	X	X	X	X				CR	NC - TX Br	a
Barbatia domingensis	X	X	X					CR	NC - TX Br	a
GLYCYMERIDIDAE										
Glycymeris americana		X	X	X				CR! CB!	NC - FL TX Br	a
Glycymeris pectinata		X	X					CR CB?	NC - FL TX Br	a
MYTILIDAE										
Botula fusca	X	X						CR CB?	NC - FL WI Br	c
Brachidontes exustus	X	X						CR!	NC - TX WI Br	a
Gregariella coralliophaga		X						CR	NC - TX WI Br	c
Lithophaga aristata		X	X					CR	NC - TX FL WI	a
Lithophaga bisulcata	X	X						CR!	NC - TX FL Br	a
Modiolus americanus	X	X						CR	SC - FL Br	a
Modiolus modiolus squamosus	X	X						CR	NC - TX - Car	c
Musculus lateralis	X	X	X					CR!	NC - FL TX WI Br	a
PINNIDAE										
Atrina rigida	X	X						CR	NC - FL-S Cb	c
Atrina seminuda	X	X	X					CR	NC - TX - AG	c?
Atrina serrata	X	X	X					CR	NC - FL TX WL	c?
PTERIIDAE										
Pteria colymbus	X	X	X					CR	NC - FL TX WL Br	a
OSTREIDAE										
Cryptostrea permollis	X	X						CB	NC - FL WI? GM	c
PLICTULIDAE										
Plicatula gibbosa		X	X	X				CR CB?	NC - FL TX WI Br	a
PECTINIDAE										
Aequipecten muscosus		X	X					CR? CB	NC - FL TX - Br	a

Table 4 (continued)

	Depths (m)									
	0-10	11-62	63-100	101-246	247-445	446-940	940	Faunal Group	Published Range	Dens.
Chlamys benedicti			#	#				CR	FL-S - TX	a
Lyropecten (*Nodipecten*) *nodosus*		X	X	X				CR CB?	NC - FL TX Br	a
AMOMIIDAE										
Pododesmus rudis		X	X					CR CB	SC - FL TX Br	c
LIMIDAE										
Lima pellucida	X	X	X					CR	NC - FL TX Br	a
Limatula setifera		X	X	X				CR CB	NC - WI	c
Limea bronniana		X	X	X				CR CB?A	NC - FL WI	c
LUCINIDAE										
Linga (*Parvilucina*) *blanda*		X	X					CR CB	NC - Br	a
Lucina leucocyma			X					CR CB	NC - FL Bah	c
UNGULINIDAE										
Diplodonta punctata	X	X	X	X				CR! CB!	NC - FL Br	a
Diplodonta semiaspera	X	X						CR ?CB	NC - FL TX WI Br	c
CHAMIDAE										
Arcinella cornuta		X	X					CR	NC - FL TX MX	a
Chama congregata	X	X	X	X				CR! CB!	NC - TX Br	a
Chama macerophylla		X	X	X				CR CB	NC - FL Br	a
Pseudochama radians		X	X					CR CB	NC - TX WI Br	a
CARDITIDAE										
Glans dominguensis			X					CR CB	NC - FL-SE WI	c
Pteromeris perplana		X	X	X	X	X	X	CR CB BTH and A	NC - FL-S	a
ASTARTIDAE										
Astarte nana			X					CR CB	NC - FL GM	a
CRASSATELLIDAE										
Eucrassatella speciosa		X	X					CR	NC - FL WI	a
CARDIIDAE										
Laevicardium laevigatum		X	X					CR	NC-CurBh - FL Br	a
Papridea soleniformis		X	X	X				CR CB	NC - FL Br	c
Trachycardium egmontianum	X							CR	NC - FL-S WI	a
Trachycardium muricatum	X							CR	NC - FL TX AG 1	a
Trigoniocardia (*Americardia*) *media*		X	X	X				CR CB	NC - FL-SE Br	c
MACTRIDAE										
Anatina anatina	X							CR	NC - FL TX Br	c
Mactra fragilis	X	X						CR	NC - FL TX WI Br 1	c ?
Spisula raveneli	X	X						CR	NC - FL	a
MESODESMAIIDAE										
Ervilia concentrica		X						CR CB	NC - FL Br	a
TELLINIDAE										
Strigilla mirabilis	X	X						CR!	NC - TX Car Br	a
Tellina aequistriata	X	X						CR!	NC - TX Br	a
Tellina alternata	X	X						CR! CB!	NC - FL -TX	a
Tellina americana			X					CR CB	NC - MS Bar	c
Tellina iris	X	X						CR!	NC - FL TX	c
Tellina listeri		X	X					CR	NC - FL-S Br	a
Tellina nitens		X	X					CR	NC - TX Br	c
Tellina squamifea				X				CB	NC - FL - TX	c
Tellina sybaritica			X					CB CB	NC - FL Br	a
DONACIDAE										
Donax parvula	X							CR	NC-OC - TX 4	c
SEMELIDAE										
Abra aequalis	X	X	X					CR! CB!	NC - TX WI Br	a
Semele bellastriata		X	X	X				CR! CB!	NC - FL TX WI Br	a
Semele proficua	X							CR	NC - FL TX Br	a
Semele purpurascens		X	X	X				CR CB	NC - FL-S WI Br	a
Semelina nucloides		X	X					CR CB	NC - GM WL	a
PSAMMODIIDAE										
Solecurtus cuminguanus		X	X					CR!	NC - FL-S TX Br	c
VENERIDAE										
Calista eucymata		X	X	X				CR CB	NC - FL-S TX B	c
Callista (*Macrocallista*) *maculata*		X	X					CR	NC - FL TX Br	a
Callista (*Macrocallista*) *nimbosa*	X	X						CR!	NC - FL TX Br 1	a
Chione cancellata	X							CR CB	NC-CurBh - FL TX Br	a
Chione cancellata mazycki		X	X					CR CB		c
Chione grus	X	X	X					CR CB	NC - FL TX	a
Chione intapurpurea	X	X	X					CR CB	NC - TX WI Br	a
Chione latilirata		X	X					CR! CB!	NC-CurBh - FL TX Br	a
Dosinia elegans		X						CR!	NC - TX Cb	c
Gouldia cerina		X	X	X				CR CB	NC - FL WI Br	a

Table 4 (continued)

	Depths (m)									
	0- 10	11- 62	63- 100	101- 246	247- 445	446- 940	940	Faunal Group	Published Range	Dens.
Mercenaria campechiensis	X							T2 CR?	GSL - FL GM	a
Pitar fulminatus			X	X				CR CB	NC - FL WI Br	a
Ventricolaria rugatinaria			X	X				CB	NC - FL-SE WI	a
PERTICOLIDAE										
Petricola typica	X	X						CR	NC - FL Br	c
CORBULIDAE										
Corbula barrattiana	X	X	X					CRCB?BTH	NC - FL Br	a
Corbula dietziana	X	X	X	X				CR CB	NC - FL-SE WI Br	a
GASTROCHAENIDAE										
Gastrochaena hians	X	X	X	X				CR CB	NC - TX WI Br	a
HIATELLIDAE										
Panopea bitruncata	X							CR	NC - FL TX	c ?
PHOLADIDAE										
Martesia cuneiformis	X	X						CR	NC - TX Br	a
Pholas campechiensis	X?							CR	NC - TX Br	c
TEREDINIDAE										
Bankia fimbriatula								?CB ?CR	NC - FL-S WI Br	c
PANDORIDAE										
Pandora arenosa		X	X					CR! CD!	NC - WI MX	c
Pandora bushiana		X	X					CR	NC - FL TX WI Br	c
LYONSIIDAE										
Entodesma beana		X						CR	NC - FL WI Br	a
CUSPIDARIIDAE										
Cardiomya costellata		X	X	X	X	X		CR!BTH A?	NC - FL WI	c
DENTALIIDAE										
Dentalium americanum ?f	X							CR	NC - TX	c
Dentalium laqueatum laqueatum		X	X					CB	NC - FL-S WI	a
Episiphon sowerbyi		X	X					CB	NC - FL TX LAnt	c
Graptacme eborea	X	X						CR CB!	NC - FL TX WI	a
SIPHONODENTALIIDAE										
Cadulus tetraschistus		X	X					CR CB?	NC - FL WI Ber	a

1 Rehder, 1981
2 Radwin, 1978
3 Cernohorsky, 1976
4 Morrison, 1971
5 Ferreira, 1985

Table 5. Abyssal and bathyal province marine mollusks of North and South Carolina waters. Only live-collected species densities are included; published NC-SC or UNC-IMS collection living depths are indicated by an "X". Note Table 2.

	DEPTHS (m)										
	0-10	11-45	46-80	81-100	101-246	247-445	446-940	940	Faunal Group	Published Range	Dens.
TROCHIDAE											
Solariella infundibulum									A	MA - NC Ber Br	s
SKENEIDAE											
Ganesa proxima								X	A	NC -FL FR	s
NATICIDAE											
Polinices (*Lunatia*) *pallidus*							X	X	A AB!	ASea NC 1 MNAm Europe	s
CASSIDAE											
Oocorys sulcata							X		A BTH	NC - LAnt BNA	s
BUCCINIDAE											
Colus obesus								X	A	MA - FL-FR	s
Colus pubescens			X	X	X	X	X	X	AB A	ASea - SC	c
Mohnia caelatulus								X 2	A B !	GB - NX BNAm	s
TURRIDAE											
Drillia cf. *oleacina*							X		BTH A?	GM Cuba 3	s
Gymnobela agassizii							X	X	T1 A	S of MV - WI BNAm	s
Oenopota subvitreus								X	A EN	NC	s
Pleurotomella atypha							X	X	EN A BTH	NC-CF	s
Pleurotomella bairdii							X	X	A BTH	off DB & ChB BNAm	s
Pleurotomella sp.								X	A		s
Propebela subvitrea								X	A EN	NC	s
PYRAMIDELLIDAE											
Pyramidella lissa						X			?EN BTH	NC-CH	s
SCAPHANDRIDAE											
Scaphander punctostriatus						X	X	X 2	T2 A	ASea - FL WI BNew	s
LIMACINIDAE											
Limacina inflata								X	WW A	N-At - FL Br WW	c
Limacina lesueurii								X	WW A	MA - Br Pacific	s
Limacina trochiformis									A	MA - GM Ber Br	s
CAVOLINIIDAE											
Cavolinia gibbosa								X	A WW	WW	s
Cavolinia longirostris	X	X	X	X	X	X	X	X	WW A	WW	a
Cavolinia tridentata	X	X	X	X	X	X	X	X	WW A	NFD - GM WW	c
Cavolinia uncinata								X	WW A	NFD - Br WW	c
Clio recurva									WW A	NY - GM	s
Creseis acicula								X	WW A	AT and Pacific	c
Creseis virgula virgula									?WW A	AT	s
Diacria quadridentata								X	WW A	WW	c
Diacria trispinosa								X	WW A	NS - Br WW Pacific	c
Hyalocylix striata								X	WW A	NS - GM Br	c
PERACLIDAE											
Peracle reticulata								X	A WW	WW Pacific	s
Peracle triacantha								X	A ?WW	N-AT off Ber	s
ARGONAUTIDAE											
Argonauta argo									A WW	WW	s
MALLETIIDAE											
Mallentia obtusa								X	A	MA - NC BNAm BCan	s
LIMIDAE											
Limatula subauriculata			X	X	X				A T2	Gr - PR MX Alaska	c
THYASIRIDAE											
Thyasira tortuosa								X	B A	MA - NC BNAm	s
CARDITIDAE											
Pteromeris perplana		X	X	X	X	X	X	X	CR CB BTH A	NC - FL-S	a
SEMEDIDAE											
Abra longicallis americana							X	X	T2 A	Asea - WI BNew BNA	s
CORBULIDAE											
Corbula swiftiana	X	X	X	X					T1 A	MA - FL TX WI	a
CUSPIDARIIDAE											
Cardiomya costellata		X	X	X	X	X	X		A CR BTH	NC - FL WI BAm BGM	c
DENTALIIDAE											
Dentalium entale stimpsoni									?T2 A	NS - MA-CC BNAm 2	s
Fissidentalium meridionale verrilli								X	B A	MA - NC BNAm	c

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1 Franz and Merrill, 1980b
2 Clarke, 1962
3 Dall, 1881

Table 6. Endemic marine mollusca of North and South Carolina waters. Only live-collected species included - see Table 2 for abbreviations.

	Density	NC-SC Depth (m)	Published Range
CHAETODERMATODAE			
Falcidens sp. (?)	vr[1]	650	NC-CH
TURRIDAE			
Drillia amblytera	vr	260	NC-CH
Glyphostoma elsae	vr	40	NC
Mangelia leuca	vr	1103	NC-CL
Pleurotomella atypha	s	597-1900	NC-CF
Pleurotomella chariessa phalera	s	680-1338	NC-CF
Pleurotomella leptalea	vr	1184	NC-CF
Pleurotomella sulcifera	vr	1184	NC-CF
Oenopta subvitrea	s	1543	NC
MATHILDIDAE			
Mathilda scitula	s	55-119	CH
PYRAMIDELLIDAE			
Odostomia teres	c	3-44	NC-SC
Pyramidella lissa	s	260	NC-CH
DORIDIDAE			
Chromodoris morchi	vr		NC-CL
Chromodoris aila	s	<3	NC
POLYCERATIDAE			
Polycera chilluna	vr	<3?	NC-B
DENDRODORIDIDAE			
Doriopsilla leia	s	<3?	NC-B
ALLOPOSIDAE			
Heptapus danai	vr (?)	100	Off NC

[1] Sheltema, 1985

Table 7. Percent species per province and overlapping provinces.

Faunal Areas	% Species	
	live collected	total collected
Arctic-Boreal	1	1
Boreal	5	4
Transhatteran	22	12
Carolinian	26	14
Caribbean	10	18
Bathyl	< 1	2
Abyssal	4	9
Endemic	3	4
Worldwide	2	3
Unknown	< 1	7
Abyssal + Artic-Boreal	< 1	1
Abyssal + Boreal	2	4
Abyssal + Transhatteran	3	4
Arctic-boreal + Boreal	< 1	< 1
Arctic-boreal + Transhatteran	< 1	< 1
Boreal + Transhatteran	< 1	< 1
Transhatteran + Carolinian	0	< 1
Carolinian + Caribbean	18	10
Caribbean + Bathyl	1	1
Bathyl + Abyssal	1	2
Abyssal + Arctic-Boreal + Transhatteran	0	< 1
Abyssal + Boreal + Transhatteran	0	< 1
Carolinian + Caribbean + Bathyl	< 1	< 1
Caribbean + Bathyl + Abyssal	0	2
Bathyl + Abyssal + Boreal	< 1	< 1
Carolinian + Caribbean + Bathyl + Abyssal	< 1	< 1
% non-overlapping faunas (endemic, worldwide, Unknown not included)	68	60
% overlapping faunas	26	26
Total species	640	1548

Table 8. Percent species per province and overlapping provinces.

Faunal Areas	% Species Live Collected	% Total Species Collected
Arctic-Boreal	1	1
Boreal	5	4
Transhatteran	22	12
Carolinian	26	14
Caribbean	10	18
Bathyl	< 1	2
Abyssal	4	9
Endemic	3	4
Worldwide	2	3
Unknown	< 1	7
Abyssal + Artic-Boreal	< 1	1
Abyssal + Boreal	2	4
Abyssal + Transhatteran	3	4
Arctic-boreal + Boreal	< 1	< 1
Arctic-boreal + Transhatteran	< 1	< 1
Boreal + Transhatteran	< 1	< 1
Transhatteran + Carolinian	0	< 1
Carolinian + Caribbean	18	10
Caribbean + Bathyl	1	1
Bathyl + Abyssal	1	2
Abyssal + Arctic-Boreal + Transhatteran	0	< 1
Abyssal + Boreal + Transhatteran	0	< 1
Carolinian + Caribbean + Bathyl	< 1	< 1
Caribbean + Bathyl + Abyssal	0	2
Bathyl + Abyssal + Boreal	< 1	< 1
Carolinian + Caribbean + Bathyl + Abyssal	< 1	< 1
% non-overlapping faunas (endemic, worldwide, Unknown not included)	68	60
% overlapping faunas	26	26
Total Species	640	1548

Table 9. Percent provinces north or south of Cape Hatteras: n = total number of species north or south of Cape Hatteras - species having worldwide distribution not included.

	Percent			
Provinces	N. of Cape Hatteras	N. of Cape Hatteras[1]	S. of Cape Hatteras	S. of Cape Hatteras[1]
Arctic-Boreal	5	8	1	1
Boreal	14	23	2	3
Transhatteran #2	9	14	5	6
Transhatteran #1	21	34	11	14
Carolinian	5	8	22	28
Caribbean	3	5	29	36
Bathyl	< 1	< 1	6	8
Abyssal	40	-	21	-
Endemic	4	6	4	5
n	915	551	1733	1369

[1] n = total number of species less number of abyssal species.

Table 10. Percent habitat and feeding type of North and South Carolina Gastropoda by faunal region - gastropods having "very rare" density not included.[1,5]

		HABITAT TYPE[3]							FEEDING TYPE[3]							
FAUNAL REGION	NUMBER GASTROPOD SPECIES[2]	HARD S.	SOFT S.	SESSILE	PELAGIC	SWIM.	COMM.	UNKNOWN	HERB.	GRAZ.	DEP.F.	PLANK.	CARNIV.	PAR.	SCAV.	UNKNOWN
Arctic-boreal[4]	2 21	0 45	100 64		0 5				0 36	0 41		0 5	100 55	0 5	50 10	
Boreal	14 24	36 29	93 92			0 4			7 17	7 22			57 42	29 38	21 12	
Arctic-boreal+ Boreal	17 26	24 32	94 82		0 4	6 4			6 21	0 18		0 4	59 43	29 32	24 14	
Transhatteran#2	14 16	50 50	57 75	7 6		7 6			14 25	14 12		7 6	43 44	14 12	14 12	
Transhatteran#1	52 62	65 65	77 76	6 5	2 2	6 5	0 2	0 2	17 18	23 21	2 2	12 10	58 56	8 10	4 5	
Total Transhatteran	64 78	62 60	67 71	6 5	2 1	6 5	0 1	0 1	17 19	22 19		8 6	53 54	8 10	6 6	
Abyssal (>100 m)[4]	27 149	33 37	89 77		11 4				11 32	11 31	0 4	11 4	78 58	0 6	0 6	
Endemic[4]	14 43	29 33	71 81				0 14	7 7	0 19	21 14	0 5		57 53	14 14		7 2
Carolinian	145 189	66 69	83 75	1 1	0 1	0 1	3 5	1 1	19 23	17 22	1 2	3 2	63 59	7 5	7 6	
Caribbean	101 271	73 66	76 76	1 2	1 1	1 <1	1 5	1 4	17 20	9 18	2 22	4 3	71 61	4 9	7 4	0 1
Bathyal	16 46	50 42	75 60		0 2	0 2	0 2	12 4	38 35	38 33			56 59	6 4	6 11	

[1] Gastropod habitat and feeding types based on: Abbott, 1944 and 1974; Andrews, 1971; Bandel, 1976; Cernohorsky, 1970; Clark and Franz, 1969; Clench and Aguoya, 1943; Clench and Turner, 1964; Eyster, 1979, 1980 and 1981; Franz, 1967; Fretter and Graham, 1969; Houbrick, 1978; Hughes and Hughes, 1981; Hyman, 1967; Jensen and Clarke, 1983; Kerwin, 1972; LaFollette, 1977; Maes, 1983; Moore, 1969 and 1972; Purchon, 1968; and Robertson, 1958.

[2] Number of live-collected species on left; total number of species on right.

[3] % of live-collected species on left; % of total species on right.

[4] Data includes all densities as faunal region data is from only a few collections.

[5] Abbreviations: S. = substrate; SWIM. = swimming; COMM. = commensal; HERB. = herbivorous; GRAZ. = grazer; DEP. F. = deposit feeder; PLANK. = plankton; CARNIV. = carnivorous; PAR. = parasitic; SCAV. = scavenger.

Table 11. Percent habitat and feeding types North and South Carolina Bivalvia by faunal region - bivalves having "very rare" density not included.[1] See Table 2 for abbreviations.

Faunal Region	Number Bivalve Species[2]	Habitat Type[3]								Feeding Type[3]			
		Hard S.		Soft S.		Sessile		Comm.		Dep. F.		Plank.	
Arctic-Boreal[4]	20	50	45	75	73			0	9	50	36	50	64
Boreal	20	26	37	52	80	0	13			11	20	52	80
Arctic-Boreal + Boreal	43	46	40	75	78	4	2	7	5	25	22	75	78
Transhatteran #2	25	10	40	90	80	10	8	5	4	19	16	81	84
Transhatteran #1	59	52	51	82	83	4	3	2	2	12	12	88	88
Total Transhatteran	84	51	49	85	83	6	5	3	2	17	14	93	93
Abyssal (>100m)[4]	97	0	6	100	90			0	2	75	35	25	65
Endemic[4]	16	0	12	0	37			0	56	0	6	0	94
Carolinian	116	70	64	77	78	6	6	1	1	13	13	93	87
Caribbean	107	84	63	76	76	7	7	0	3	11	22	91	78
Bathyal	12	50	33	100	67	0	8			50	33	50	58

[1] Bivalve habitat and feeding types based on: Abbott, 1974; Hackney, 1985; Harry, 1985; Prezant, 1981; Purchon, 1968; Smith, 1945. Multiple habitat types were listed for many species, thus, total percentages generally exceeded 100%.

[2] Number of live-collected species on left; total number of species on right.

[3] % of live-collected species on left; % of total species on right.

[4] Data includes all densities as faunal region data is from only a few collections.

Table 12. Published Gulf of Mexico and Caribbean molluscan faunas and their overlap into North and South Carolina faunal zones. Unless otherwise noted, data is percent to species overlapping North and South Carolina Provinces of "abundant" or "common" density species within these waters. Referenced faunas indicated.

North Carolina - South Carolina Faunal Zones	Gulf of Mexico Faunas							Caribbean Faunas						
	A	B	C	D	E	F	G	H	I	J	K	L	M	N
Arctic-Boreal											1			
Boreal	<1						1							
Transhatteran #2	7	3	9	21	6	8	9	4	2		4			
Transhatteran #1	36	41	40	66	33	29	36	22	18	22	18		8	
Carolinian	35	47	31	10	35	58	34	32	52	26	28	100	32	61
Carolinian + Caribbean	17	9	18		21	4	15	30	18	25	37		27	26
Caribbean	2				3		2	8	8	18	8		18	13
Caribbean + Bathyal	<1		2	3			1	2	2		3		5	
Bathyal														
Abyssal														
Worldwide - Pelagic					2			1		8	2			
?	3													
% Transhatteran (#2, + #1) + Carolinian.	77	92	80	97	74	95	79	58	72	48	50	100	40	61
% Carolinian + Caribbean - Caribbean + Bathyal.	19	9	20	3	24	4	18	40	43	43	48	-	50	39
% Species of "abundant" & "common" densities in NC-SC waters.	57	62	62	81	71	73	46	30	27	55	30	10	11	18
% Species, all densities, in NC-SC waters.	76	65	79	86	82	82	64	48	58	80	51	26	40	48
% Of species not in NC-SC waters.	24	35	21	14	18	18	36	52	42	20	49	74	60	52
Number of species, "a" or "c" density, in NC-SC waters.	183	32	116	29	108	24	119	89	40	72	104	2	22	23
Number of species, all densities, in NC-SC waters.	247	34	147	31	126	27	186	140	85	105	173	5	82	60
Total published number of species.	323	52	186	36	153	33	186	292	147	131	342	19	207	125

References and locations:

A. Andrews, 1971. Texas coast.
B. Hildebrand, 1954. West Gulf of Mexico.
C. Sykes & Hall, 1970. Boca Ciega Bay, Florida.
D. Taylor, Hall & Saloman, 1970. Hillsborough Bay, Florida.
E. Tunnell & Chaney, 1970. One-half Fathom Reef, N.W. Gulf of Mexico.
F. Vokes & Vokes, 1983. "Characteristic" Gulf of Mexico fauna.
G. Vokes & Vokes, 1983. Total possible Gulf of Mexico species; includes "characteristic" and species of similar habitat but less occurrence.
H. Radwin, 1969. Caribbean Coast off southeastern Panama in shallow water.
I. Rice & Kornicker, 1962. Alacran Reef, Campeche Bank, Mexico. Includes additional species in an Addendum published in Rice & Kornicker, 1965.
J. Rice & Kornicker, 1965. Deeper waters of N.W. Campeche Bank, Mexico.
K. Treece, 1980. Yucatan, Mexico.
L. Vokes & Vokes, 1983. "Diagnostic" Caribbean East Coast fauna.
M. Vokes & Vokes, 1983. Total possible Caribbean East Coast fauna; include "diagnostic" and species of similar habitat but less occurrence.
N. Work, 1969. Los Roques, Venezuela - shallow water fauna.

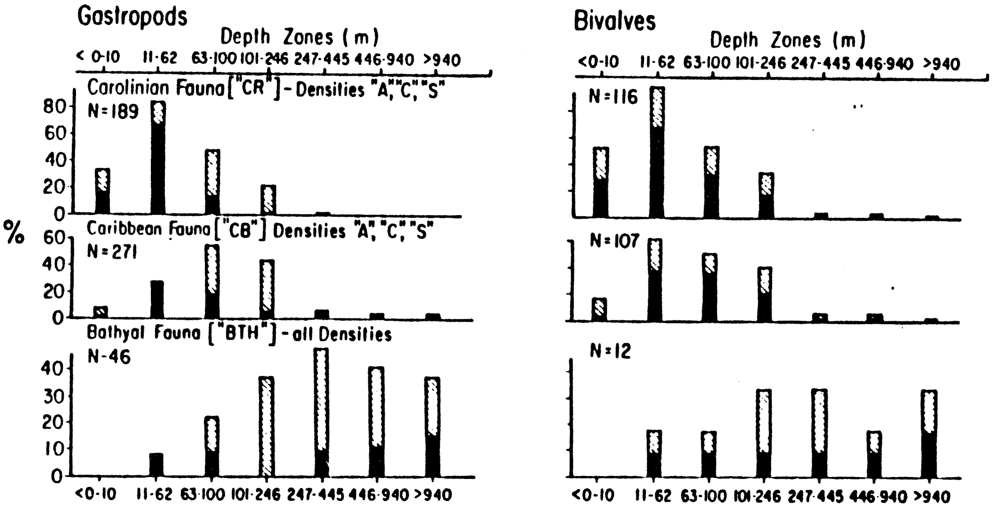


Figure 1. Percent gastropod and bivalve species per depth zone in each North and South Carolina, Carolinian, Caribbean, and Bathyal faunal province. "N" = total number gastropod or bivalve species of specifed densities believed occurring in each region; this includes species, the range of which includes North and South Carolina waters, but, within which, may never have been collected there.

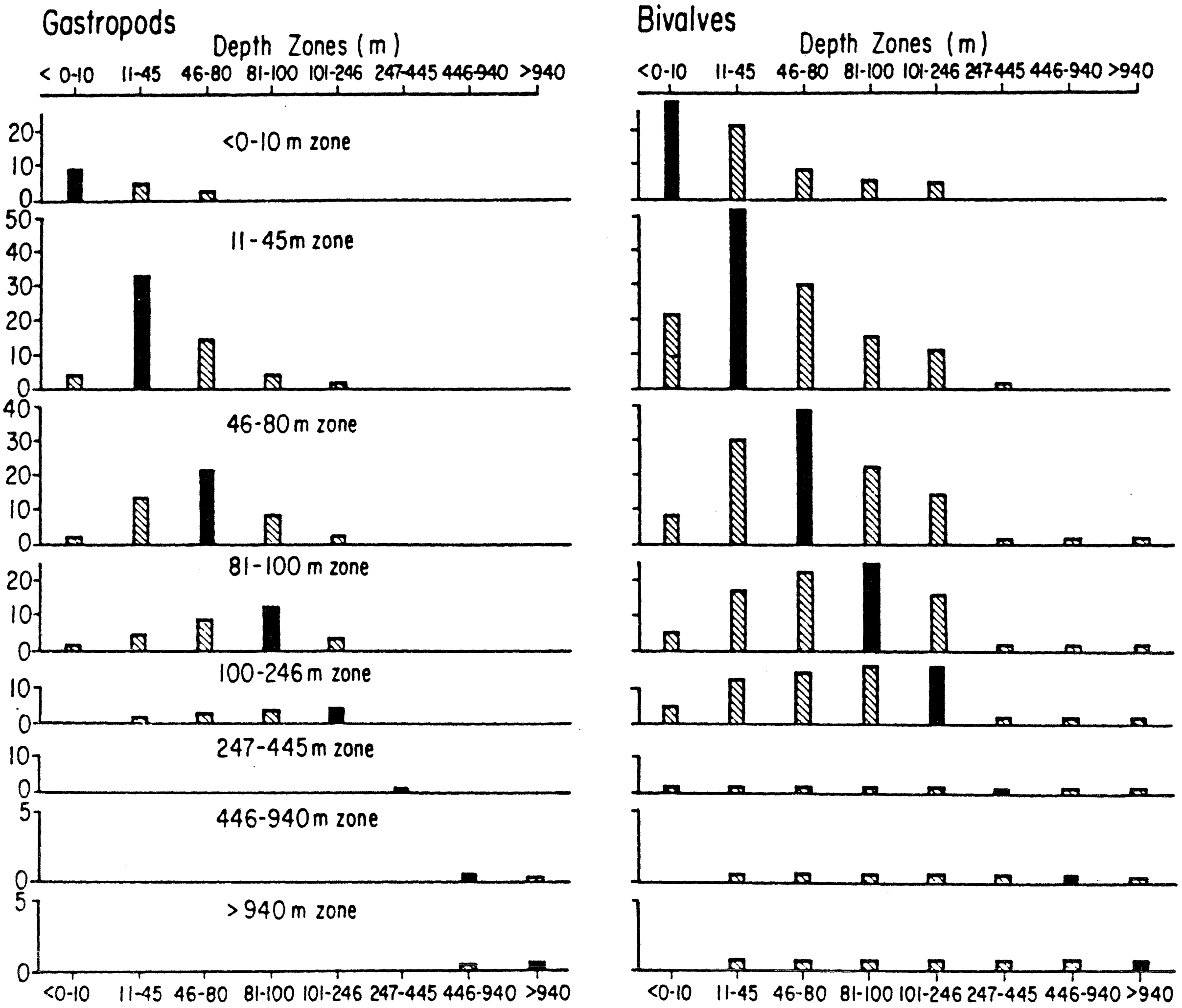


Figure 2. Percent overlap of species of each depth zone into neighboring depth zones. Solid block = percent species of a specific depth zone. Cross-hatched block = percent overlap of species of a specific depth zone at adjoining depth zones. Percent = percent of total live-collected gastropod or bivalve species (a, c, or s densities - note Table 2) of combined Carolinian, Caribbean and Bathyal province data. Gastropod n = 396; bivalve n = 163.

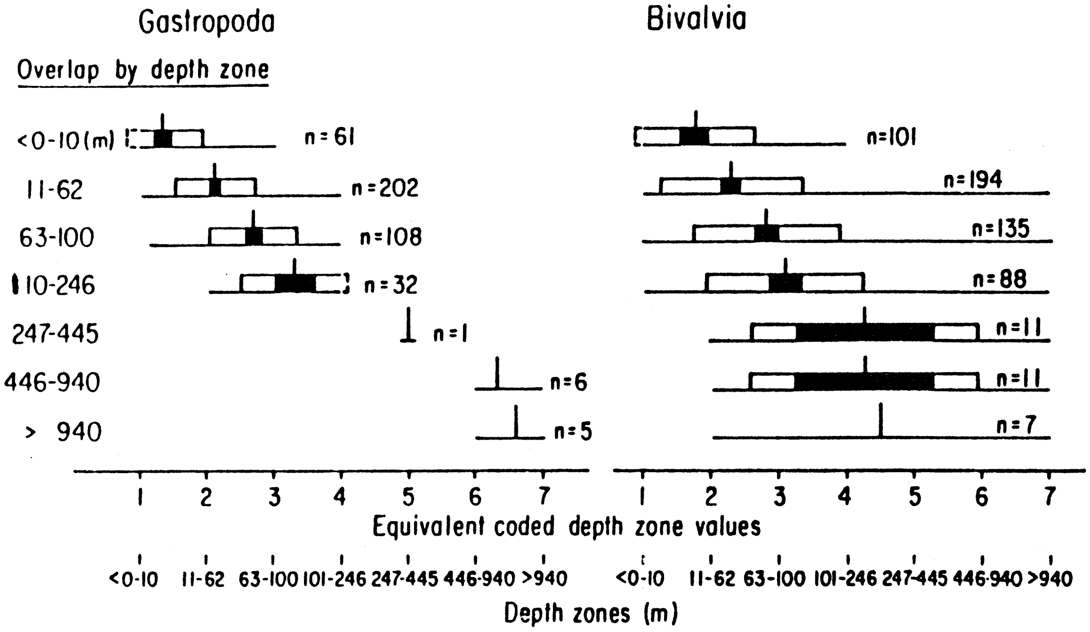


Figure 3. Depth overlaps (gastropod and bivalve species) by depth zones south of Cape Hatteras. Original depth parameters 11-45, 45-80 and 81-100 replaced by 11-62 and 63-100, see text. Depth zone values coded to facilitate analysis. Block diagrams adapted from Hubbs and Hubbs (1953); horizontal lines = range of data; vertical lines = mean coded depth; hollow blocks = range of + one standard deviation about mean; solid blocks = range of + two standard errors about mean. Considerable reliance can be placed on significance between samples (depth zones) if the solid blocks do not overlap by more than 33% of smaller solid block.

THE COMMUNITY OF SMALL MACROINVERTEBRATES ASSOCIATED WITH ROCK OUTCROPS ON THE CONTINENTAL SHELF OF NORTH CAROLINA

William W. Kirby-Smith
Duke University Marine Laboratory, Beaufort, N.C. 28516

ABSTRACT

Communities of small benthic organisms associated with rock outcrops on the continental shelf of North Carolina were examined for patterns in community structure related to season and depth. The communities were dominated by polychaetes, amphipods and molluscs. The number of species per $0.5m^2$ ranged from 40 to 214 and the number of individuals from 180 to 1657. Diversity was high with H' values of 4 to 6. Diversity was slightly greater at middle shelf stations as compared to inner and outer shelf. The number of species and individuals was greatest at all three locations in the spring and fall and least in the winter and summer: a pattern similar to that of temperate coastal plankton. An index of community similarity indicated the presence of cold (winter/spring) and warm (summer/fall) communities at each of the three locations. Moreover at the middle and inner shelf the communities were more related to season (cold and warm) than to location (inner and middle). Outer shelf communities also had a strong seasonal component but were very different when compared with the middle and inner shelf communities. Different sampling gear (grabs versus diver suction) may explain some of the outer shelf uniqueness.

INTRODUCTION

Wherever rock outcrops or biogenic structures occur in the ocean a community dominated by sessile epibenthic organisms develops. Marine ecologists have focused considerable experimental research on two very different types of hard bottom epibenthic communities: Coral Reef and Rocky Intertidal. Coral reefs have attracted attention due to the diversity of organisms and because of the very complex and extremely interesting biological interactions among organisms. On the other hand, rocky intertidal communities offer dramatic examples of how both physical and biological forces can interact to influence community organization. Other epibenthic communities have received less attention perhaps because of difficulty in their study or because they represent less distinct community types.

An excellent example of epibenthic communities which share biological characteristics with coral reefs but which are physically stressed are the temperate zone communities associated with rock outcrops on the continental shelf of the South Atlantic Bight. The rock outcrop epibenthic communities in the South Atlantic Bight have been referred to by numerous names - e.g. hard bottoms (Wenner et al., 1983; Sedberry and

VanDolah, 1984), reefs or reef-like structures (Chester et al., 1984; Parker et al., 1983; Miller and Richards, 1980; Avent et al., 1977; Cain, 1972; Pearse and Williams, 1951), sponge-coral (Wenner, 1983; Powles and Baranes, 1980), coral patch (Huntsman and Macintyre, 1971), and live bottom (Cummins et al., 1962; Struhsaker, 1969; South Carolina Wildlife and Marine Resources Department et al., 1981, 1982). These terms all refer to communities of organisms associated with rock outcrops upon which sponges and corals dominate. In addition, there is a wide diversity of plants and animals of all sizes and the benthic communities attract an equally interesting community of nekton.

Rock outcrop communities stand out on the continental shelf as biologically rich and diverse islands of varying size separated by the apparently barren adjacent sandy bottom areas. Interest in studying these communities has arisen not out of an effort to answer basic questions as to the nature of ecological community structure and function but rather because of recognition that such communities were the basis for important sport and commercial fisheries (Struhsaker, 1969; Miller and Richards, 1979). However the detailed results of several recent applied ecological research investigations (Duke University Marine Laboratory, 1982; South Carolina Wildlife and Marine Resources Department et al., 1982) do provide an excellent basis upon which basic experimental research is proceeding. The purpose of the paper presented here is to call attention to the diverse epibenthic communities of the North Carolina continental shelf by describing some of the results of an intensive investigation of these systems.

Rock outcropping is frequent in Onslow Bay, North Carolina (Cleary and Pilkey, 1968) due to a low rate of sedimentation, and a variety of types of rocky outcrops occur in this area. Outcrop strata of Oligocene and younger ages with generally low relief are widespread in the mid-shelf region of Onslow Bay (Huntsman and Macintyre, 1971; Schneider, 1976; Riggs et al., 1985) where winter bottom temperatures as low as 10.6°C have been recorded (Macintyre and Pilkey, 1969). These areas are often covered with a thin layer of sand which probably shifts during storms (Kirby-Smith and Ustach, 1986; Vaughan et al., 1987). In shallower water near the shoals of Cape Fear and Cape Lookout there are outcrops of moderate to high relief. The Cape Lookout systems are composed of late pleistocene rock outcropping (Mixon and Pilkey, 1976) probably exposed as a result of erosion by strong currents. Southeast of Cape Fear in approximately 25-30 m depth is a large area of moderate to high relief of Pliocene or Pleistocene carbonate rock (Hine and Riggs, 1986) with relief maintained by bioerosion of the ledges by the bivalve Lithophaga. Offshore along the continental shelf break is a ridge system that extends from Cape Hatteras, North Carolina, to Cape Canaveral, Florida (Blackwelder et al., 1982). This system was originally thought to be an algal reef that flourished in shallow water about 20,000 years ago (Menzies et al., 1966). Later evidence has indicated this ridge is algal limestone, sandstone, and sediment forming a veneer of predominantly Holocene, relict shallow water deposits (Macintyre and Milliman, 1970). The rock outcrop characteristics of this area probably result from the scouring action of the Gulf Stream which keeps the area free of sediments.

The South Atlantic Outer Continental Shelf Living Marine Resource Study of which this study was a part, has described in great detail the characteristics of these continental shelf epibenthic communities. Prior to this study there were few published papers available on the abundance and distribution of invertebrate species associated with rock outcrop habitats off North Carolina. Algae have been studied more intensively than invertebrates (Hoyt, 1920; Schneider, 1976; Searles and Schneider, 1980; Schneider and Searles, 1979; Peckol, 1980). Pearse and Williams (1951) described the flora and fauna of a shallow water rock outcrop. Studies of outcrop invertebrates have been limited to descriptions of specific habitats (Wells et al., 1954; Menzies et al., 1966; McCloskey, 1970; Cain, 1972) and have not treated the continental shelf as a whole. Several studies have dealt with soft-bottom habitats off North Carolina (Cerame-Vivas and Gray, 1966; Grassle, 1967; Day et al., 1971) and biogeographical analyses of the western North Atlantic (Parr, 1933; Briggs, 1974; van den Hoek, 1975; Searles and Schneider, 1980); these studies indicate that the Carolina shelf is a transitional zone where algal and invertebrate species of both northern and southern affinities can be found but with a dominance of southern taxa. Changes in water masses and annual variations in the temperature and light penetration in waters over most of the continental shelf create a changing physical environment which may dramatically influence algal and invertebrate species (Cerame-Vivas and Gray, 1966; Peckol, 1980) and, perhaps, community structure.

Earlier research on the South Atlantic on rock outcrop communities (summarized by Environmental Research Technology, Inc., 1979) had suggested that major changes in flora and fauna occur as depth increases. In more recent studies (Wenner et al., 1983) from Georgia and South Carolina (using the same sampling techniques as reported here) differences in communities were found associated with seasons and with depth in the winter but not the summer. Collections from inner and middle shelf areas formed two groups from each depth in the summer while outer shelf collections formed one major group. However, in the winter no groups associated with depth differences were identified. Diversity and density were reported to be high relative to previous studies of continental shelf soft bottom habitats. In addition to these observations the importance of sponges and corals in enhancing the total number of species and abundance of macroinvertebrates has been well documented in recent studies by Wendt et al. (1985).

In the investigations reported here three depth zones were identified: inner shelf (19-27 m), middle shelf (27-55 m) and outer shelf (55-100 m). The research was divided into two phases: a preliminary summer sampling in 1980 and a seasonal study (winter, spring, summer, fall) done in 1981. This paper presents the results of quantitative benthic sampling of five communities; two Inner Shelf, one Middle Shelf and two Outer Shelf.

METHODS

Location

Five rock outcrop areas from three distinct bathymetric zones were sampled on the continental shelf off North Carolina in Onslow Bay (Figure 1, Table 1). Two inner shelf stations were sampled, IS04 and IS05. IS04 is a rock outcrop located north of Cape Hatteras which was identified by Dr. D. Swift of the Marine Geology and Geophysics Laboratory, NOAA, Miami, Florida. This feature appears to be a relict beach rock approximately 3.7 km long and 0.9 km wide with an orientation perpendicular to the normal depth contours of the continental shelf. IS04 was selected as an example of a rock outcrop located in the colder waters of the Virginian biogeographical province. Sampling did not continue at this spot in 1981 because high turbidity and the extremely rough topography made remote sampling difficult. For these reasons a new site, IS05, was selected for the 1981 sampling effort. IS05, located south of Cape Lookout Shoals, was selected based upon detailed studies of the algae and, to a lesser extent, the benthic macroinvertebrate fauna at this location (Peckol, 1980; Peckol and Searles, 1983, 1984). The middle-shelf station (MS04) was located northeast of the shoals of Cape Fear. The general location for the MS04 site was selected by R.B. Searles (personal communication) based upon his experience sampling algae on rock outcrops in Onslow Bay. The specific area for MS04 was selected based upon preliminary sampling by the R/V EASTWARD in the summer of 1980. OS04, located approximately 46 km east-southeast of Ocracoke Inlet at the edge of the continental shelf, was selected to be representative of the northern limit of Macintyre and Milliman's (1970) reef structure (their profile A). Sampling in the summer of 1980 indicated that relief in the area was too great for trawling. For this reason the outer shelf sampling in 1981 was moved to OS05, further south along the same reef structure.

Sampling Periods and Vessels

IS04, MS04, OS04 were sampled between 15 August and 19 September in the summer of 1980. Two research vessels, R/V EASTWARD and the R/V DAN MOORE, and two commercial dive boats were used in field sampling.

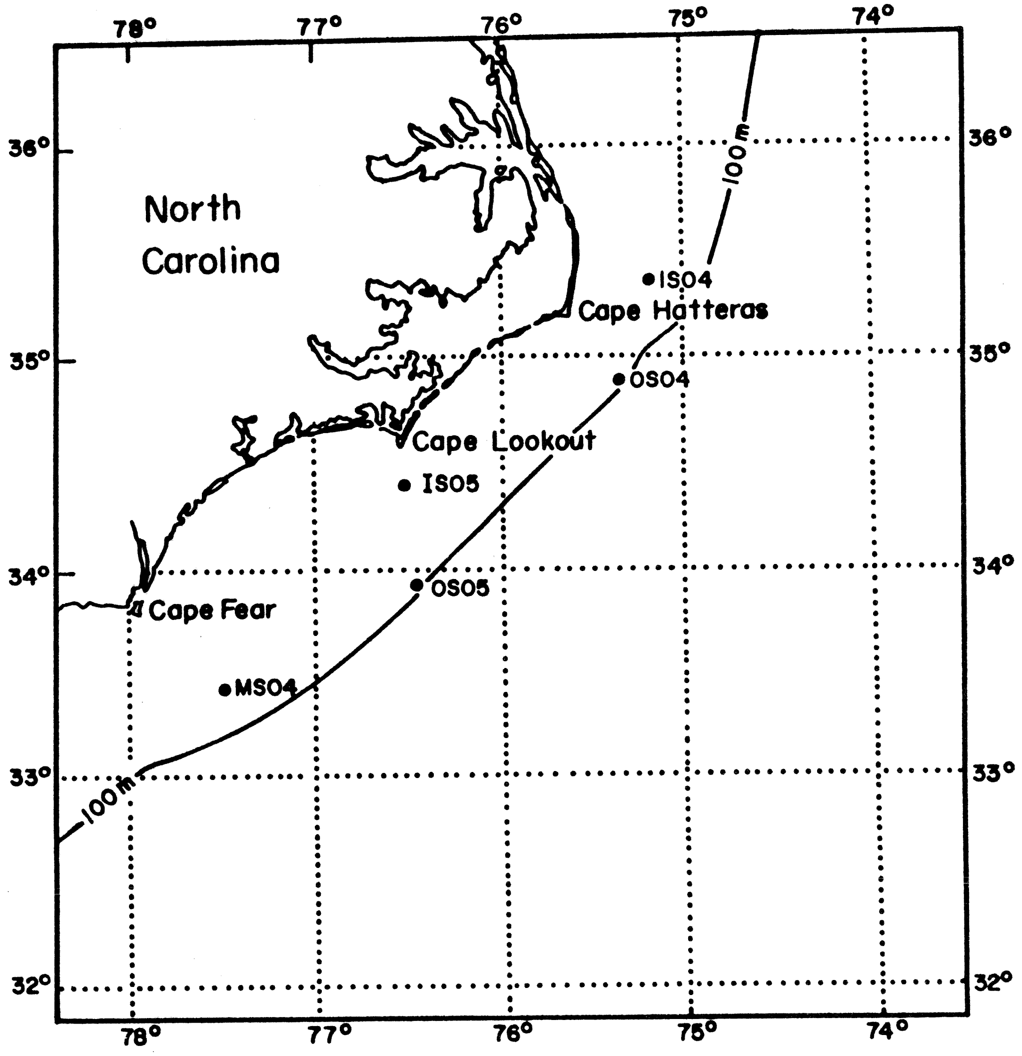


Figure 1. Location of rock outcrop site sampled in 1980 (IS04, MS04 and OS04) and 1981 (IS05, MS04, OS05).

Table 1. Location and physical characteristics of rock outcrop study sites on the North Carolina continental shelf

Site	Location		Depth (m)	Relief
	Latitude	Longitude		
IS04	32°20.5'N	75°21.6'W	16-27	very high
IS05	34°23.0'N	76°34.0'W	17-25	high
MS04	33°31.0'N	77°25.0'W	27-35	moderate
OS04	34°51.8'N	75°31.0'W	54-98	high
OS05	33°49.0'N	76°33.5'W	50-109	high

IS05, MS04 and OS05 were sampled quarterly during 1981 to provide seasonal data. Winter samples were collected between 6 February and 11 March, spring samples between 27 April and 19 May, summer samples between 15 July and 14 August, and fall samples between 5 October and 30 November.

Remote sampling in the winter was done from the R/V BLUEFIN (Skidaway Institute of Oceanography) and the R/V EASTWARD (Duke University Marine Laboratory). In the spring and summer the R/V DAN MOORE (N.C. Division of Marine Fisheries) was used and in the fall the R/V CAPE HATTERAS (Duke/University of North Carolina Oceanographic Consortium) was employed. Diver sampling was done from the R/V ONSLOW BAY (National Marine Fisheries Service) and commercial workboats. Loran C navigation was used in positioning all vessels.

Equipment and Methods

During the project communities were sampled with fathometer, TV and still camera, dredge, trawl, benthic sled, airlift suction and grab. Since only quantitative data derived from suction and grab are presented here only those sampling techniques are described. Fathometer, TV and diver observation (Duke University Marine Laboratory, 1982) were used to provide the physical characterization of the study sites.

Quantitative suction samples of smaller benthic invertebrates that were not adequately sampled by dredge and trawl were obtained at IS04, IS05 and MS04 by scuba diving. Using Loran C for positioning, divers obtained five replicate samples at each station from an area on the rock outcrop avoiding the edge of ledges and avoiding large patches of sand commonly found at the sites. A disc with five equally spaced radial marks was dropped to the bottom and a 3-m line, fastened to the center of the disc, was then used to place five open-ended quadrat boxes (0.1 m^2, 10cm walls) equidistantly around the disc. Exact positioning of the quadrat boxes was accomplished by randomly pre-selecting one of nine possible quadrat areas from a larger grid frame attached to the 3-m line. Fauna within the quadrat was sampled by scraping the area while simultaneously operating an airlift suction device similar to that described by Chess (1979). All suction samples were collected in 1.0-mm mesh bags and brought to the surface for preservation. On deck, each sample was relaxed in Epsom salts seawater, preserved in a 10% buffered seawater-formalin solution and returned to the laboratory.

At OS04 and OS05, where water depth precluded the use of a diver-operated suction device, quantitative 0.1-m^2 samples were collected with a modified Smith-McIntyre grab. Five replicate samples were collected during each season. After retrieval, each sample was placed on a 1.0-mm sieve, washed to remove the finer sediment, relaxed in Epsom salts seawater and preserved in 10% buffered seawater-formalin solution. During the summer sampling period in 1981, five replicate grab samples were also collected at IS05 and MS04 for comparison with the suction samples taken at those sites.

Biological samples collected with suction and grab were separated from non-living and inorganic material, sorted to major taxa, preserved in 50% isopropyl alcohol, and identified to the lowest taxonomic level possible. A voucher collection composed of every identified taxon was prepared. Sponges, colonial invertebrates, the polychaete Filograna implexa, and algae are not included in the analysis here because numbers of individuals could not be determined.

Cluster analysis was used to elucidate patterns of similarity among species and collections for abundance data collected by suction and grab. Replicates were pooled and data sets were reduced prior to cluster analysis because of computational constraints (computer core) and because some of the taxonomic groups could not be classified as separate species. In 1980 data sets were reduced prior to analysis by elimination of species which occurred in only one collection. In 1981 samples species which occurred in fewer than four collections were eliminated plus additional taxa because of classification problems. For gear comparison a separate cluster analysis was performed using the extra grab samples collected in the summer at IS05 and MS04 together with the grab samples from OS05.

The Bray-Curtis measure (Bray and Curtis, 1957) was used to cluster quantitative data (log transformed) collected with airlift suction and grab samplers. Normal classifications, in which collections are clustered as entities with species presence or abundance as attributes (Williams and Lambert, 1961a) were produced for each data set. Community diversity (H') was estimated by the Shannon index (Pielou, 1975).

Cluster analysis for suction and grab comparisons was done using the weighted pair-group linkage method (Sokal and Sneath, 1963) and Morisita's index of similarity (Grassle and Smith, 1976).

RESULTS AND DISCUSSION

Physical Characterization of Study Areas

Inner Shelf Stations

IS04 was approximately 3.2 km^2 with a depth range of 16-27 m. Fathometer tracings revealed an area of extremely high relief characterized by large broken ledges and isolated boulders greater than 5 m in height. There was no distinct orientation of the ledges; instead here jagged relief was indicated by sonar tracking. Because of limited visibility no television transects were made at IS04.

The second inner-shelf station IS05 consists of a flat-topped rock outcrop approximately 18-20 m deep. The irregularly shaped rock extends in an east-west direction approximately 3 km with a width of 1 km. Although fathometer tracings in this project did not delineate the rock completely, a bathymetric chart (N.O.A.A. #11520) suggests that it comes to a point on its westermost end and merges with the 10-fathom (18-m) contour of Cape Lookout shoals on its eastern end. Sharp undercut ledges 3-4 m in relief occur along the 20-m contour on the south face of this rock. To the northeast of the large rock are numerous undercut "table" rocks of varying sizes which are surrounded by sand-covered bottom. Most of these rocks were too small to appear in the fathometer tracing, although they appeared in television transects and were observed by divers. A coarse sand bottom approximately 24 m deep surrounded the rock outcrop areas sampled. Sharp undercutting of the rock areas suggested that strong currents are eroding the edge of this feature. The top of the rock area is relatively smooth with depths averaging about 18 m. Near the edges of the rock there was little sediment cover; away from the edges, however, a coarse sand veneer covered most of the rock reducing the density of attached organisms.

Middle-Shelf Station

The middle-shelf station MS04 is an extensive area of uneven bottom with moderate relief. Numerous ledges, approximately 30 m deep at their tops, occur with various orientations, but they are generally arrayed along an east-west axis. Areas to the north (33-m depth) and south (28-m depth) are relatively smooth. Although some of the ledges seen in fathometer and television transects are sharp drops of approximately 3 m, many of the ledges are relatively smooth and, while not undercut, still have approximately 3 m of relief. All of the ledges had little sediment cover and were covered with attached organisms. Away from the ledges, areas of sand were more frequent; however, there were numerous ridges of approximately 0.5 m relief which were completely covered with organisms. Even in the sandy area corals and algae were frequently seen; thus the sand veneer probably was fairly thin. Bottom erosional features (undercut ledges, broken rock) were much less apparent than at IS05.

Outer Shelf Stations

Sonar tracking indicated that rock outcrops at OS04 covered a very large area. A smaller area, 5 km^2, ranging in depth from 54-98 m, was delineated for extensive study. The fathometer transects indicated this area is a continuous reef structure with a northeast-southwest orientation and gradual rather than abrupt changes in depth along the north-south axis. Although OS04 did not appear to have the type of ledges occurring at both IS04 and MS04, the depth range at this station was much greater than at either the inner or middle shelf site. TV analysis indicated that this site, like MS04, contained extensive rock outcrop areas. In contrast to the low profile indicated by sonar tracking, the TV suggests that OS04 had a large number of boulders and ledges. Many of the ledges seen along the television transects were not distinguished by fathometer. OS04 has little sediment accumulation on the rock outcroppings; however, there was a great amount of material in the water column (suspended sediment) during television reconnaissance and transect work.

Station OS05 was located at the edge of the continental shelf southwest of OS04 and had a depth range of 50-100 m. The area between 50 and 70 m has a gently sloping, relatively smooth area with a thick to thin sand veneer. There were few rocks, yet sessile rock outcrop fauna (corals, sponges) were frequently seen on television transects. Between 70 and 100 m the slope of the bottom increases dramatically and the number of rock outcrops increases, particularly in the center of the areas studied. These rocks are generally rounded on top with a relief of approximately 1 m and few sharp ledges. In this area the rocks are often sediment-free and covered with rock outcrop organisms, particularly crinoids; they appear to be the emergent part of a larger geological structure and are probably kept sediment-free by the scouring action of the Gulf Stream. At approximately the 100 m depth there is the relict structure (Macintyre and Milliman, 1970) with a landward trough approximately 5 m deeper than the top of the ridge. This ridge area consists of rock rubble with fist-sized "lithothamnion balls" with a great diversity of motile invertebrates.

The physical characteristics of rock outcrop areas at IS04, IS05, MS04, OS04 and OS05 are representative of the range of relief (low, moderate and high) and depth ranges on which epibenthic communities occur off North Carolina. All three areas experience moderate to strong bottom currents (Kirby-Smith and Ustach, 1986) and thus are probably maintained by erosion and lack of sedimentation. None of the areas (with the possible exception of the "lithothamnion" ridge at OS05) could be considered as reefs in the geological sense of structures constructed by organisms; however, they all support a rich rock outcrop community, including the pelagic community (fish) attracted to such structures.

Distribution Patterns

Suction and grab sampling in rock outcrop areas of Onslow Bay, N.C. collected a diverse assemblage of small invertebrates belonging to five major taxonomic groupings (Table 2). Polychaetes, amphipods and molluscs were dominant with varying numbers of additional decapods and echinoderms. On a 0.5 m^2 basis (5 replicate 0.1 m^2 samples) the number of species collected ranged from a low of 70 at OS04 in the summer of 1980 to a high of 214 at MS04 in the fall of 1981. Total number of individuals ranged from 180 at OS04 in the summer of 1980 to 1657 at MS04 in the spring of 1981.

Diversity of these communities (Table 2) was high with most values greater than 5.0. The lowest diversity occurred at IS04 in the summer 1980 (H'=4.20), the station located in the Virginia province. In comparison to the other more diverse communities, this moderate diversity was due to reduced species richness coupled with dominance of three amphipods. Diversity OS05 in the spring of 1981 was also reduced (H'=4.32) due to the fact that of a total of 1379 individuals 580 belonged to the amphipod species Rildardanus laminosa. Diversity above 6.0 was found in collections at MS04 in the spring, summer and fall 1981 and at OS05 in the fall 1981. These data suggest that diversity of midshelf stations is generally greater than that found on the inner shelf or outer shelf.

The comparison of suction with grab sampling in the summer of 1981 indicated that the number of species, number individuals and the diversity of grab samples taken at IS05 and MS04 was very similar to data from suction samples taken at the same general locations. Thus, at least as far as these indices of community structure were concerned, the two techniques were similar.

Sampling in the summer of 1980 only 14 species occurred with a total abundance (all replicates at all stations=15) of 10 or more individuals (Table 3). Six of the taxa were amphipods and non-decapod crustaceans, three were molluscs, three were echinoderms and two were polychaetes. Ten of the 14 were found

Table 2. The number of species (Sp) and individuals (In) in each major taxonomic group in five replicate (0.1 m^2 each) suction (S) and grab (G) samples. Amph.+ = Amphipoda and arthropods other than Decapoda; Polyc. = Polychaetes; Mollu. = Mollusca; Decap. = Decapoda; Echin. = Echinoderms. H' = diversity

	Polyc.		Amph.+		Mollu.		Decap.		Echin.		Tot.	Tot.	H'
	Sp	In	Sp	In	Sp	In	Sp	In	Sp	In	Sp	In	
Summer 1980													
IS04 (S)	20	64	11	190	31	113	12	21	5	35	79	423	4.20
MS04 (S)	25	47	21	98	21	35	11	23	13	42	91	245	5.62
OS04 (G)	32	104	8	31	26	34	3	9	1	2	70	180	5.35
Winter 1981													
IS05 (S)	49	159	27	536	39	171	16	40	5	28	136	934	5.42
MS04 (S)	41	135	35	196	15	16	9	18	9	22	109	387	5.63
OS05 (G)	62	325	6	30	10	29	10	48	9	15	97	447	5.28
Spring 1981													
IS05 (S)	39	155	36	726	55	518	22	108	11	34	163	1541	5.38
MS04 (S)	91	847	39	489	48	243	16	32	12	46	206	1657	6.22
OS05 (G)	75	643	21	638	14	71	8	20	5	7	123	1379	4.32
Summer 1981													
IS05 (S)	33	145	22	113	57	442	21	92	8	23	141	815	5.82
IS05 (G)	23	153	33	222	46	322	23	82	8	23	133	802	5.74
MS04 (S)	43	283	20	32	51	109	19	32	10	59	143	515	6.22
MS04 (G)	44	275	40	417	61	220	10	17	7	50	163	979	6.04
OS05 (G)	36	193	20	161	15	30	10	17	5	11	86	412	5.11
Fall 1981													
IS05 (S)	44	372	28	108	58	581	25	151	10	53	165	1265	5.96
MS04 (S)	54	726	38	158	74	308	32	124	16	252	214	1568	6.06
OS05 (G)	41	403	30	212	25	65	1	1	4	14	101	695	6.40

at IS04, nine at MS04 and five at OS04. Four species common to all three stations included an amphipod, *Unicola laminosa*, two echinoderms, *Ophiothrix angulata* and *Arbacia punctulata* and one mollusc *Nassarius albus*. Six of the 14 species occurred at both IS04 and MS04 while 4 species distribution overlapped from MS04 and OS04. None of these species occurred at IS04 and OS04 without also being found at MS04; an observation which is not surprising given that IS04 was located in the Virginian province north of Cape Hatteras while OS04 was located along the edge of the shelf south of Hatteras under the Gulf Stream.

Table 3. Abundance by station of invertebrates taken during the summer 1980 by suction and grab. Total number collected in five 0.1 m^2 replicates. Only taxa having a total abundance of 10 or more individuals (0.15 individuals/m^2) are included. A=Amphipoda + Nondecapod crustaceans; E=Echinodermata; M=Mollusca; P=Polychaeta

Species	IS04	MS04	OS04
(A) *Melita appendiculata*	98	2	
(A) *Lembos smithi*	64		
(M) *Anachis lafresnayi*	45		
(A) *Lembos unicornis*	4	35	
(A) *Unicola laminosa*	3	3	21
(P) *Prionospio* sp.B			23
(E) *Ophiothrix angulata*	17	5	1
(P) *Hydroides uncinata*	16		
(E) *Ophiostigma isocanthum*		15	
(E) *Arbacia punctulata*	9	1	4
(A) *Amphithoe* sp.A		13	
(A) Phyllocarida A		11	
(M) *Urosalpinx* sp.A	10		
(M) *Nassarius albus*	8	1	1

In 1981 seasonal sampling 51 taxa of a total of 615 had 50 or more individuals or a density of 0.12/m^2 when summed over all seasons and stations (Table 4). In these samples polychaetes dominated the taxa with 22 groups followed by amphipods and non-decapod crustaceans with 13, molluscs with 11, echinoderms with 3 and decapods with 2. These species are a diverse assemblage of both epifauna and infauna attesting to the complexity of the physical environment. The community consists of animals attached to rock, animals living on colonial species or animals

Table 4. Abundance by season and station of invertebrates collected in five 0.1 m^2 suction (ISO5, MSO4) and grab (OSO5) samples, including only those taxa (51-615) that had a total abundance for the year of 50 or more individuals (0.12/m^2). Grab samples taken at ISO5 and MSO4 in the summer for gear comparison are not included. (P)=polychaete, (A)=amphipoda, (M)=mollusc, (D)=decapod, (E)=echinoderm.

Taxa (in order:rank by abundance)	Winter			Spring			Summer			Fall		
	ISO5	MSO4	OSO5	ISO5	MSO4	OSO5	ISO5	MSO4	OSO5	ISO5	MSO4	OSO5
(A) *Rildardanus laminosa*		3	10	1	7	580		1	90		1	26
(M) *Chione grus*	45			271	25		148	6		27	37	
(P) *Syllidae* (undetermined)		2	2	2	21	3	5	1	13	126	245	97
(A) *Erichthonius brasiliensis*	177	49		152	40	1	18			2	3	
(P) *Spiophanes bombyx*			101		137	90		3	4		5	
(A) *Photis* sp.	20	15		94	91		1	1	10	1	2	3
(E) *Ophiostigma isacanthum*	8	11		13			3	26		10	144	
(A) *Gammaropsis* sp.	26	10		93	38	3	4	1				14
(P) *Lumbrineris inflata*	7	7		23	13		37	16			23	53
(A) *Luconacia incerta*	18	15		71	38					10	1	24
(P) *Syllis spongicola*	1	3	11			32		4		3	117	2
(M) *Lithophaga bisulcata*	3			24	5		27	1		103	2	
(A) *Photis pugnator*	103	6		26	22			3	3	1		
(A) *Ampithoe* sp. A	62	8		50	19		16	1		4	3	
(M) *Cumingia tellinoides*	15			23	1		32	5		41	25	
(A) *Ampelisca schellenbergi*	16	4		44	18	1	22	4		21	4	
(D) *Paguristes tortugae*	10			42			27	3		33	17	
(P) *Syllis hyalina*	3	1	8	1	14	29	5	14	3	21	18	14
(A) *Lembos smithi*	6			21	67	1	1		8	5	1	16
(A) *Podocerus* sp.	24	5		24	54		4		1	4	4	2
(P) *Chone americana*	2		9	1	19	14		8	46	7		10
(M) *Laevicardium multilineatum*		1			96		1	5	2	3	2	3
(P) *Syllis regulata carolinae*			25	3	37	36	1		9		1	
(M) *Chaetopleura apiculata*			19	2	4	47	1	1	11			22
(P) *Exogone dispar*	21	3		23	27		10	21				
(D) *Pagurus carolinensis*	12			18	1		24	4		33	11	
(A) *Caprella equilibra*	6	11		57	2	1				2	2	20
(P) *Notomastus latericeus*			8			35	2	15	6	1	25	7
(M) *Gastrochaena hians*	5			24	4		14	3		43	4	
(M) *Turbonella* D							9	2		81	4	

which live in the unconsolidated sand and shelf fragments covering the rock.

Analysis of the overlap in the fauna among seasons reveals that 40 of the 51 (78% of the taxa Table 4) were present at all seasons. Additionally there is little evidence of any pattern of seasonality among the 11 taxa which were missing during one or more seasons. Analysis of degree of overlap among stations in presence/absence of the 51 taxa is presented in Figure 2. The percent of the fauna restricted to a particular depth zone was low (7-9%). As might be expected based upon distance and depth, overlap among stations was least for IS04 and OS05 (4%), somewhat greater for MS04 and OS05 (15%) and greatest for IS04 and MS04 (35%). In addition there was a relatively high overlap (23%) of taxa found at all three stations. These data suggest that there is a gradual rather than discrete change in fauna as water depths increase across the shelf.

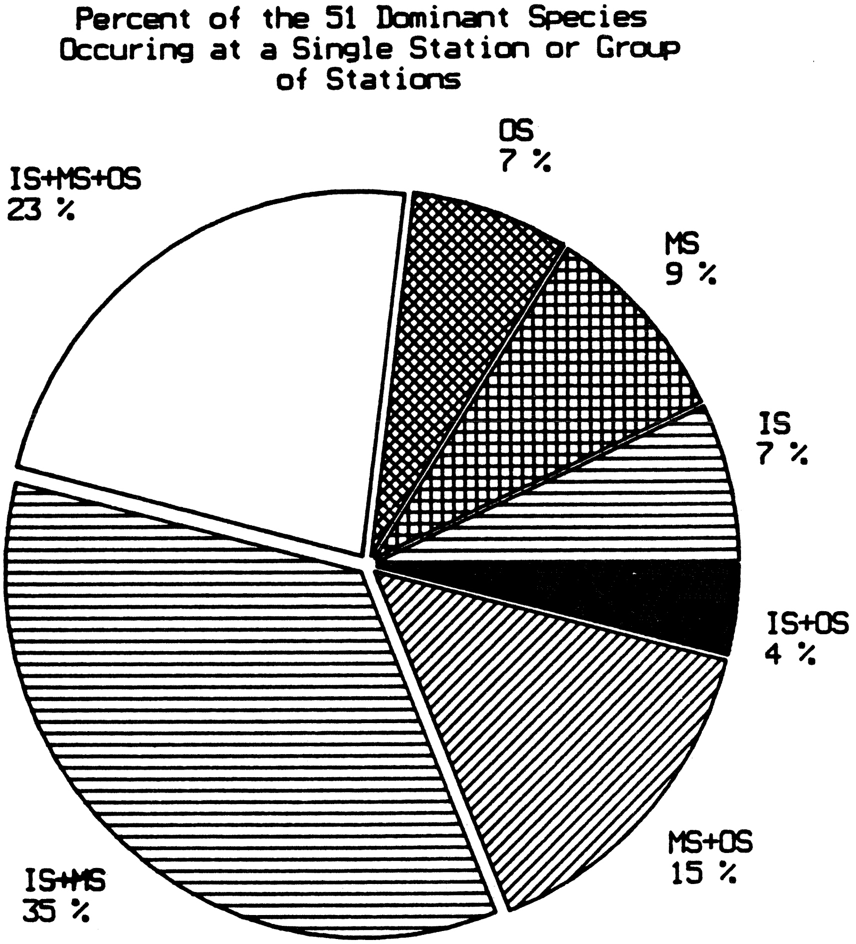


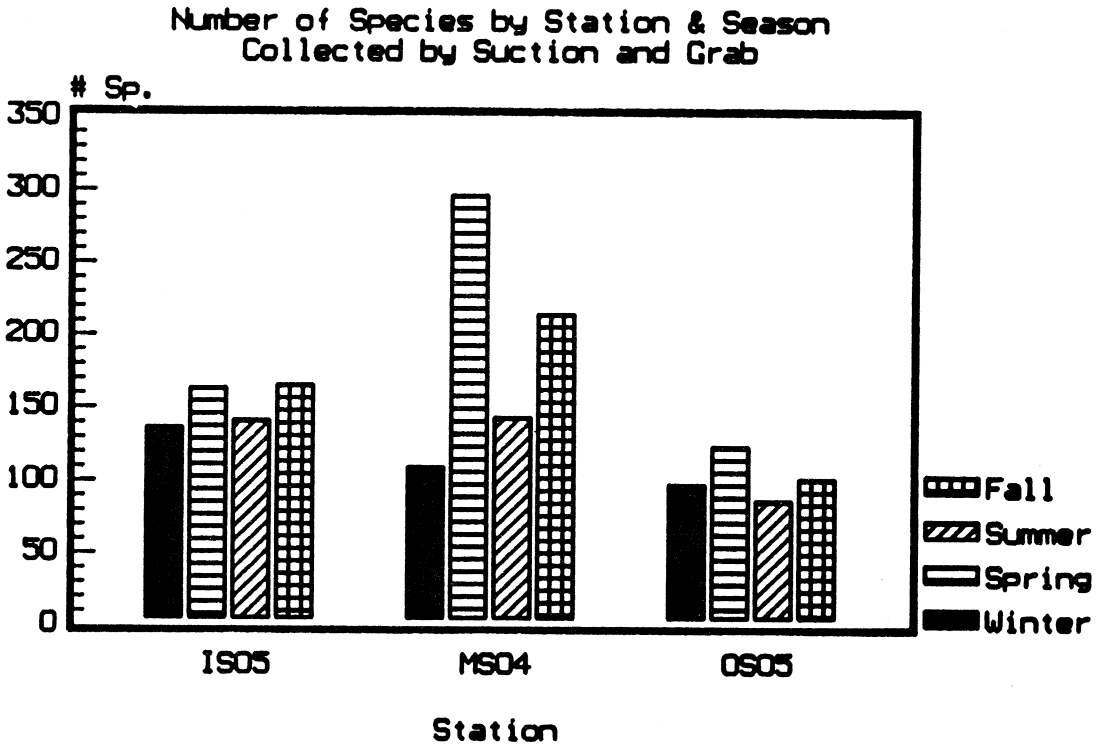
Figure 2. Overlap in the distribution of dominant taxa collected in 1981 from IS05 (IS), MS04 (MS) and OS05 (05).

Graphic presentation (Figure 3) of the variations in total number of species and individual samples at the three depths in 1981 shows that OS05 in general had the fewest species and individuals while MS04 had the greatest. This difference is probably real and not related to gear type as indicated by suction/grab comparisons (Table 2) where similar numbers of species and individuals were collected with the different gear. Strong seasonal differences are indicated by the observation that at all three stations the winter and summer samples had fewer species and individuals than did the spring and fall. Since this pattern was observed at all three stations, it appears to be predictable although the cause is not obvious. The differences were greatest at MS04 where the numbers of individuals in the winter and summer were approximately 1/3 to 1/4 the number in the winter and spring.

The patterns in seasonal changes in different groups of taxa at each station are shown in Figures 4, 5 and 6. At IS05 (Figure 4) molluscs, followed by polychaetes and then amphipods, were dominant in number of species. This pattern was also present at IS04 in the summer of 1980 (Table 2). In numbers of individuals, amphipods were dominant at IS05 in the winter and spring followed by molluscs in the summer and fall. Polychaetes were generally less abundant except in the fall. Patterns of seasonality were mixed and group dependent obscuring general patterns discussed about (Figure 3). At MS04 (Figure 5) polychaetes and molluscs were usually dominant in species. Polychaetes were dominant in numbers in the spring, summer and fall, amphipods were most abundant in the winter. The pattern of spring/fall dominance in totals shown in Figure 3 apparently was due primarily to the variation in numbers of polychaetes and secondarily to amphipods. At OS05 (Figure 6) polychaetes were by far the most numerous in terms of species followed by amphipods and molluscs with approximately equal numbers. A similar pattern was observed at OS04 in the summer of 1980. In terms of individuals at OS05 molluscs were very few with polychaetes showing dominance with amphipods. Once again the summer maximum in total number (Figure 3) is primarily due to variations in polychaetes and secondarily amphipods. In summary, polychaetes appear to be slightly less important at the inner shelf compared to the midshelf and outer shelf, amphipods are more or less equally important across the shelf while molluscs are much less important at the outershelf than in the midshelf or inner shelf. Molluscs were much more abundant in individuals at the inner shelf than elsewhere. Seasonality was particularly influenced by variations in polychaetes and amphipods.

Community Structure

Cluster analysis (Figure 7) of pooled replicates collected by station and season in 1981 revealed distinct differences among communities, which are correlated with location and time. The greatest degree of similarity was seen in the seasonal



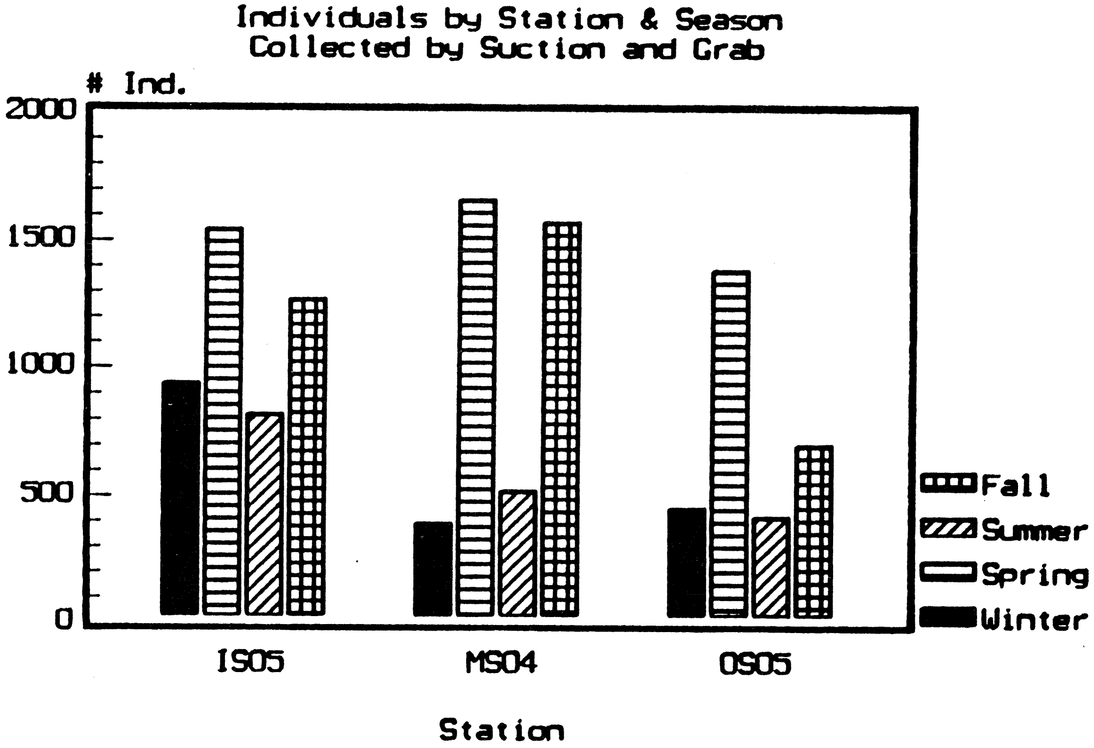


Figure 3. Total numbers of species and individuals collected in 5 replicate (0.1 m^2 each) samples during each season.

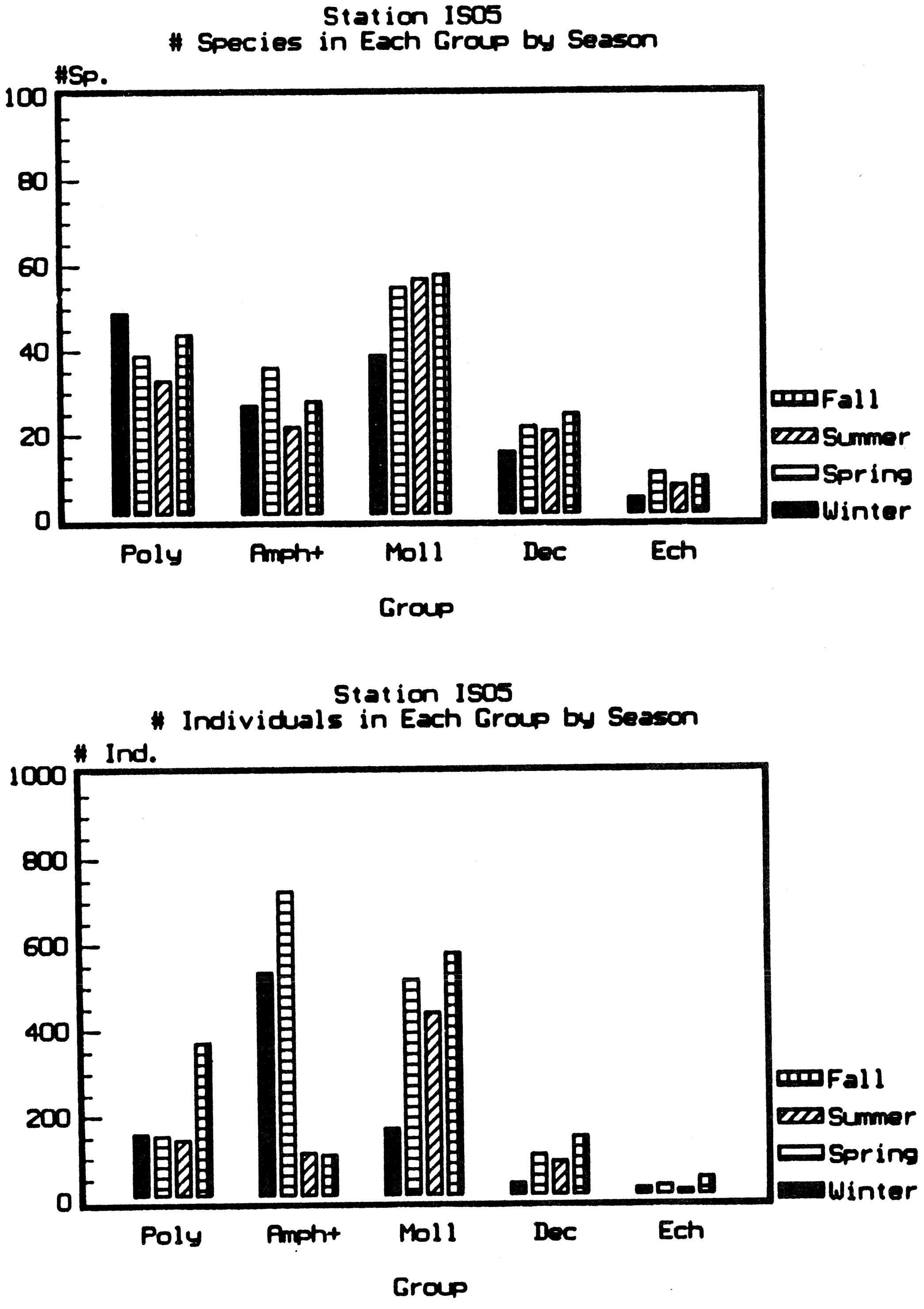
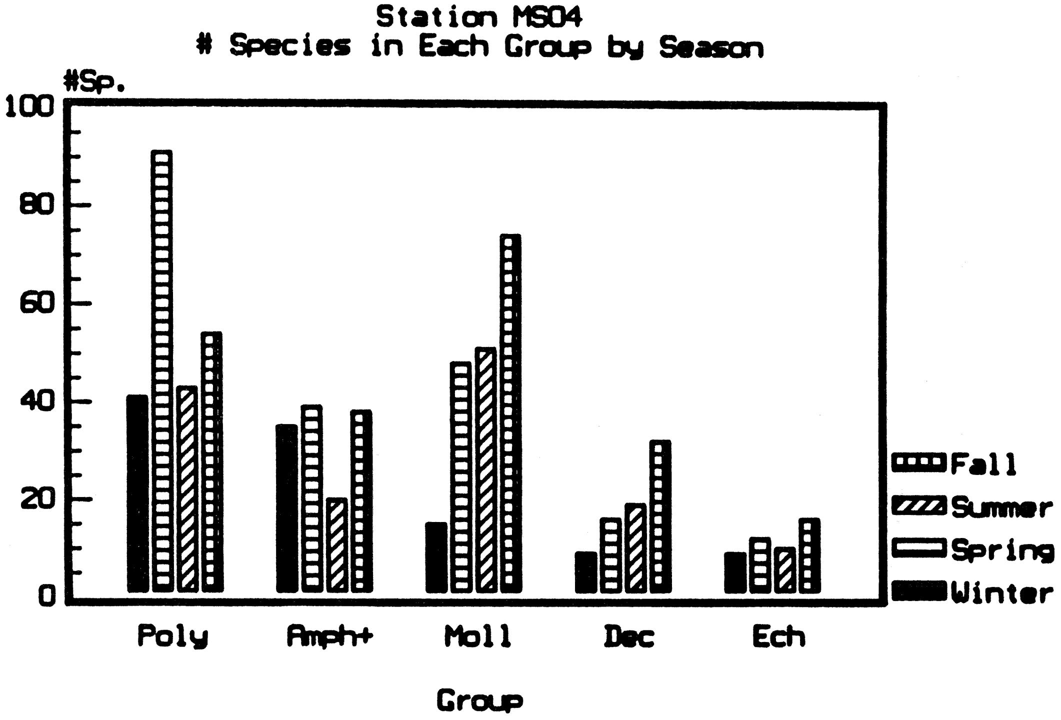


Figure 4. Taxonomic composition of species and individuals collected in 5 replicate (0.1 m^2 each) samples at IS05 during each season (Poly = Polychaete, Amph+ = Amphipods plus all non decapod crustaceans, Moll = Mollusca, Dec = Decapods, Ech = Echinoderms).



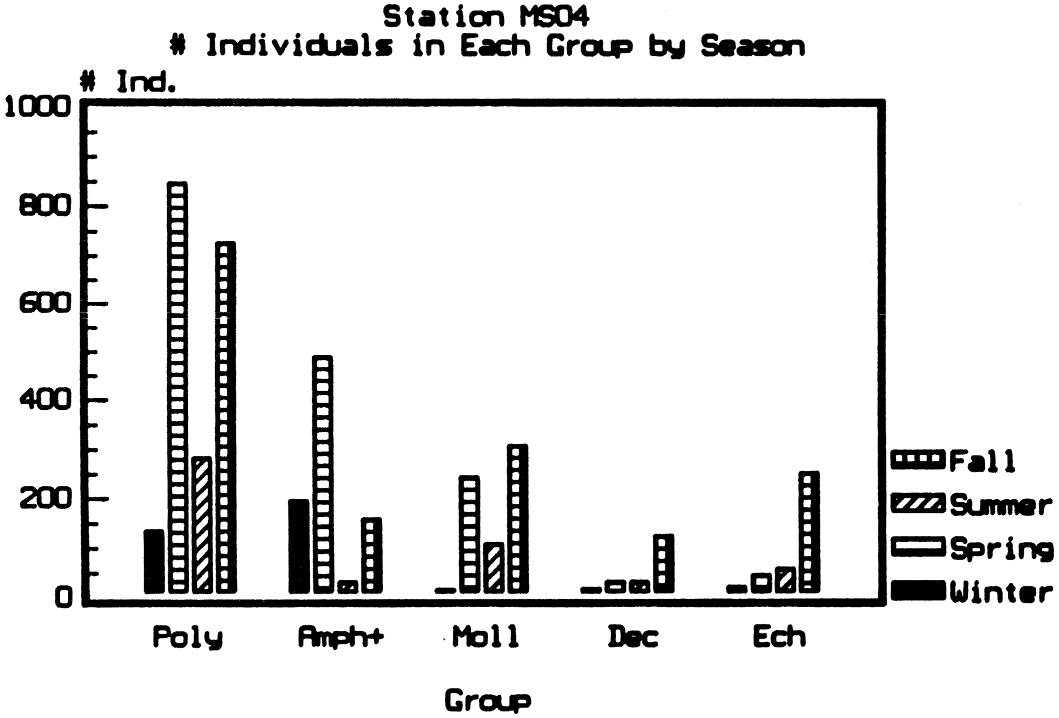
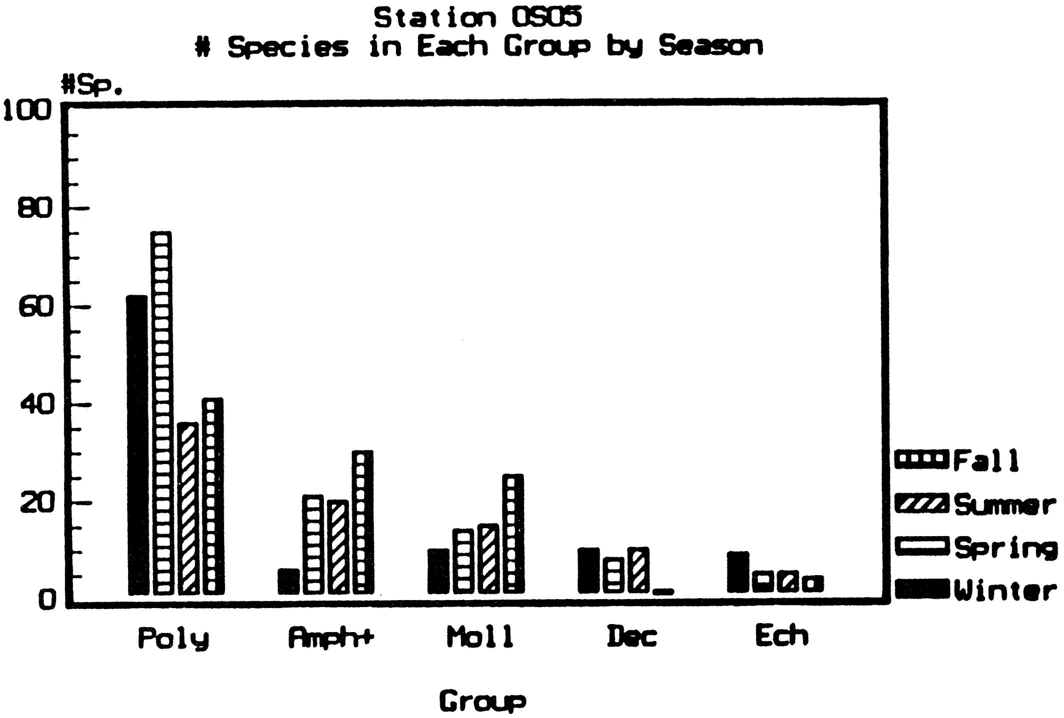


Figure 5. Taxonomic composition of species and individuals collected in 5 replicate (0.1 m^2 each) samples at MS04 during each season (Poly = Polychaete, Amph+ = Amphipods plus all non decapod crustaceans, Moll = Mollusca, Dec = Decapods, Ech = Echinoderms).



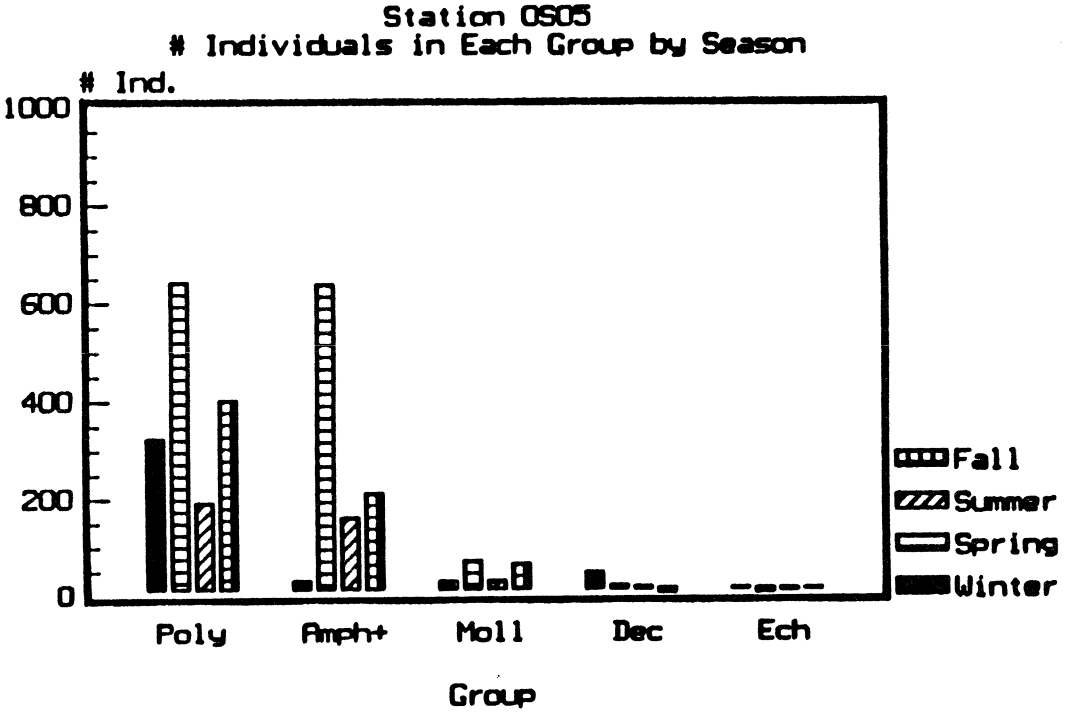


Figure 6. Taxonomic composition of species and individuals collected in 5 replicate (0.1 m^2 each) samples at OS05 during each season (Poly = Polychaete, Amph+ = Amphipods plus all non decapod crustaceans, Moll = Mollusca, Dec = Decapoda, Ech = Echinoderms).

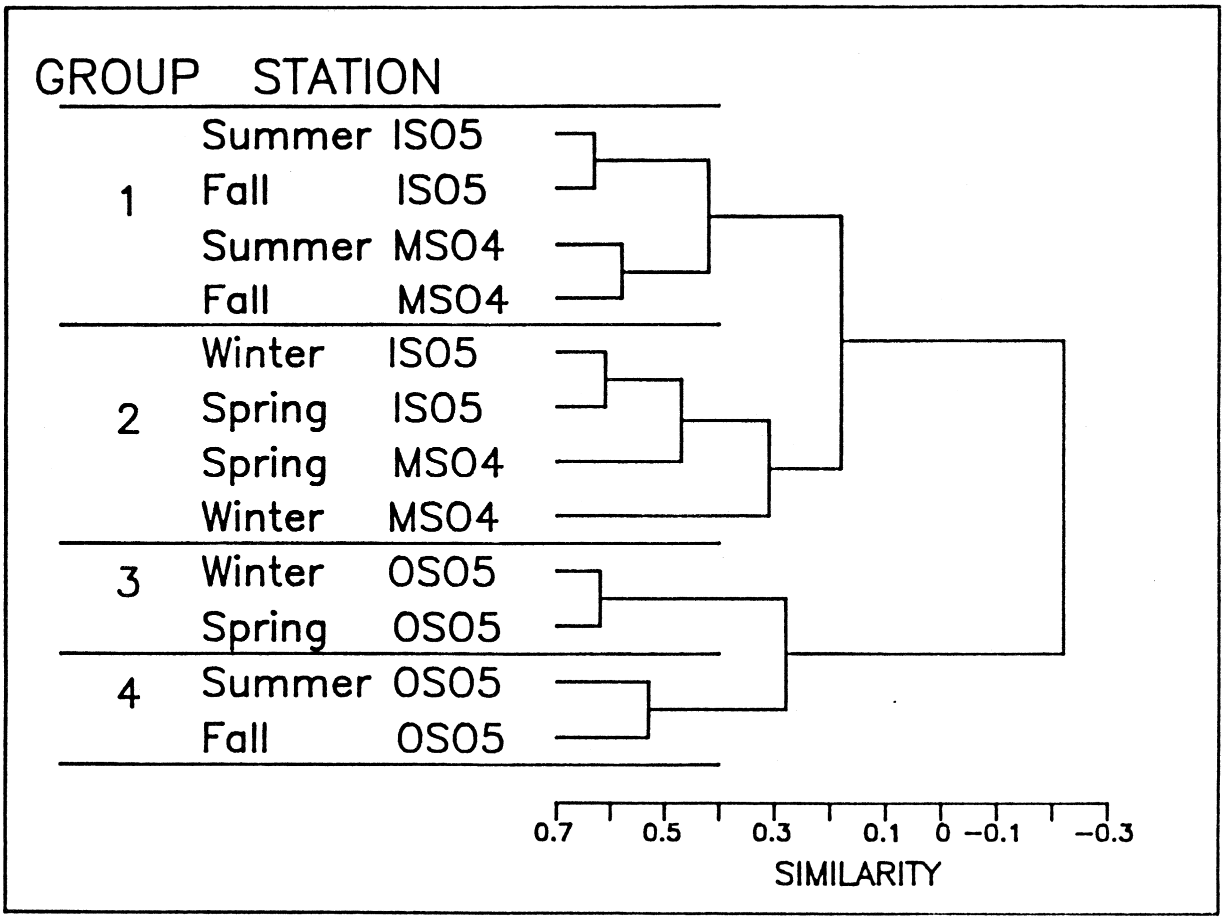


Figure 7. Cluster analysis showing similarities among collections at each station and season. Four major groups are delineated.

patterns. At all three stations the colder weather communities in the winter and spring were separated from the warm summer fall communities. Furthermore the overlapping similarities between communities at IS05 and MS04 resulted in a seasonal classification (groups 1-2), which was much stronger than location. The OS05 collections all clustered separately from the IS06 and MS04 suggesting a strong location difference between the inner and midshelf compared with the outer shelf. However, even on the outer shelf the winter/spring collections clustered separately from the summer/fall. These data suggest that there are definite seasonal differences among communities between winter/spring versus summer/fall or cold weather versus warm weather all across the continental shelf of N.C. Furthermore the data suggest that the inner shelf and midshelf are more closely related to each other than either is the outer shelf community. However this locational difference is confounded by the fact that the inner and middle shelf station were sampled with suction by divers while the outer shelf station was sampled by grab.

In an effort to determine the effect of sampling techniques on community structures a comparison of grab and suction sampling was done in the summer 1981 at IS05 and MS04. The data (Table 5) suggest that there is more similarity in species caught within a gear type and among stations than there is within stations and between gear type. The types of organisms were similar but the communities sampled appeared to be very different. To document these community similarities a cluster analysis was done to compare the three stations sampled in the summer 1981 by grab (IS05, MS04, OS05) with the two stations sampling by suction (Figure 8). Communities were all very dissimilar, however there was greater similarity within gear type at all stations (grab = 0.13, suction 0.21) than among stations. IS05 and MS04 grabs were slightly more similar to each other (0.22) than the two were to the OS05 grabs. These data suggest that both gear type and depth (location) are significant in determining the structure of the community sampled based upon species composition.

CONCLUSIONS

Very diverse communities of small macroinvertebrates are associated with rock outcrops on the continental shelf off North Carolina. Like most marine soft bottom communities these communities are dominated by polychaetes, amphipods and molluscs suggesting the importance of a thin sediment cover and animals (corals and sponges) in providing a diversity of physical nitches for these small organisms. Diversity was generally slightly greater in the middle shelf than outer or inner shelf but these differences were slight. The number of taxa collected were less at the outer shelf than at the middle or inner shelf. At all three stations both taxa and individuals attained maximum numbers in the spring and fall and minimum numbers in the winter and summer. This pattern is similar to what is classically observed in standing crop biomass of phytoplankton and zooplankton in temperate coastal waters. Whether or not these observed changes are associated with the same causes of such cycles in the plankton is unknown.

Although only slight differences were observed among stations in diversity, the structure of the communities across the continental shelf and through time was different. In general, molluscs were most important at the inner shelf and least on the outer shelf while polychaetes had a reverse trend. Amphipods were equally important across the shelf. In spite of these differences approximately 25% of the taxa were found at all three depth zones. Even though abundances alternated seasonally from low winter to high spring to low summer to high

Table 5. Comparison of abundance by station of invertebrates taken during the summer 1981 (five replicate 0.1 m^2) by suction and grab at ISO5 and MSO4. Only taxa with 10 or more individuals are included

Species	ISO5		MSO4	
	S	G	S	G
(M) *Chione grus*	148	3	6	-
(P) *Lumbrineris inflata*	37		16	-
(M) *Cumingia tellinoides*	32		5	
(M) *Lithophaga bisulcata*	27		1	
(D) *Paguristes tortugae*	27		3	
(D) *Pagurus carolinensis*	24		4	
(A) *Amplisca schellenbergi*	22		4	
(M) *Vermicularia knorrii*	20		1	
(M) *Lithophaga aristata*	18			
(A) *Erichthonius brasiliensi*	18			
(M) *Gouldia cerina*	17	12	5	1
(E) *Ampithoe* sp.	16		1	
(M) *Nassarina glypta*	14		2	
(M) *Gastrochaena hians*	14		3	
(A) *Heterophlias seclusdus*	11			
(M) *Cerithium atratum*	11		2	
(P) *Exogone dispar*	10		21	
(M) *Mangelia regirima*	12		2	
(P) *Exogone* sp.			46	
(P) *Eunice vittata*			31	
(E) *Ophiostigma isacanthum*	3		26	
(P) *Notomastus lateralis*	2		15	
(P) *Syllis hyalina*	5		14	
(P) Maldanidae			13	
(E) *Amphiodia pulchella*	2	4	11	37
(M) *Parvilucina multilineata*		133		2
(M) *Tellina subaritica*		42		13
(A) *Lembos smithi*		42		1
(A) *Bowmaniella* sp.		33		
(P) *Glycera* sp.	2	29		12
(A) *Apseudes* sp.B		24		107
(A) *Photis* sp.		23		46
(P) Spionidae	4	22	9	10
(P) *Lumbrineris impatiens*		20		1
(A) *Melita sppendiculata*		20		1
(D) *Pagurus hendersoni*		20		
(P) *Bhawania goodei*	1	14		26
(P) *Owenia fusiformis*		14		
(P) *Paraprionospio pinnata*		12		
(A) *Pananthura formosa*		12		
(M) *Acteocina cnadei*		12		1
(M) *Varicorbula operculata*		11		8
(A) Amphipoda E		3		88
(P) *Hemipodus roseus*				32
(P) *Pisione remota*				28
(M) *Cassinella lunulata*		5	6	27
(P) Nereidae	9	2	3	25
(A) *Maera* sp.	3	2	1	19
(M) *Ervilia concentrica*			1	17
(A) *Liljeborgia* sp.A				17
(A) *Unicola* sp.A		1		16
(P) *Syllis regulata carolina*	1	1		16
(A) *Lembos unicornis*	1	1	4	14
(M) *Cadulus* sp.		8		13
(M) *Laevicardium multilineata*	1	6	5	12
(A) Bodotriidae B				12
(P) Syllidae	5		1	12
(P) Cirratulidae		4	4	12
(A) *Tiron tropakis*		1		11
(M) *Cadulus quadratentatus*		9		5
(M) *Chaetopleura apiculata*	1	6	1	5
(M) *Lyonsia hyalina*		3		7

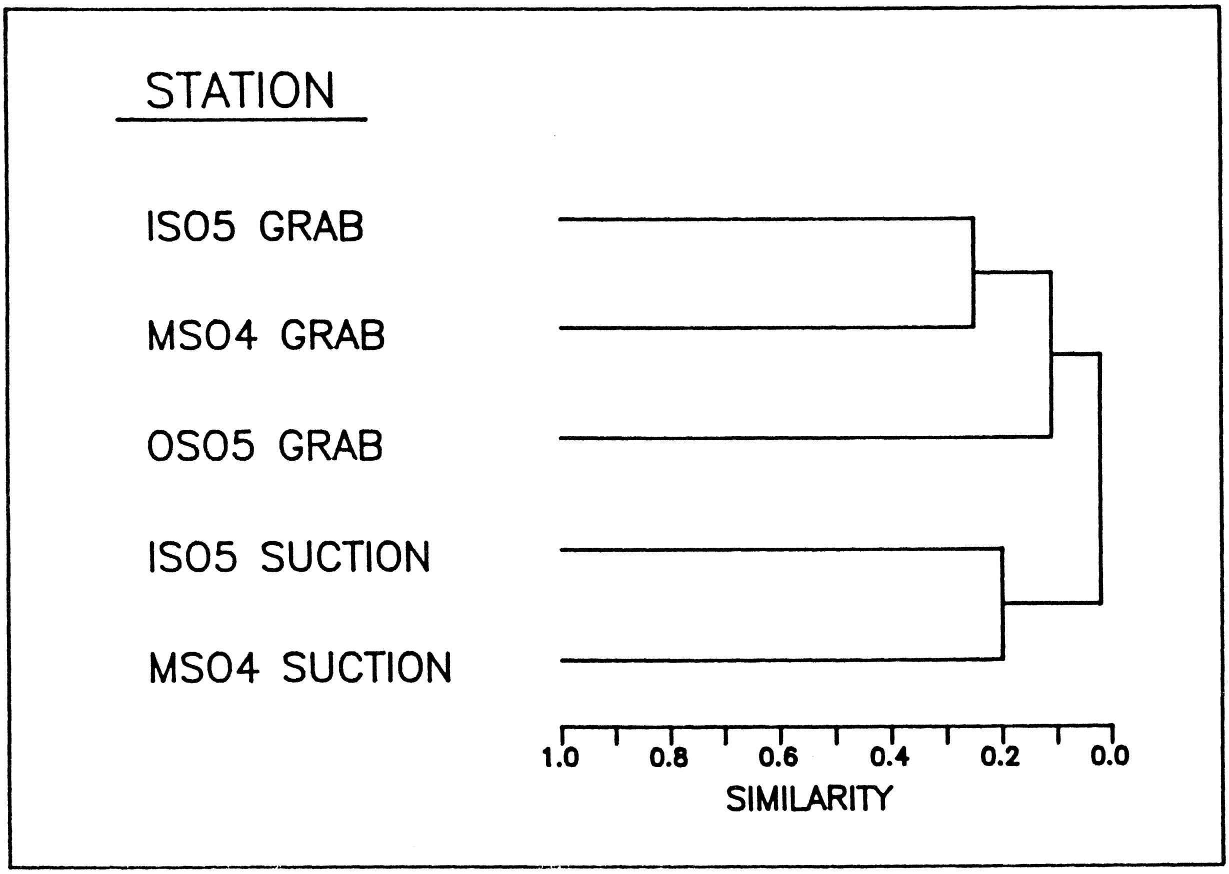


Figure 8. A comparison of collection techniques using cluster analysis of communities collected by suction and grab in the summer 1981.

fall the structure of the communities varied dramatically from cold (winter/spring) to warm (spring/fall) with inner and mid shelf communities more similar to each other at a given season than within a location across seasons.

In summary, continental shelf rock outcrop communities off North Carolina have the following patterns:

1. High and generally constant species diversity (H') all across the shelf and through all seasons.
2. Changes in the importance of major groups related to depth.
3. Alteration through seasons in number of taxa and individuals, primarily associated with polychaetes, which have the appearance spring and fall "blooms".
4. Season changes in community structure so that at all locations there is a cold weather (winter/spring) and a warm weather (summer/fall) fauna even though the annual water temperature

changes are greatest in inner shelf and mid shelf (10-15°C) and decrease to become an slight (2°-4°C) on the outer shelf.

ACKNOWLEDGEMENTS

This study was supported by the Minerals Management Service of the U.S. Department of Interior under Contract AA551-CT1-18. R. Van Dolah and his staff at the Marine Resources Research Institute, South Carolina Wildlife and Marine Resources Department provided detailed planning, specified techniques, checked the identification of specimens and provided computer services, all of which were necessary to insure comparability between the North Carolina study and a similar study done off Georgia and South Carolina. Technical help at the Duke University Marine Laboratory was provided by a number of personnel both at sea and ashore. Particularly important to this part of the project were E.K. Barber, P.K. Fowler, T. Handsel, P. Peckol, S. Ross and L.L. Wood.

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BIOLOGY AND ECOLOGY OF SEA TURTLES FREQUENTING NORTH CAROLINA

Frank J. Schwartz
Institute of Marine Sciences
University of North Carolina
Morehead City, North Carolina 28557

ABSTRACT

Five species of rare and endangered sea turtles frequent North Carolina's coast. Their abundance and seasonality is influenced by water mass and Gulf Stream currents, seasonal water temperatures, and effects of natural and man's alteration of the available habitat. Annually, 200-500 loggerhead nests are found on state beaches. Green turtles have nested in recent years on only six occasions. The pattern of nesting varies depending on position of the Gulf Stream and seasonal water temperatures. Natural causes (cold stunning or attacks by sharks) account for some turtle deaths. A limited number of deaths result from ingestion of artificial substances. Most deaths are man induced. Recent, often meager, conservation efforts have attempted to protect incubating nests by screening or removal to hatcheries. A sanctuary was established off one of the most productive beaches in the state (Onslow Beach) to lessen fishing fleet influence on adult turtles. Accommodation must be made by man to further protect sea turtles, otherwise a valuable heritage will be lost forever.

INTRODUCTION

Five species of sea turtles are found in North Carolina (Schwartz, 1977a,b). They are, in terms of decreasing frequency of abundance and occurrence: Atlantic loggerhead, Caretta caretta; Atlantic green, Chelonia mydas; Atlantic leatherback, Dermochelys coriacea; Atlantic ridley, Lepidochelys kempi; and Atlantic hawksbill, Eretmochelys imbricata. All are considered threatened and/or endangered and are now protected by the Rare and Endangered Species Acts of 1973 and 1978 (Bjorndal, 1981; Mager, 1985; Schwartz, 1977a,b, 1978a; WATS, 1984).

This report condenses information on how each species contributes to the North Carolina herpetofauna in terms of seasonality, occurrence, abundance, nesting sites, behavior, and strandings. It documents aspects of their biology as affected by natural and artificial actions of man or nature. Recent conservation efforts to protect or improve survival and status are also discussed.

Seasonality and Abundance

Sea turtles, primarily loggerheads, greens, leatherbacks, and to some extent ridleys, are found year-around in North Carolina (Fahy, 1954; Lee and Palmer, 1981; Schwartz, 1977a,b, 1978a), usually in offshore waters associated with the west wall of the Gulf Stream (Hoffman and Fritts, 1982). They may be carried or migrate northward from southern waters, where they are more common and abundant (WATS, 1984) by the northerly moving waters of the Gulf Stream (Witham, 1976; Witham and Carr, 1968; Witham and Futch, 1977). Six records of hawksbills being found in the state are known (Schwartz, 1977b, 31 July 1973 and 16 July 1988 at Frisco). As shelf or coastal waters warm between March and August turtles move shoreward in order to breed, nest or feed (Figure 1). Offshore or southerly movements are apparent after September and during winter as inshore waters cool.

Inshore movements are dependent, to some extent, on the nearness of the Gulf Stream to the coast. Undisturbed the Gulf Stream is "normally" farthest offshore in the southern part of the state and nearest at Cape Hatteras (Blanton, 1971; Steffanson et al., 1971). Deflection of the stream away from the southern coast may also be affected as the stream flows past the Charleston bump (Brooks and Bane, 1983; McClain and Atkinson, 1985; Pietrafesa et al., 1985). Winds out of the southeast, northeast or east actively move the stream onto or away from the coast. They also cause folding of the stream back on itself or create anticyclonic eddies, water masses that are carried southward or shoreward along the North Carolina shelf (Pietrafesa et al., 1985). The latter often carry warm waters ashore during the winter, where they are broken down or mixed with colder inshore winter waters. Such eddies often contain sea turtles that, once the eddy dissipates, find themselves ashore or in Pamlico Sound in December to February, where cold winter water temperatures substantially below their tolerance survival levels kill them (Schwartz, 1978b). As a result of this interplay of winds, eddies, and water currents spring inshore movements by sea turtles may occur earlier in some years in waters north of Cape Lookout than in areas or waters south of Cape Lookout or in the southern part of the state (see Oceanographic Monthly Summaries, NOAA, National Environmental Satellite Data and Information Service, Washington, D.C.

While some sea turtles are known to migrate southward from North Carolinian waters in the fall and winter, many move offshore to spend the winter in the warmer waters near the Gulf Stream. This need to vacate sound and colder shelf waters stems from observations, for loggerheads, greens, and ridleys at least, that low water temperatures are lethal when they fall below 9-10°C (Schwartz, 1978b; Figure 2). Depending on size and species, survival in such waters would be 18-24 h at most. Younger turtles would withstand lethal waters slightly longer than would adults (Schwartz, 1978b; Figure 3).

Local folklore and some published reports (Carr et al., 1980; Felger et al., 1976; Ogren and McVea, 1982) believe sea turtles hibernate by muddying (digging) in, especially at Cape Lookout Bight in North Carolina or the Cape Canaveral ship

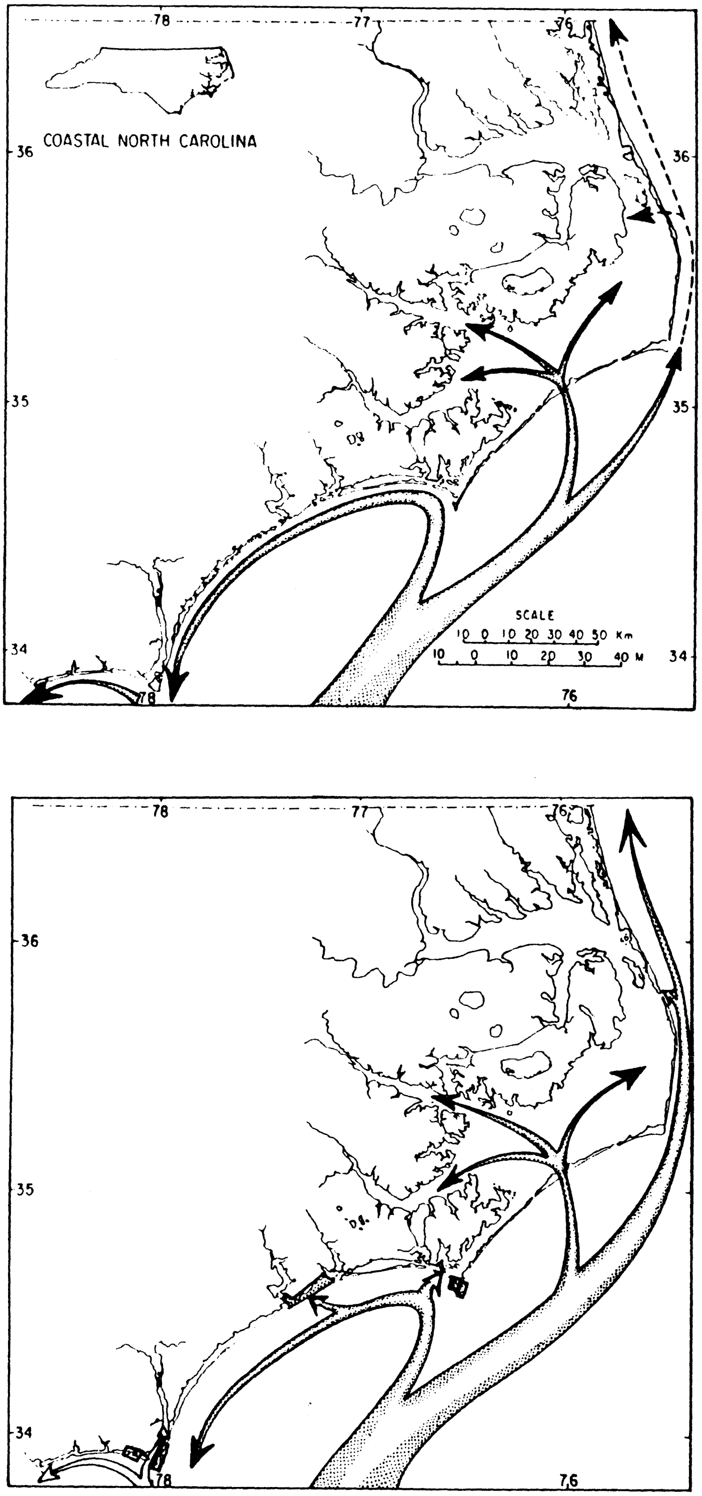

Figure 1. Map illustrating movement by loggerhead (top) and green (bottom) sea turtles in the oceanic and inshore waters of North Carolina. Squares denote major loggerhead or green nesting beaches. Dashed line is incomplete inferences about northern green turtle movements in the Gulf Stream (wide aspect of arrow).

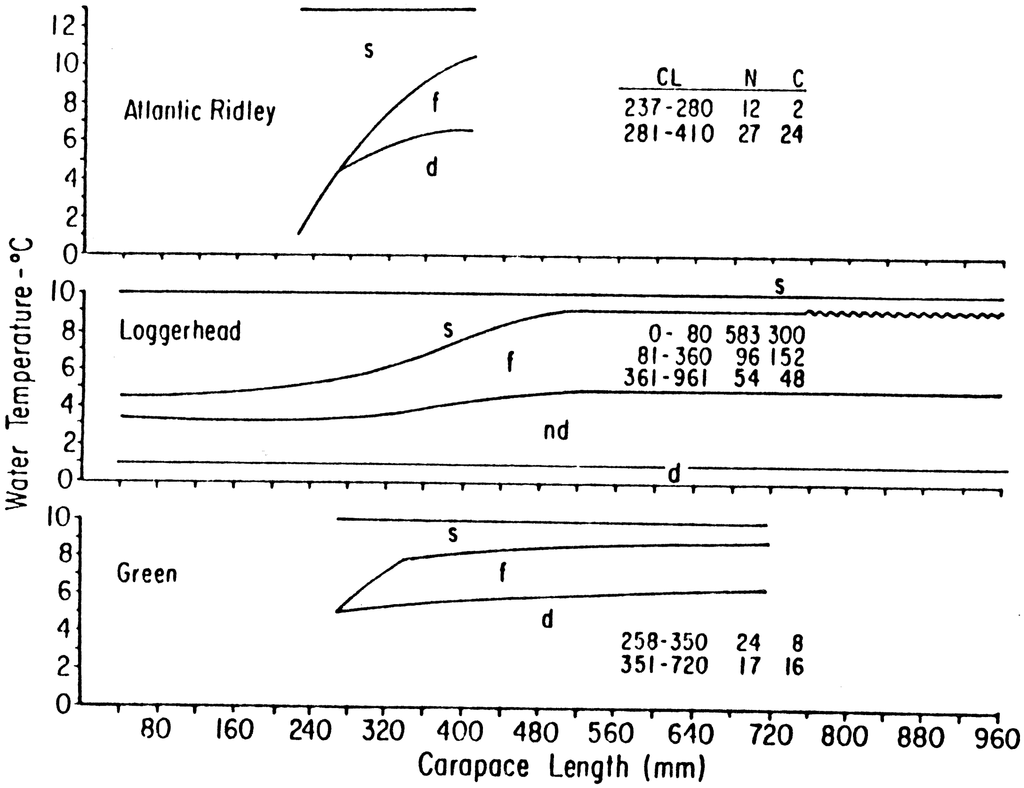

Figure 2. Behavior responses by experimental hatching, subadult, and/or adult ridley, loggerhead, and green turtles to decreasing water temperatures. CL = carapace length; N = number; C = controls; S = swimming; F = floating; ND = near dead; D = dead.

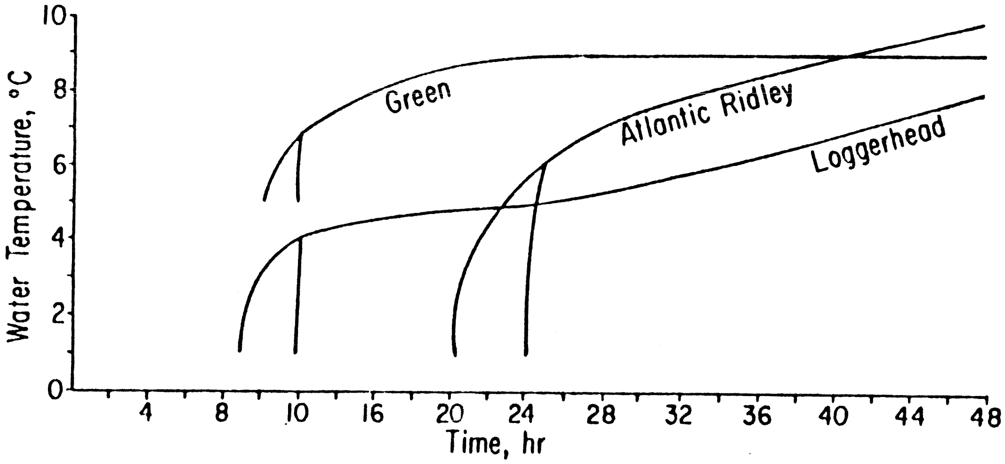

Figure 3. Survival time curves for hatching, subadult, and adult green, ridley, and loggerhead turtles when exposed for prolonged periods of time to water near or below their lethal endurance. In each case, young of each species survive longer (right vertical of each curve) than do adults.

channel, Florida. Schwartz (1978b) has shown that to be impossible. Cold affected turtles would naturally float to the surface prior to death making it impossible for them to dig in to hibernate. Sea turtles, contrary to Felger et al., 1976, do not hibernate. Instead, muddying in is a response by the turtle to keep from floating upward. Muddying in or wedging under the nearest ledge or object keeps and helps them from floating to the surface. Although body pits of non-nesting turtles are often found dotting the Cape Lookout Bight substrate in April and early spring, turtles frequenting the bight have also been found with mud adhering to their plastrons. However, it is highly unlikely that they would survive if they dug into the substrate to "hibernate". Cape Lookout muds contain high levels of H_2S (3-6 mM) (Chanton, 1985; Crill, 1984), concentrations that would, if exposed for long periods of time, be detrimental to skin and turtle alike. It is possible that the same would be true for Cape Canaveral ship channel sea turtles, although marine sediments from that area have not yet been analyzed.

Floating-moribund reactions by sea turtles to cold waters have been documented for North Carolina, Long Island Sound, and off Florida (Ehrhart, 1983; Meylan and Sadore, 1986; Provancha et al., 1986). The Long Island Sound observation pertained to ridleys, those in Florida to greens. Windrows of moribund or dead sea turtles are noted almost annually off North Carolina. The largest concentration occurred 25 February 1976 when groups of 200 or more were seen simply floating at the surface in the typical head-flippers down condition preceding death by cold (Schwartz, 1978b; Manooch, pers. comm., 1986). Divers have also found lethargic turtles, mostly loggerheads, at various depths, almost annually between December and February, in the offshore waters north of Cape Lookout. Winter kills, December to February, of juvenile green, ridley, and subadult loggerheads occur annually in North Carolina. These are turtles that have spent the summer in the sounds or that have been carried into the sounds via Ocracoke Inlet and/or are waifs of offshore eddy disintegrations and have failed to vacate the southern portion of Pamlico or northern parts of Core Sounds. Apparently leatherback turtles that also are present offshore at this time are protected by their blubber-like skin or can heat regulate (Greer et al., 1972) as specimens are seen offshore throughout all seasons, but none are ever cold stunned or winter killed. Although wind rows of loggerhead turtles were noted in inshore cold waters extending from Cape Lookout south to Masonboro Inlet during the November 1987-March 1988 red tide (Ptychodiscus brevis) incidence, no turtles succumbed to the infestation.

Attempts to determine population estimates for each species have proven inaccurate, feeble, or almost impossible (Carr and Carr, 1974; Crouse, 1984, 1985; Davis and Whiting, 1977; Eckert, 1987; LeBuff and Hagen, 1978; Shoop et al., 1985). Such efforts have been compounded seasonally in that the time spent near or at the surface, when state or federal aerial survey flights are attempted, vary widely, Further, aerial and ground truth surveys often are unable to distinguish between old or new crawls thereby compounding nesting estimate inaccuracies (Crouse, 1985). This inaccuracy has led to large population estimate inaccuracies for often many turtles are or could be out of sight (deeper) (Shoop et al., 1985) rather than at the surface. Beach crawl data is also suspect for the number of crawls seen does not signify each was made by a nesting female. Population estimates based on tag presence or absence are often over or under-estimated respectively; whereas survival is usually under-estimated (Eckert, 1987).

Based on nesting and stranding data, loggerheads are the most frequently encountered sea turtle along the North Carolina coast (Table 1). They frequent the coast, usually south of Corolla, North Carolina, the sounds, and even survive extended periods of time in freshwater. For example, one remained from 9 May-16 June 1980 in the freshwaters of Chowan River, a tributary to Albemarle Sound with no ill affects prior to being relocated to saline waters near Oregon Inlet (N.C. Marine Fisheries observation). Young or immature green turtles are next most often encountered whereas adults are known from four individual turtles nesting at Onslow Beach, Camp Lejuene, one each in 1980, 1985 (Peterson et al., 1985; Schwartz et al., 1981), and two in 1987, two at Caswell Beach in 1985, one on Bald Head Island in 1987, and one near Cape Hatteras in 1988. Other large greens have been reported off Cape Lookout and the Outer Banks but no confirmed nesting has occurred there. Many young greens (30-45 cm carapace length) enter state waters, following northward movement as head start releases from Florida (Witham and Carr, 1968; Witham and Futch, 1977) and occupy the sounds of North Carolina. Leatherbacks are found abundantly in offshore or coastal waters, especially north of Cape Lookout (Lee and Palmer, 1981; pers. obs.). Fishermen often capture leatherbacks in ocean pound or stop nets set south of Oregon Inlet. None enter sound waters unless dead or injured. The only recorded nesting of a leatherback was at Cape Lookout in 1966 (Schwartz, 1977b) and was based on hatchlings found at the Coast Guard Station at Cape Lookout. Otherwise, leatherbacks of 2-2.5 m and up to 405 kg (pers. obs.) frequent coastal waters annually.

Atlantic ridleys, perhaps the most endangered of the western Atlantic sea turtles, are encountered sporadically year round in near offshore as well as inshore or sound waters and the lower reaches of coastal Carolina rivers. Their numbers, depending on season or locality, vary from several to 35 sightings or captures per year. Most weight 1.3 to 16 kg. The largest ridley from North Carolina (29.4 kg) was found dead in the Morehead City harbor at the Fort Macon Coast Guard Station, Beaufort Inlet, on 28 August 1980. Ridleys, like greens, frequent or are carried into Pamlico or Core Sounds late in the fall or winter and are subject to winter kills there. No mating is known. The temperate or tropical inhabiting hawksbill is a rarity in North Carolina. Six specimens have been known from North Carolina waters, two were collected at the Beaufort Inlet Bar and four from offshore areas north of Cape Lookout (Schwartz, 1977a,b; N.C. Marine Fisheries, Cape Hatteras National Seashore Park, obs.). The latest record was of a specimen at King's Point, Pamlico Sound near Frisco, N.C. 16 July 1988 (Carapace curve length 190 mm). No abundance estimates are possible for hawksbills nor is nesting known in the state.

Table 1. Number of reported sea turtle nests and strandings along North Carolina's coast, species combined, 1979 through 1988.

Year	Number	
	Nests	Strandings
1979	332	41+
1980	284	159
1981	339	133
1982	337	273
1983	257	109
1984	318	132
1985	479	203
1986	509	131
1987	248	194
1988	285	308

Nesting

Loggerhead turtles gather en masse, especially at Cape Lookout bight, to mate prior to the extensive annual nesting season of 13 May-28 August. Occasionally nesting pairs are seen in the ocean well offshore of Cape Hatteras (Anon., 1985). Mating males are about 95 cm in carapace length and 120 kg in weight and as many as 40 have been seen at one time in Cape Lookout bight. Once mating occurs males are rarely seen or captured throughout state waters. Depending on year and environmental conditions following mating, loggerheads populate state waters by fanning out either to the north or south of Cape Lookout. In years when waters are cooler to the south of Cape Lookout, nesting commences initially (e.g., 1979, 1982, and 1985) in the northern part of the state, followed by activity later in the season on beaches south of Cape Lookout. Cool waters throughout the state apparently influenced fewer turtles to nest in 1980 and 1983, when only 284 and 257 nests, respectively, were recorded (Table 1). Cold waters off Camp Lejuene also account for the poor nesting there in 1988. The reverse is true when waters in the southern part of the state are warmer (1976, 1977, 1978, 1986, and 1988). However, nesting generally begins in May in southern waters, especially on Bald Head Island, and then increases in a northerly direction toward Nags Head by late May. Why the total number of nests varies between years is unexplained. The best nesting beaches, in descending order of use or nests deposited, are Bald Head Island, Onslow Beach (Camp Lejuene), Hammocks Beach, Caswell Beach, and Cape Lookout National Seashore including Core Bank beaches. The number of nests on Bald Head Island has varied (data from period 1980 through 1988, Brooks unpubl.) between 72 and 196, the latter occurring in 1986. All other areas of the state provide few nests to the overall nestings recorded annually. Whether female loggerheads are nest site specific (Carr and Carr, 1972) is uncertain. Green turtles that have nested in North Carolina do return almost to the same nest site (Peterson et al., 1985). Leatherbacks have been noted mating off Core Banks (10 May 1982) but have not nested there in recent years.

A single female loggerhead has been known to nest four times per season in North Carolina (Camp Lejuene data). Nesting females are usually larger than 63 cm carapace length. Clutch size varies between 47 and 220 eggs (Schwartz et al., 1980; Figure 4). Although Schwartz et al., (1980) published a formula by which one could calculate the number of days needed for a clutch to incubate before hatching, refinement of additional data now finds (187 nests, Figure 4) that estimates should be based on the formula log y (days) = 1.946 - .0472 log x (eggs). This formula produces estimates of 68-72 days as the time needed for most nests (average 120 eggs/nest) to hatch in North Carolina. Lows of 53 to highs of 87 days incubation are known from Cape Lookout and Camp Lejuene data, Table 2. Incubation periods of 105 days have been recorded for nests in the state (pers. obs.). Elsewhere, incubation periods of 58-100 days are known (Baldwin and Lofton, 1959; Kraemer, 1979; Mann, 1977). In North Carolina nests that do not hatch in 100+ days are usually those lain late in August or that hatch after 15 October when ground temperatures are below lethal limits of 10°C (Schwartz, 1978b). Percent hatch of eggs in a natural nest may vary from 0-100% (Figure 5), yet if lain in June, July or August the mean percent hatching decreases from 82.1 to 72.9 and 59.8%, respectively, as the summer progresses. In terms of egg deposition, the number of eggs in a clutch varies little from summer month to month although June eggs require 71.5 days (range 57-82), July 68.6 (range 51-90), and August 73.6 (range 53-78) days to hatch (Figure 5). This find agrees with Frazer and Richardson (1985b). Laboratory incubated eggs take longer to incubate and the hatch success for July is lower than for June and August eggs (Camp Lejuene 1980 data; Table 4). Whether size, shell shape, and body depth of the female (Congdon and Gibbons,

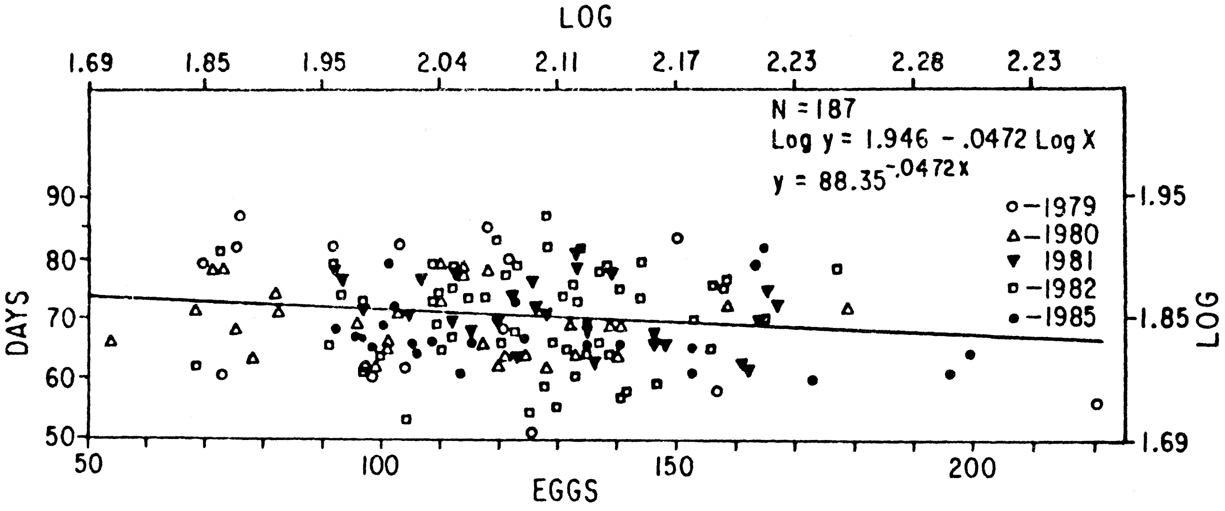

Figure 4. Regression data for loggerhead nests (1979-1985) that permits estimates of days needed for incubation when the clutch size is known (Camp Lejuene data).

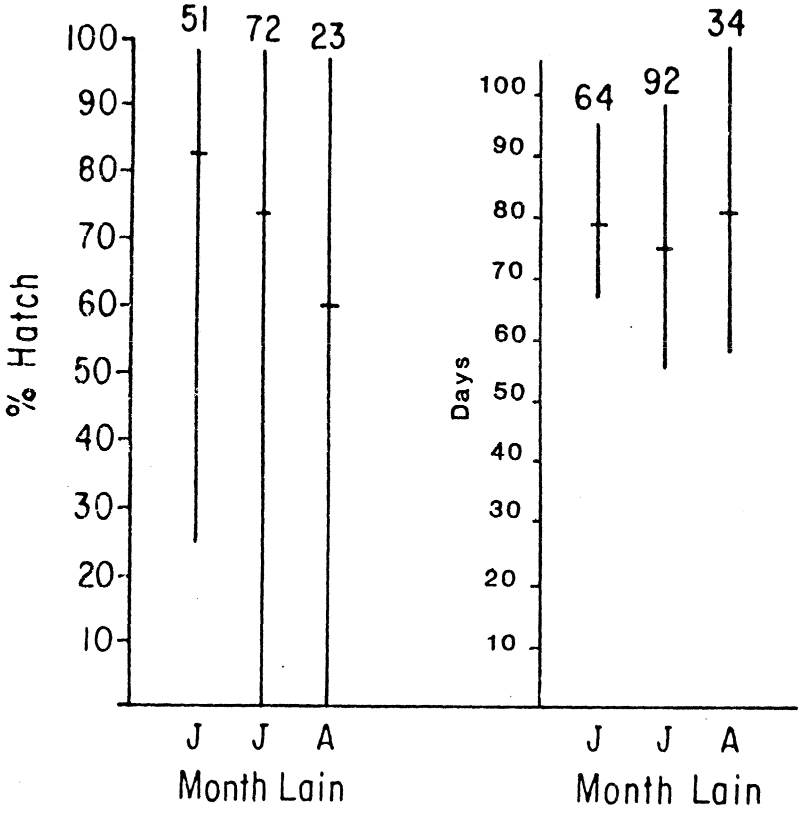

Figure 5. Mean and range hatching success (left) of loggerhead eggs and range and mean number days for a clutch to hatch (right) when lain in June, July, or August. Numbers above bar indicate number nests studied.

1985; Stoneburner, 1980) controls the number of eggs produced per clutch in North Carolina rather than the number of clutches per season is under investigation and may account for the difference in average North Carolina clutch size of 120 versus 100 as one reaches Florida. Frazer and Richardson (1985b, 1986) found a correlation between a clutch size and carapace length for Georgia loggerheads and Caldwell (1959), and Hirth (1980) also commented on the relationship between body size and clutch size, but the issue warrants additional investigation.

Table 2. Number and hatching success, mean incubation time and range for wild nests lain and successfully hatched at Cape Lookout National Seashore (CALO) and Camp Lejuene, Onslow Beach (CL) 1981-1986, including number of tagged recaptures of nesters per year.

Year	Nests Hatched	Total Number	Hatching Success (%)	Incubation Mean Days	Range	Tag Returns
				CALO		
1982	14	28	72.0	65.8	58-74	6
1983	23	31	75.0	62.0	57-76	85
				CL		
1981	51	86	61.2	57.0	57-87	40
1982	55	60	57.7	68.6	53-83	28
1983	42	42	80.9	63.5	54-85	21
1984	63	63	57.0	67.9	55-81	17
1985	28	36	80.1	64.5	60-79	38
1986	32	32	77.0	64.8	50-80	25

Loggerhead nesting usually commences on flooding tides between the hours of 1000 and 0400 (Frazer, 1983). Nest construction and egg deposition take less than two hours. Seven daylight nestings by loggerheads occurred in North Carolina in 1980. Five occurred between 0930 and 1700 h on the Outer Banks from Cape Lookout northward to Coquina Beach near Oregon Inlet. Two daylight nestings occurred in 1980 on Bogue Banks during the same hours. All daylight nestings occurred between 10-30 June and 19-22 July 1980 and during ebb tides (Cape Hatteras and Cape

Lookout, pers. obs.). Whether nesting loggerheads employ sand temperature probing prior to nest site selection, as suggested by Stoneburner and Richardson (1981) and now considered questionable, is uncertain. Best nesting has been found to occur when nests were lain in sands with a grain size of 0.25-0.125 mm (Kraemer, 1979; Schwartz, 1982; statewide data). Nests in coarse or very fine sands do poorly (Schwartz, 1982) and hatch fewer eggs than nests in medium grain sands. Whether excessive freshwater from rains during nest incubation influences nest incubation and hatching success in North Carolina is uncertain (Kraemer and Bell, 1980; Ragotzskie, 1959). One albino and one two-headed loggerhead hatchlings are known from the thousands hatched in the state; these were recorded at Cape Lookout in 1983 (R. Harriet, obs.). The green turtle that nested four times in 1980 and five times in 1985 at Camp Lejuene (Peterson et al., 1985 deposited 819 and 893 eggs respectively. The 1.04 m green that nested near Cape Hatteras 7 July 1988 produced 158 hatchlings between 30 August and 2 September 1988 (Cape Hatteras National Seashore, pers. obs.). Whether increased nesting in North Carolina by greens is a result of an increased green population off Florida (as has been historically documented by Dodd, 1981) is uncertain. Natural incubation of two of the 1980 Camp Lejuene green nests produced hatches of 80 and 87%, whereas laboratory incubation (3 nests) varied between .006 and 42.8% (Table 3). Hatch data is not available for the green turtle nests lain at Caswell beaches in 1985 or Bald Head in 1987. One albino and several deformed greens were found in the Camp Lejuene 1980 nests (Schwartz and Peterson, 1984).

Emergence of hatchlings (pers. obs.) occurs in North Carolina en masse or in stages. In the latter case, a few emerge the first day, the bulk the second day, and stragglers a day or so after hatching in the nest. Emergence originally believed to occur from 0300 h until sunrise or when the beach sands are the coolest, agreeing with Mrosovsky (1968) has now been shown to occur anytime between 1800 and 0400 h (Neville et al., 1988). The number of hatchlings that reach the sea is usually low as they are actively preyed upon, location dependent, by such nocturnal predators as foxes, raccoons, and ghost crabs.

Hatchlings upon emergence race frantically toward the sea, not just because it is downhill from the nest but because they apparently perceive a lighter background at the sea/beach interface than landward behind them (Ferris, 1986; Freck, 1976; Grossman et al., 1984; Ireland, 1979; Stoneburner et al., 1982; Van Rhijn, 1979; Van Rhijn and Van Gorkam, 1983). Ferris (1986) has shown that locally the revolving light of the Cape Lookout lighthouse or even nighttime glow from nearby cities or lights will reorient hatchlings from their seaward movements landward. Hatchlings face another gauntlet in their race to the sea, Overland Recreational Vehicular (ORV) ruts (Hosier et al.,

Table 3. Mean and range carapace straightline length (CL of normal and deformed green turtles from natural and laboratory incubated nests lain on Onslow Beach, Camp Lejuene, North Carolina, summer 1980.

Date Lain	N measured	Hatching Success (%)	CL mm		Wgt (g)		Days Incubation
			Mean	Range	Mean	Range	
			Wild nest				
25 June	145 of 168	86.3	50.8	47.6-53.8	25.8	22.8-29.9	58
8 July	148 of 183	80.9	52.0	47.3-54.6	26.4	23.7-28.3	58
25 June	albino		50.5		26.8		
25 June	deformed		48.4		24.7		
8 July	deformed		52.8		27.0		
			56.2		27.2		
			47.3		25.3		
		Laboratory Incubated (IMS) at 27-32°C					
21 July	1 of 166	.006	47		19.2		49
2 Aug	32 of 157	20.4	47.9	46.5-51.0	23.0	21.3-24.9	55
17 Aug	62 of 145	42.8	47.8	46.5-50.0	23.0	20.0-24.5	59

1981). ORV ruts left on the beach present obstacles to hatchlings as they usually cannot climb out once they fall into them. Once in an ORV rut, death results following aimless wanderings, and inability to climb out of the rut, and dehydration. If the hatchlings reach the sea, their frantic swimming efforts carry them offshore where they have been seen at distances of 40 km (pers. obs.) or in Sarganum (Schwartz, 1988). Whether they will return to North Carolina when mature remains unknown, even though thousands of hatchling loggerheads and greens have been flipper tagged with internal binary coded wire tags (Schwartz, 1981). Only time will answer that question.

Many have shown that the sex of a developing sea turtle is influenced or controlled by the nest incubation temperature. If the egg is developed at temperatures below 29 or 30°C, males are produced, females develop from eggs incubated above 30°C (Bull et al., 1982; Dimond and Mohanty-Hejmadi, 1983; McCoy et al., 1983; Mrosovsky, 1982, 1988; Mrosovsky et al., 1984; Mrosovsky and Yntema, 1980; Vogt and Bull, 1982; Whitmore et al., 1985; Yntema and Mrosovsky, 1980). Mrosovsky (1987, 1988) now feels that the pivotal sex determining incubation temperature is

29.1°C. Controlled incubation tests at the Institute of Marine Sciences, Morehead City, have shown (same eggs as in Table 4) that, for North Carolina, the pivotal temperature is 29.7°C (clutches from Camp Lejuene lain in 1980). This translates into nature producing more male hatchlings in June and August than July in North Carolina (Schwartz et al., 1980; Webster and Gouveia, 1988) for average air and/or beach temperatures are at least June 24.4, July 26.7, and August 25.7°C (Porter, 1985). Sampling elsewhere Pritchard (1979) and Wibbels et al. (1984) suggested that the reverse would be true in areas south of North Carolina as they would have warmer incubating temperatures, thereby producing more females than males. Perhaps this is nature's way of balancing the male-female sea turtle ratio, but more work will be needed before that aspect is resolved.

Local folklore believes nesting is most intense or best during a full moon. Data from Cape Hatteras, Cape Lookout, Hammocks Beach, and Camp Lejuene indicate that there are just as many nestings during other stages of the moon as during a full moon. Likewise, although most nesting occurs during flooding or high tides (598 of 598 observations statewide), tides are not the only controlling agent of nesting (Brooks and Webster, 1988). Flooding tides only help the turtle reach a higher point on the beach before it has to crawl toward a choice fore dune nest site. Frazer (1983) felt there was a real tidal effect, if the tide was greater than ±2 m. Stormy or rainy nights do tend to frighten sea turtles from North Carolina's beaches (pers. obs.). Nesting, when it does occur, usually occurs above the high tide mark at or near the fore dune base. Occasionally, energetic smaller nesters will climb over and behind the fore dune to nest among the grasses, but these actions account for less than 5% of the nestings in North Carolina.

Table 4. Number of nests by month, eggs lain and hatched, and hatching success for loggerhead eggs lain in 1980 at Camp Lejuene, Onslow Beach, but incubated (IMS) at temperatures between 27 and 32°C

	Number			Days to Hatch		Percent
Month	Nests	Eggs	Hatched	Mean	Range	Hatch
June	7	769	371	66.2	62-73	48.2
July	12	1442	608	70.0	60-84	42.2
August	13	1321	667	80.0	46-128	50.5

Movement

Interesting movement has been recorded for tagged North Carolina logger heads. As many as 85 turtles per year (Table 2) have moved between Camp Lejuene and Cape Lookout or Bald Head Island. Fewer have moved from Cape Lookout to Bald Head Island than to Camp Lejuene. Turtles north of Cape Lookout never seem to move onto beaches south of the Cape. Whether they are members of other subpopulations in the Atlantic remains unresolved, yet it has been suggested that subpopulations do occur in the lower United States but not in North Carolina (Caine, 1986; Frazier et al., 1985).

Growth and longevity

The literature is replete and confused as to how long sea turtles live, the sizes at those ages or what influences their growth rates (Bjorndal, 1981; Frazer and Ehrhart, 1985; Rebel, 1974). Much of the confusion stems from the inability of scientists to accurately age turtles (Zug et al., 1983, 1986). To resolve these problems eggs of loggerhead and green turtles were incubated at IMS in 1968 and 1978. The resultant turtles have been kept in captivity for periods of 11 and 21 years respectively. Their growth rates have been recorded in order to determine growth by sex and species under seemingly as natural conditions as possible. Schwartz and Frazer (1984) and Frazer and Schwartz (1984) reported the growths (then 14 years) for a single male and female loggerhead turtle reared under such conditions (Figure 6). Those same two turtles, as of 31 October 1988, now measure and weigh: male 83.2 cm carapace (straightline length) and 110.3 kg, female 78.8 cm CL and 98.6 kg. Younger loggerheads reared from Florida, Cape Romain, South Carolina, and Pea Island, North Carolina eggs for 11 years have also shown similar logistic growth rate curves (pers. obs.).

Body-organ weight relationships for 56 wild, hatchling to adult, loggerheads collected off Bogue Banks in 1979 and 1980, revealed that hypermegalistic growth occurs with size for the liver, digestive tract, kidney, flippers, carapace, and plastron (Schwartz, 1985). Little growth changes occurs for the heart, lungs and trachea, muscle and bone, head or tail. Differences, however, were correlated to poor food and ecological environmental conditions off North Carolina in 1980. Although most loggerheads and other sea turtles feed extensively on jellyfish or crustaceans (Bjorndal, 1981; Rebel, 1974) captive loggerheads will feed on fishes or any organism except pipefish (Schwartz and Carter, 1984). Whether this is a negative response to something produced by the skin of a pipefish is unknown. Greens and ridleys will also feed on fishes although ridleys prefer shrimp and crustaceans when kept in captivity (pers. obs.).

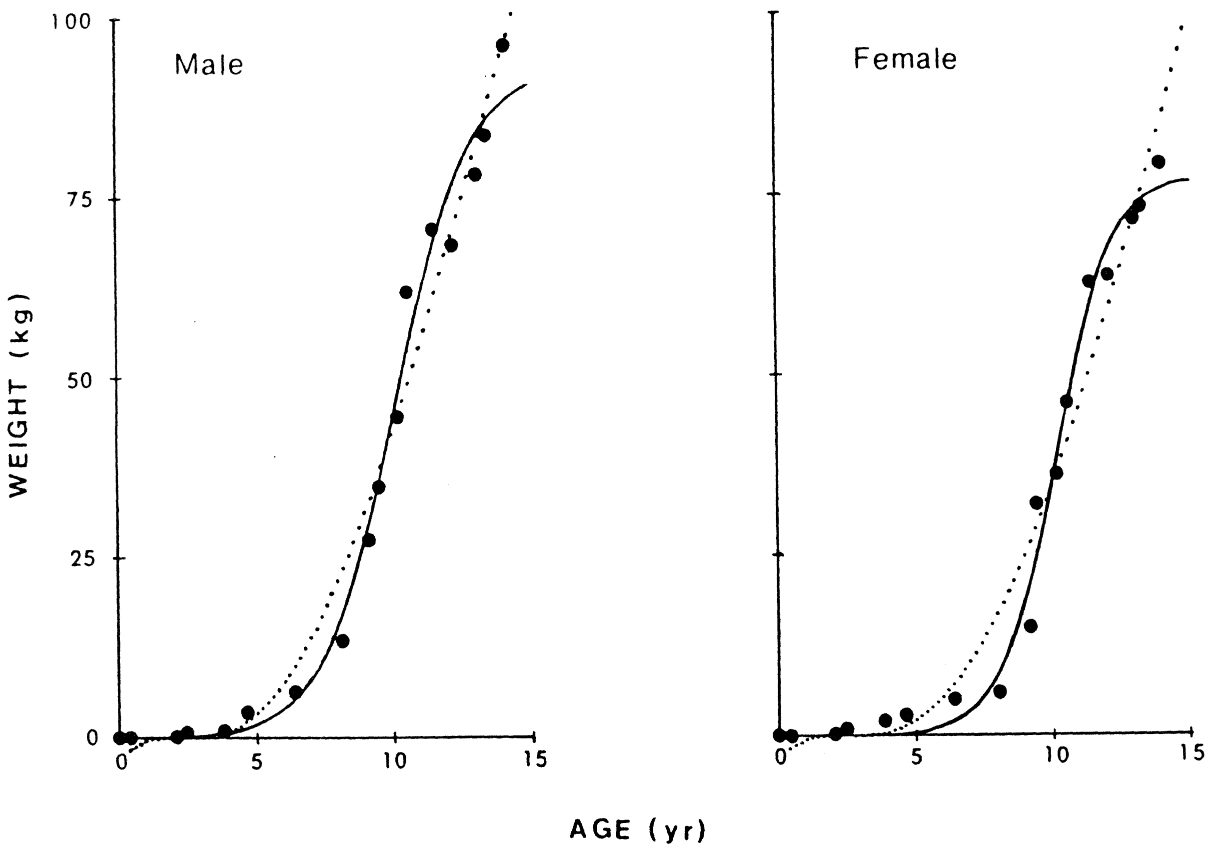

Figure 6. Weight growth curves for a male and female loggerhead turtle born and reared in captivity for 14 years at the Institute of Marine Sciences, North Carolina. Growth has continued (see text) beyond the curves projected by Frazer and Schwartz (1984). Solid line is actual, dotted predicted.

Wild adult North Carolina loggerheads are often found covered with the barnacle Platylepas hexastylas (Schwartz, 1960) and are subject to heavy infestation of the marine leech Ozobranchus margoi (Schwartz, 1974), as are greens, but not ridleys or leatherbacks. The shark sucker Echeneis naucrates is the most frequent external fish associate of the loggerhead yet it causes no damage to the turtle (Schwartz, 1977c). Whether the shark sucker acts as a parasite picker, as is claimed by Cressey and Lachner (1970), is unresolved.

Stranding and Death

Annually a growing concern has developed that more and more sea turtles are being found stranded along the United States coasts (Shoop and Ruckdeschell, 1982). Less than 300 sea turtles wash ashore or strand each year in North Carolina, exhibiting conditions varying from fresh to decomposed or mutilated bodies (Table 1). While strandings occur where and when shrimp or flounder fisheries exist, there is a tendency to blame those industries for the turtle's demise. No empirical data have shown that most of the deaths can be attributed to shrimping operations. Five percent or less of the turtles, mostly loggerheads, greens, or ridleys, found in North Carolina have propeller damage to the body or shell. The incidences of death from bullets has dropped dramatically to one or two per year since the enactment of the endangered species act. Damage to dead turtles by sharks is extensive. Perhaps this results after the turtle is returned to the water.

Strandings during the 1981-1988 seasons varied between 109 and 308 per season (Table 4). Fewer turtles stranded in years when shrimping was reduced, as a result of poor environmental conditions effecting shrimp larval survival and adult production (N.C. Marine Fisheries obs.). The only fishery where trawling seems to be directly tied to turtle strandings and death is the December-February flounder fishery off Ocracoke and Cape Hatteras. There, if the fall-winter weather season is warm, as a result of the Gulf Stream's persistence near the coast, a greater likelihood occurs for the fishery to encounter sea turtles. Such encounters have produced 52 turtles strandings along the Outer Banks from Cape Hatteras to Ocracoke (1985 Cape Hatteras data). Usually fewer than 10 turtles are affected during the flounder fishing season for the Gulf Stream is farther offshore and away from the spawning flounder populations that inhabit waters of 20 m or less off Cape Hatteras and Ocracoke. Elsewhere strandings, by county, are most frequent in areas where active concentrations of fishing fleets exist. These concentrations are off Ocracoke (Hyde County), Morehead City (Carteret County), Wrightsville Beach (New Hanover County), and Southport (Brunswick County). A fall fishery for menhaden existed off Southport until 1985 and occasional strandings occurred following their operations. Only one other fishing activity caused appreciable turtle strandings in North Carolina, the temporary gill net fishery for sturgeon off Bald Head Island and Caswell Beach in April 1981. Such operations are now prohibited by state law. Yearly, depending on cold surges or inshore eddy movement, a number of loggerheads, mostly greens and some ridleys, are killed and stranded (6 to 20 per year, pers. obs.) in southern Pamlico and northern Core sounds. Annually, cold stunned turtles, if found in time, have been rehabilitated (warmed) at the Manteo and Pine Knoll Shores Aquaria for subsequent return by helicopter to offshore warm waters in order to prevent further deaths or strandings.

Effects by Man

Other than the effects of cold snaps, cold water temperatures, and beach accessibility, man's activities present the greatest threats to the sea turtles of North Carolina. Beach availability problems stem from natural and man-made causes. Natural causes are beach erosion during coastal spring and winter storms or hurricanes (Pilkey et al., 1980). Many areas north of Cape Hatteras, along Bogue Banks, and south of Topsail Island, North Carolina (especially south of Masonboro Inlet, Kure, and Carolina beaches) are high energy beaches that are annually eroded by storms (Pilkey et al., 1980). Each year cities in those affected areas spend millions of dollars trying to rebuild the beach (with Corps of Engineers beach replenishment efforts) by pumping sand onto the beach prior to the next storm or hastily building bulkheads, groins, etc. to stem the storm's affects. As a result the beach sands used in replenishment are the wrong size (see earlier; Schwartz et al., 1980), too coarse, and have been easily washed away during the next storm. Bulkheads are undercut by subsequent storms and waves leave areas behind or next to them threatened, thereby increasing erosion. Man's most detrimental action is bulldozing the beachfront to create a new beach or fore dune. This action steepens the beach and leaves the area more vulnerable to destruction by storms and the sea. Available beach habitat for turtle nestings is thus under constant change or alteration. The results are fewer nestings in populated areas each year. Increased public use of the beaches also constantly disturbs the beach sands. Elaborate condominium construction has greatly altered sea turtle nesting behavior, especially from Nags Head northward, off Bogue Banks, and off Wrightsville Beach as too many lights now illuminate the beaches during the night. An example of the effects of this construction and lighting is Bogue Banks where 20-30 nests were once common on the eastern end of the island in the 60's and early 70's (per. obs.), only 13 and 2 occurred in 1987 and 1988. Nesting has shifted to the western end of the island towards Hammocks and Onslow beaches or to the east at Cape Lookout. Hatchlings born in areas impacted by man readily fall prey to bright lights that distract them from their intended movement to the sea. Losses of upwards of 900 hatchling loggerheads have been recorded for short spans of Bogue Banks beaches alone, especially during the 1 August through 15 October period of each emergent period (pers. obs.). Few turtles have been affected by oil tar balls (Witham, 1978) or dense concentrations of Portuguese man-of-war or cabbage head (Stomolopus) jellyfishes. They have been, as elsewhere (Anon., 1983; Fritts and McGehee, 1982), affected by ingested floating styrofoam or plastics (Anon., 1983; Mrosovsky, 1981).

Conservation

Although stiff penalties, levied as a result of the Rare and Endangered Species Act, have deterred public use of or lessened sea turtle strandings or their use as food, mutilations are still encountered. Efforts that specifically protect sea turtles in North Carolina are the regulations prohibiting gill netting off Bald Head Island, erecting wire screens around nests to prevent wild animal predation, and the creation (Schwartz, 1980; N.C. Fishery Laws) of the only sea turtle sanctuary in the continental United States. The sanctuary extends from New River Inlet to Bogue Inlet and off Hammocks and Onslow beaches and annually serves as an area where sea turtles are safe and can stage prior to nesting nearby (Figure 7). The sanctuary is an example of how man and sea turtles can safely coexist as the sanctuary permits a historical shrimp and fish fishery to exist without conflict to turtles or man. Fishermen are permitted to fish in only two specific areas (Figure 7). This compromise has led to a reduction of strandings in the area from 40 to less than one per year.

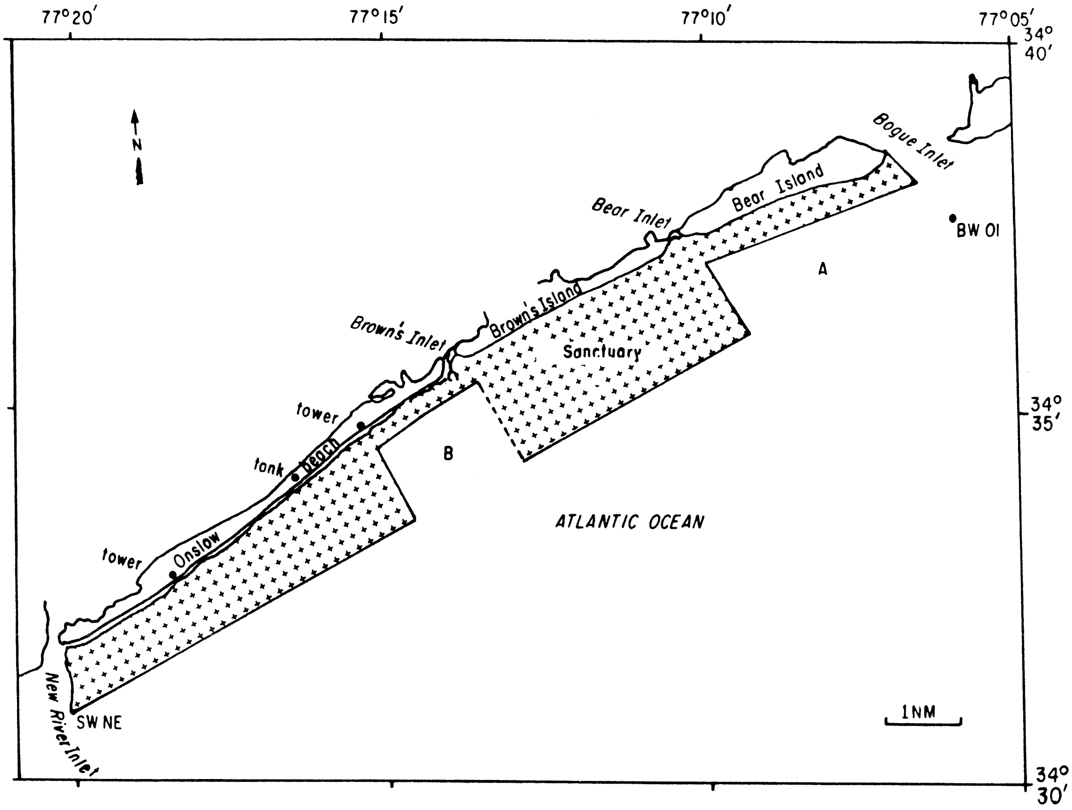

Figure 7. Location of sea turtle sanctuary in North Carolina established by law in 1980. Sanctuary extends from New River to Bogue Inlet. Areas marked a and b are restricted areas open to shrimping.

CONCLUSIONS

Five species of rare and endangered sea turtles are known from North Carolina. Their abundance, seasonality, nesting, and existence is interwoven by the effects of environment, habitat, and man. If left to their own resources it appears that sea turtles would persevere and perhaps increase in numbers. Man needs to make the biggest change in his use and alteration of the available habitat and populations. A compromise must be struck, otherwise one of North Carolina's natural heritages, the sea turtles, will be lost to all generations.

ACKNOWLEDGMENTS

Many have contributed in obtaining data on North Carolina's sea turtle nestings, strandings, hatch success, and laboratory incubation and growth experiences. Special thanks are extended the personnel at Cape Hatteras National Seashore Park, Pea Island National Seashore Park, Cape Lookout National Seashore Park, Fort Macon State Park (Bogue Banks), Hammocks Beach State Park, Camp Lejuene (Onslow Beach), Carolina Power and Light Lab at Southport, Marine Resources Center (now Aquaria) at Manteo, Pine Knoll Shores, and Ft. Fisher. North Carolina State Ferry Service, Cedar Island, Ocracoke, Hatteras Inlet, North Carolina Marine Fisheries Division, Morehead City, N.C., F. Berry and B. Schroeder, NMFS, Miami, Fl., and the many private volunteer citizens who faithfully reported data year after year. Special thanks to IMS staff who helped with maintaining the hatchling and experimental sea turtles: J. Tate, J. Purifoy, G. Safrit, and O. Lewis. Dr. N. Frazer, Mercer College, Macon, Ga., R. Witham, Florida Department Natural Resources, Jensen Beach, Fl., C. Peterson, Camp Lejuene, N.C. and Dr. W.D. Webster, University of North Carolina at Wilmington, reviewed the manuscript and provided timely comments for its improvement. V. and H. Page produced Figures 1-7. B. Bright typed the text.

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Chapter 6. Continental Shelf-Slope Biota

Chairpersons - Dr. William Hogarth &
Dr. Lisa Levin

ZOOGEOGRAPHY AND ECOLOGY OF FISHES INHABITING NORTH CAROLINA'S MARINE WATERS TO DEPTHS OF 600 METERS

Frank J. Schwartz
Institute of Marine Sciences
University of North Carolina
Morehead City, North Carolina 28557

ABSTRACT

More than 685 species of fishes within 149 families are known to occur in waters that extend from the inshore high tide mark seaward to offshore depths of 600 m off North Carolina. These waters include estuarine, coastal, continental shelf, and slope habitats. The fishes are treated by province, depth distribution, habitat, type of fish, type of migrant, seasonality, and where known. Comments are presented on a species' biology and interaction with a specific community or environment located in the Middle and South Atlantic bights. The interplay and influence or control of their abundance by geological and environmental features such as Hatteras barrier, Charleston Bump, eddies, water temperatures, salinities, rivers, and the Gulf Stream are also noted.

INTRODUCTION

More than 685 species of fishes within 149 families are known to occur in waters that extend from the inshore high tide mark seaward to offshore depths of 600 m off North Carolina (Table 1). While many species are often cited as occurring in immediate or adjacent areas, Labrador to South America (e.g., Breder, 1929; Briggs, 1958, 1974; Leim and Scott, 1966; Robins and Ray, 1986), they are not included in this faunal list unless extant specimens were located in known repositories, verified from literature records, or collected by various fishing gears. Likewise, many factors (e.g., the Gulf Stream and Charleston Bump, the latter a raised oceanic ridge off Charleston, South Carolina that deflects the Gulf Stream offshore, Pietrafesa et. al., 1985) or events may directly or indirectly influence a species' range extension, disjunction, occurrence, or absence from North Carolina. This paper addresses those fishes captured in or frequenting North Carolina's estuarine, coastal or continental shelf and slope waters, and factors that influence their occurrence. They are treated by province, habitat, type of fish, type of migrant, depth distribution, seasonality, and physical and geological features. Where known, additional comments are presented on a species' biology and interaction with specific communities or environments located within the Middle and South Atlantic Bights.

Table 1. Fishes known from estuarine and marine waters of North Carolina and adjacent areas to depths of 600 m in relation to family, province, and habitat occupied by species.

	Province			Habitat					
	VA	Car	Carib	E	C	OS	R	SE	LS
Myxinidae									
Myxine glutinosa - Atlantic hagfish	X	X						X	X
Petromyzontidae									
Petromyzon marinus - sea lamprey	X	X	X	X	X	X			
Hexanchidae									
Heptranchias perlo - sharpnose sevengill shark		X	X					X	X
Hexanchus griseus - sixgill shark		X	X			X		X	
Odontaspididae									
Eugomphodus taurus - sand tiger	X	X	X	X	X	X	X	X	
Alopiidae									
Alopias superciliosus - bigeye thresher	X	X	X		X	X		X	
Alopias vulpinus - thrasher shark	X	X	X		X	X	X	X	
Lamnidae									
Carcharodon carcharias - white shark	X	X	X		X	X		X	X
Cetorhinus maximus - basking shark	X	X			X	X			
Isurus oxyrinchus - shortfin mako	X	X	X		X	X	X	X	
Isurus paucus - longfin mako	X	X	X			X	X	X	X
Lamna nasus - porbeagle	X	X	X		X	X		X	
Orectolobidae									
Ginglymostoma cirratum - nurse shark		X	X		X	X	X	X	
Rhincodontidae									
Rhincodon typus - whale shark		X			X	X		X	
Scyliorhinidae									
Apristurus laurussonni - flathead catshark			X					X	X
Scyliorhinus meadi - blotched catshark		X	X			X		X	X
S. retifer - chain dogfish	X	X	X		X	X		X	X
Carcharhinidae									
Carcharhinus acronotus - blacknose shark		X	X		X	X			
C. altimus - bignose shark	X	X	X		X	X		X	
C. brevipinna - spinner shark	X	X	X		X	X		X	
C. falciformis - silky shark	X	X	X		X	X		X	
C. isodon - finetooth shark	X	X	X		X	X		X	
C. leucas - bull shark	X	X	X	X	X	X			
C. limbatus - blacktip shark	X	X	X		X	X			
C. longimanus - oceanic whitetip shark	X	X	X		X	X		X	X
C. obscurus - dusky shark	X	X	X	X	X	X		X	
C. plumbeus - sandbar shark	X	X	X	X	X	X			
C. signatus - night shark	X	X	X		X	X		X	
Galeocerdo cuvieri - tiger shark	X	X	X		X	X	X	X	
Mustelus canis - smooth dogfish	X	X	X	X	X	X			
Negaprion brevirostris - lemon shark	X	X	X	X	X	X	X	X	
Prionace glauca - blue shark	X	X	X		X	X		X	X
Rhizoprionodon terraenovae - Atlantic sharpnose shark	X	X	X	X	X	X			
Sphyrnidae									
Sphyrna lewini - scalloped hammerhead	X	X	X		X	X		X	
S. mokarran - great hammerhead	X	X	X		X	X		X	
S. tiburo - bonnet head	X	X	X	X	X	X		X	
S. zygaena - smooth hammerhead	X	X	X		X	X			
Squalidae									
Dalatias licha - kitefin shark			X			X		X	X
Deania profundorum			X					X	X
Etmopterus bullisi			X					X	X
E. gracilispinis - broadband dogfish			X					X	X
E. hillianus - blackbelly dogfish			X					X	X
Somniosus microcephalus - greenland shark	X	X				X		X	
Squalus acanthias - spiny dogfish	X	X	X	X	X	X			
S. cubensis - Cuban dogfish		X	X			X			
S. mitsukurii - short spine spurdog		X	X			X			
Squatinidae									
Squantina dumerili - angel shark	X	X	X		X	X		X	
Pristidae									
Pristis pectinata - smalltooth sawfish	X	X	X		X	X			
Rhinobatidae									
Rhinobatos lentiginosus - Atlantic guitarfish	X	X	X		X	X			
Torpedinidae									
Benthobatis marcida - deep-sea electric ray			X			X		X	X
Nacine brasiliensis - lesser electric ray	X	X	X		X	X			
Torpedo nobiliana - Atlantic torpedo	X	X	X		X	X			
Rajidae									
Bathyraja richardsoni			X					X	X
Breviraja atripinna - black-fin skate		X	X			X		X	

Table 1 (con't)	Province			Habitat					
	VA	Car	Carib	E	C	OS	R	SE	LS
B. plutonia		X	X			X		X	
B. spinosa	X	X	X			X		X	
Dactylobatus armatus			X					X	?
Raja eglanteria - clearnose skate	X	X	X	X	X	X			
R. erinacea - little skate	X	X				X		X	
R. floridana		X	X			X		X	X
R. garmani - rosette skate	X	X	X			X		X	X
R. laevis - barndoor skate	X	X	?			X		X	X
R. ocellata - winter skate	X	X	X			X		X	
R. radiata - thorny skate	X	X	X		X	X		X	X
R. senta - smooth skate	X	X	X			X		X	X
Dasyatidae									
Dasyatis americana - southern stingray	X	X	X	X	X	X			
D. centroura - roughtail stingray	X	X	X		X	X			
D. sabina - Atlantic stingray	X	X	X	X	X	X			
D. sayi - bluntnose stingray	X	X	X	X	X	X			
Gymnura altavela - spiny butterfly ray	X	X	X	X	X	X			
G. micrura - smooth butterfly ray	X	X	X	X	X	X			
Urolophus jamaicensis - yellow stingray	X	X	X		X	X			
Myliobatidae									
Aetobatus narinari - spotted eagle ray	X	X	X	X	X	X			
Myliobatis freminvillei - bullnose ray	X	X	X	X	X	X			
M. goodei - southern eagle ray		X	X		X	X			
Rhinoptera bonasus - cownose ray	X	X	X	X	X	X			
Mobulidae									
Manta birostris - Atlantic manta	X	X	X	X	X	X	X		
Mobula hypostoma - devil ray	X	X	X		X	X			
M. mobular - devil ray	?	X	X			X		X	
Acipenseridae									
Acipenser brevirostrum - shortnose sturgeon[a]	X	X		X	X				
A. oxyrhynchus - Atlantic Sturgeon[a]	X	X	X	X	X				
Lepisosteidae									
Lepisosteus osseus - longnose gar	X	X	X	X	X				
Amiidae									
Amia calva -bowfin	X	X		X	X				
Elopidea									
Elops saurus - ladyfish	X	X	X	X	X				
Megalops atlanticus - tarpon	X	X	X	X	X				
Albulidae									
Albula vulpes - bonefish		X	X		X				
Halosauridae									
Aldrovandria affinis			X					X	X
A. gracilis			X					X	X
Anguillidae									
Anguilla rostrata - American eel[c]	X	X	X	X	X	X			
Muraenidae									
Gymnothorax moringa - spotted moray		X	X			X	X	X	X
G. saxicola - ocellated moray	X	X	X		X	X	X	X	
Muraena retifera - reticulate moray	X	X	X				X	X	
M. robusta		X	X				X	X	X
Congridae									
Arisoma balearicum - bandtooth conger		X	X			X	X		
Conger oceanicus - conger eel	X	X	X	X	X	X	X	X	
Paraconger caudilimbatus - margintail conger		X	X			X	X		
Synaphobranchidae									
Dysommina rugosa		X			X	X			
Ilyophis brunneus		X	X					X	X
Synaphobranchus affinis		X	X					X	X
S. kaupi - gray's cutthroat eel		X	X					X	X
Ophichthidae									
Ahlia egmontis key worm eel		X	X		X	X			
Apterichthus ansp - academy eel		X	X			X	X		
A. kendalli - finless eel		X	X			X	X		
Bascanichthys bascanium - sooty eel		X	X			X	X		
B. scuticaris - whip eel		X	X			X	X		
Echiophis intertinctus - spotted spoon-nose eel		X	X			X	X		
Letharchus velifer - sailfin eel		X	X		X	X			
Myrichthys acuminatus - sharptail eel		X	X				X		
M. punctatus - speckled worm eel	X	X	X	X	X	X			
Ophichthus cruentifer - margined snake eel	X	X	X	X	X	X			
O. gomesi - shrimp eel		X	X	X	X	X			
O. ocellatus - palespotted eel		X	X	X	X	X			
O. ophis - spotted snake eel		X	X			X			
Notacanthidae									
Polyacanthus merretti			X						X

Table 1 (con't)	Province			Habitat					
	VA	Car	Carib	E	C	OS	R	SE	LS
Nemichthyidae									
Nemichthys scolopaceus - slender snipe eel	X	X	X					X	X
Serrivomeridae									
Serrivomer beani			X					X	X
Clupeidae									
Alosa aestivalis - blueback herring[a]	X	X	X	X	X	X			
A. mediocris - hickory shad[a]	X	X	X	X	X	X			
A. pseudoharengus - alewife[a]	X	X	X	X	X	X			
A. sapidissima - American shad[a]	X	X	X	X	X	X			
Brevoortia smithi - yellowfin menhaden	X	X	X	X	X	X			
B. tyrannus - Atlantic menhaden	X	X	X	X	X	X			
Clupea harengus - Atlantic herring	X	X	X		X	X			
Dorosoma cepedianum - gizzard shad	X	X	X	X	X	X			
D. petenense - threadfin shad	X	X	X	X	X				
Etrumeus teres - round herring	X	X	X	X	X	X			
Harengula jaguana - scaled sardine	X	X	X		X	X			
Jenkinsia lamprotaenia - dwarf herring		X	X		X	X			
Opisthonema oglinum - Atlantic thread herring	X	X	X	X	X	X			
Sardinella aurita - Spanish sardine	X	X	X		X	X			
S. brasiliensis - orangespot sardine		X			X				
Engraulidae									
Anchova cubana - Cuban anchovy		X	X		X	X			
A. hepsetus - striped anchovy	X	X	X	X	X	X			
A. lyolepis - dusky anchovy		X	X		X	X			
A. mitchelli - bay anchovy	X	X	X	X	X				
Anchoviella perfasciata - flat anchovy		X	X		X	X			
Engraulis eurystole - silver anchovy	X	X			X	X			
Argentinidae									
Argentina striata - striated argentine	X	X	X		X	X		X	X
Glossanodon pygmaeus		X						X	X
Esocidae									
Esox americanus - pickerel	X	X		X	X				
E. niger - chain pickerel	X	X		X	X				
Alepocephalidae									
Bajacalifornia megalops			X					X	
Synodontidae									
Synodus brasiliensis - largescale lizardfish		X	X		X	X			
S. foetens - inshore lizardfish	X	X	X	X	X	X	X		
S. intermedius - sand diver		X	X		X	X	X		
S. normani - shortjaw lizardfish		X	X			X	X		
S. poeyi - offshore lizardfish		X	X			X	X		
S. synodus - red lizardfish		X	X			X	X		
Trachinocephalus myops - snakefish	X	X	X			X	X		
Gonostomatidae									
Cyclothone acclinidus			X				X	X	
Gonostoma elongata			X				X	X	
Sternoptychidae									
Argypelecus aculeatus - Atlantic silver hatchetfish			X					X	X
A. affinis			X					X	X
A. hemigymnus - silver hatchetfish			X					X	X
Maurolicus (muelleri)			X					X	X
Polypnis asteroides			X					X	X
Sternoptyx diaphana - transparent hatchetfish			X					X	X
Stomiidae									
Stomis boa ferox - boa dragonfish			X					X	X
Malacosteidae									
Malacosteus niger			X						X
Photastomias guernei			X						X
Chloropthalmidae									
Chlorophthalmus agassizi - shortnose greeneye			X					X	X
Evermannelidae									
Evermannella balboa			X						X
Alepisauridae									
Alepisaurus brevirostris - shortnose lancetfish			X					X	X
A. ferox - longnose lancetfish			X					X	X
Myctophidae									
Ceratoscopelus maderensis - horned lanternfish			X						X
Lampanyctus sp.			X						X
Myctophus affinis - metallic lanternfish			X						X
M. nitidulum			X						X
Moridae									
Antimora rostrata - blue antimora		X	X		X			X	X
Laemonema sp. (barbatula)			X					X	X
Physiculus fulvus			X					X	X
Cyprinidae									

Table 1 (con't)

	Province			Habitat					
	VA	Car	Carib	E	C	OS	R	SE	LS
Cyprinus carpio - common carp	X	X	X	X	X				
Notemigonus crysoleucas - golden shiner	X	X		X					
Notropis chalybaeus - ironcolor shiner	X	X	X	X					
N. petersoni - coastal shiner		X		X					
Catostomidae									
Erimyzon sucetta - lake chubsucker	X	X		X					
Moxostoma macrolepidotum - shorthead redhorse	X	X		X					
Ictaluridae									
Ameiurus catus - white catfish	X	X		X	X				
A. natatis - yellow bullhead	X	X		X	X				
A. nebulosus - brown bullhead	X	X		X	X				
Ictalurus furcatus - white catfish	X	X		X	X				
I. punctatus - channel catfish	X	X		X	X				
Noturus gyrinus - tadpole madtom	X	X		X					
Ariidae									
Ariopsis felis - hardhead catfish		X	X		X	X			
Bagre marinus - gafftopsail catfish		X	X		X	X			
Aphredoderidae									
Aphredoderus sayanus - pirate perch	X	X		X					
Batrachoididae									
Opsanus pardus - leopard toadfish		X	X		X	X			
O. tau - oyster toadfish	X	X		X	X	X			
Porichthys plectrodon - Atlantic midshipman	X	X	X	X	X	X			
Gobiesocidae									
Gobiesox strumosus - skilletfish	X	X	X	X	X	X	X		
Lophiidae									
Discolophius gastrophysus - blackfin goosefish			X			X			
Lophiodes reticulatus - reticulate goosefish			X			X			
Lophius americanus - goosefish	X	X	X	X	X	X			
Antennariidae									
Antennarius multiocellatus - longlure frogfish		X	X				X		
A. ocellatus - ocellated frogfish	X	X	X		X	X			
A. radiosus - singlespot frogfish		X	X		X	X			
A. scaber - splitlure frogfish		X	X		X	X			
Histrio histrio - sargassumfish	X	X	X	X	X	X			
Chaunacidae									
Chaunax stigmaeus - gaper			X					X	X
Ogcocephalidae									
Dibranchus atlanticus	X	X	X					X	X
Halieutichthys aculeatus - pancake batfish		X	X					X	X
Ogcocephalus corniger - longnose batfish	X	X	X		X	X	X		
O. nasutus - shortnose batfish		X	X		X	X	X		
O. parvus - roughback batfish		X	X		X	X	X		
O. radiatus - polka-dot batfish		X	X		X	X	X		
O. rostellum - palefin batfish		X	X	X	X	X	X		
Bregmacerotidae									
Bregmaceros atlanticus - antenna codlet	X	X	X	X	X				
Gadidae									
Brosme brosme - cusk	X	X			X	X			
Enchelyopus cimbrius - fourbeard rockling	X	X	X	X	X				
Gadus morhua - Atlantic cod	X	X		X	X	X		X	
Melanogrammus aeglefinus - haddock	X	X		X	X	X		X	
Merluccius albidus - offshore hake	X	X	X			X		X	X
M. bilinearis - silver hake	X	X	X		X	X			
Pollachius virens - pollock									
Urophycis chesteri - longfin hake	X	X	X					X	
U. chuss - red hake	X	X				X		X	
U. earli - carolina hake		X	X		X	X		X	X
U. floridana - southern hake		X	X		X	X			
U. regia - spotted hake	X	X	X	X	X	X		X	
Macrouridae									
Chalinura brevibarbus		X	X					X	X
Coelorhinchus c. carminatus - longnose grenadier		X	X					X	X
C. occa		X	X					X	X
Gadomus arcuatus			X						X
Hymenocephalus italicus		X	X					X	X
Nezumia aequalis		X	X					X	X
N. bairdii - marlin spike		X	X					X	X
Ventrifossa sp.		X	X					X	X
Ophidiidae									
Brotula barbata - bearded brotula	X	X	X	X					
Lepophidium cervinum - fawn cusk-eel	X	X	X	X	X	X			
L. jeannae			X					X	
L. profundorum		X	X					X	X
Ophidion beani - longnose cusk-eel		X	X		X	X			

Table 1 (con't)	Province			Habitat					
	VA	Car	Carib	E	C	OS	R	SE	LS
O. grayi - blotched cusk-eel		X	X		X	X			
O. holbrooki - bank cusk-eel		X	X		X	X		X	
O. marginatum - striped cusk-eel	X	X	X		X	X			
O. welshi - crested cusk-eel		X	X	X	X	X			
Otophidium omostigmum - polka-dot cusk-eel		X	X						
Exocoetidae									
Cheilopogon cyanopterus - margined flyingfish	X	X	X			X		X	
C. exsiliens - bandwing flyingfish	X	X	X	X	X	X		X	
C. furcatus - spotfin flying fish	X	X	X			X		X	
C. melanurus - Atlantic flyingfish	X	X	X		X	X		X	
Euleptorhamphus velox - flying halfbeak		X	X			X			
Exocoetus volitans - tropical two-wing flying fish		X	X	X	X	X			
Hemiramphus balao - balao	X	X	X		X	X		X	
H. brasiliensis - ballyhoo	X	X	X		X	X		X	
Hirundichthys affinis - fourwing flying fish	X	X	X		X	X		X	
Hyporhamphus unifasciatus - halfbeak	X	X	X	X	X	X			
Parexocoetus brachypterus - sailfin flying fish		X	X			X		X	
Belonidae									
Ablennes hians - flat needlefish	X	X	X		X	X		X	
Platybelone argalus - keeltail needlefish		X	X			X			
Strongylura marina - Atlantic needlefish	X	X	X	X	X	X			
Tylosurus acus - agujon	X	X	X		X	X			
T. crocodilus - houndfish	X	X	X		X	X		X	
Scomberesocidae									
Scomberesox saurus - Atlantic saury	X	X			X	X		X	
Cyprinodontidae									
Cyprinodon variegatus - sheepshead minnow	X	X	X	X					
Fundulus confluentus - marsh killifish	X	X	X	X					
F. diaphanus - banded killifish	X	X		X					
F. heteroclitus - mummicog	X	X	X	X	X				
F. luciae - spotfin killifish	X	X	X	X					
F. majalis - striped killifish	X	X	X	X	X				
Lucania parva - rainwater killifish	X	X	X	X					
Poeciliidae									
Gambusia holbrooki - mosquitofish	X	X	X	X	X				
Poecilia latipinna - sailfin molly	X	X	X	X					
Atherinidae									
Membras martinica - rough silverside	X	X	X	X	X				
Menidia beryllina - inland silverside	X	X	X	X					
M. menidia - Atlantic silverside	X	X	X	X	X				
Polymixiidae									
Polymixia lowei - beardfish	X	X	X		X				
Holocentridae									
Holocentrus adscensionis - squirrelfish		X	X		X	X	X		
H. bullisi - deepwater squirrelfish		X	X			X	X	X	
H. rufus - longspine squirrelfish		X	X			X	X		
H. vexillarius - dusky squirrelfish		X	X			X	X		
Myripristis jacobus - blackbar soldierfish		X	X				X		
Ostichthys trachypoma - bigeye soldierfish	X	X	X			X	X		
Zeidae									
Zenopsis conchifera - buckler dory	X	X	X			X		X	X
Grammicolepidae									
Daramattus americanus - thorny tinselfish			X					X	
Grammicolepis brachiusculus			X					X	
Xenolepidichthys dalgleishi - spotted tinselfish	X	X	X					X	X
Melamphidae									
Scopelogadus beani - Bean's blueback			X					X	
Caproidae									
Antigonia capros - deepbody boarfish	X	X	X			X		X	
A. combatia - shortspine boarfish	X	X	X			X		X	
Trachipteridae									
Desmodema polystictum - polka-dot ribbonfish		X	X			X		X	
Regalecidae									
Regalecus glesne - oarfish	X	X	X			X		X	X
Trachichthyidae									
Gephyroberyx darwinii	X	X				X			
Hoplostethus mediterraneus	X	X				X			
Fistularidae									
Fistularia petimba - red cornetfish	X	X	X			X		X	X
F. tabacaria - bluespotted cornetfish		X	X	X	X	X	X	X	
Gasterosteidae									
Apeltes quadracus - fourspine stickleback	X	X		X					
Gasterosteus aculeatus - threespine stickleback	X	X		X					
Centriscidae									
Macrorhamphus scolopax - longspine snipefish	X	X	X			X		X	

Table 1 (con't)	Province			Habitat					
	VA	Car	Carib	E	C	OS	R	SE	LS
Syngnathidae									
Acentronura dendriticus - pipehorse	X	X	X			X			
Cosmocampus albirostris - whitenose pipefish		X	X				X		
Hippocampus erectus - lined seahorse	X	X	X	X	X		X		
Micrognathus cringer - fringed pipefish		X	X	X					
Oostethus brachyurus - opposum pipefish		X	X	X	X				
Synagnathus dunckeri - pugnose pipefish		X	X			X			
S. eleucens - shortfin pipefish		X	X			X	X		
S. floridae - dusky pipefish	X	X	X	X	X				
S. fuscus - northern pipefish	X	X	X	X	X				
S. hildebrandi - dwarf pipefish			X			X			
S. louisianae - chain pipefish	X	X	X	X	X	X	X		
S. springeri - bull pipefish		X	X			X	X	X	
Centropomidae									
Centropomus undecimalis - snook		X	X	X	X				
Percichthyidae									
Morone americana - white perch	X	X		X	X				
M. saxatilis - striped bass	X	X	X	X	X				
Polyprion americanus - wreckfish	X	X				X		X	X
Synagrops bellus - blackmouth bass		X	X					X	X
Serranidae									
Anthias nicholsi - yellowfin bass			X			X		X	X
Centropristis ocyurus - bank sea bass	X	X	X	X	X	X	X		
C. philadelphica - rock sea bass	X	X	X	X	X	X	X		
C. striata - black sea bass	X	X	X	X	X	X	X		
Diplectrum formosum - sand perch	X	X	X	X	X	X	X		
Epinephelus adscensionis - rock hind		X	X				X		
E. cruentatus - graysby		X	X			X	X		
E. drummondhayi - speckled hind		X	X		X	X	X	X	
E. flavolimbatus - yellowedge grouper		X	X			X	X	X	
E. fulvus - coney			X			X	X	X	
E. guttatus - red hind		X	X				X		
E. inermis - marbled grouper			X			X	X	X	X
E. itajara - jewfish		X	X				X	X	
E. morio - red grouper	X	X	X		X	X	X	X	
E. nigritus - warsaw grouper	X	X	X			X	X		
E. niveatus - snowy grouper	X	X	X			X	X	X	
E. striatus - Nassau grouper		X	X			X	X		
Hemanthias vivanus - red barbier		X	X			X	X	X	X
Holacanthus martinicus - roughtongue bass		X	X				X		
Liopropoma eukrines - wrasse bass		X	X				X	X	
Mycteroperca bonaci - black grouper	X	X	X	X	X	X	X		
M. interstitialis - yellowmouth grouper		X	X			X	X	X	X
M. microlepis - gag	X	X	X	X	X	X	X		
M. phenax - scamp	X	X	X			X	X	X	
M. venenosa - yellowfin grouper		X	X			X	X	X	
Paranthias furcifer - creole-fish		X	X				X	X	X
Schultzea beta - school bass		X	X			X	X		
Serraniculus pumilio - pygmy sea bass		X	X		X		X	X	
Serranus atrobranchus - blackear bass		X	X				X		
S. notospilus - saddle bass		X	X				X		
S. phoebe - tattler		X	X		X	X	X		
S. subligarius - belted sandfish		X	X		X	X	X		
S. tigrinus - harlequin bass		X	X				X		
Grammistidae									
Rypticus maculatus - whitespotted soapfish	X	X	X		X	X	X		
Centrarchidae									
Acantharchus pomotis - mud sunfish	X	X		X	X				
Centrarchus macropterus - flier	X	X		X					
Elassoma zonatum - banded pygmy sunfish	X	X		X					
Enneacanthus chaetodon - blackbanded sunfish	X	X		X					
E. gloriosus - bluespotted sunfish	X	X		X					
E. obesus - banded sunfish	X	X		X					
Lepomis auritus - redbrest sunfish	X	X		X					
L. gibbosus - pumkinseed	X	X		X					
L. gulosus - warmouth	X	X		X					
L. macrochirus - bluegill	X	X		X					
L. microlophus - redear sunfish	X	X		X					
Micropterus salmoides - largemouth bass	X	X		X					
Priacanthidae									
Cookeolus japonicus - bulleye	X	X	X				X	X	
Heteropriacanthus cruentatus - glasseye snapper	X	X	X	X	X	X	X		
Priacanthus arenatus - bigeye	X	X	X	X	X	X	X		
Pristigenys alta - short bigeye	X	X	X	X	X	X	X		
Apogonidae									

Table 1 (con't)	Province			Habitat					
	VA	Car	Carib	E	C	OS	R	SE	LS
Apogon pseudomaculatus - twospot cardinalfish		X	X				X		
Astrapogon alutus - bronze cardinalfish		X				X	X		
Phaeopteryx pigmentaria - dusky cardinalfish			X				X		
Malacanthidae									
Caulolatilus chrysops - goldface tilefish		X	X			X	X		
C. cyanops - blackline tilefish		X	X			X	X		
C. microps - blueline tilefish		X	X			X	X		
Lopholatilus chamaeleonticeps - tilefish	X	X	X			X	X		
Malacanthus plumieri - sand tilefish		X	X			X	X		
Pomatomidae									
Pomatomus saltatrix - bluefish	X	X	X	X	X	X	X		
Rachycentridae									
Rachycentron canadum - cobia	X	X	X	X	X	X	X	X	
Echeneididae									
Echeneis naucrates - sharksucker	X	X	X		X	X		X	
Remilegia albescens - white suckerfish	X	X	X			X		X	
Remora brachyptera - spearfish remora	X	X	X			X		X	
R. osteochir - marlinsucker	X	X	X			X		X	
R. remora - remora	X	X	X			X		X	
Carangidae									
Alectis ciliaris - African pompano	X	X	X		X	X	X	X	
Caranx bartholomaei - yellow jack	X	X	X	X	X	X			
C. crysos - blue runner	X	X	X	X	X	X	X		
C. hippos - crevalle jack	X	X	X	X	X	X	X		
C. latus - horse-eye jack	X	X	X		X	X			
C. ruber - bar jack	X	X	X				X		
Chloroscombrus chrysurus - Atlantic bumper	X	X	X	X	X	X	X		
Decaperus macarellus - mackerel scad	X	X	X		X	X		X	
D. punctatus - round scad	X	X	X		X	X	X		
D. tabl - redtail scad		X	X			X			
Elegatis bipinnulata - rainbow runner	X	X	X			X	X	X	
Hemicaranx amblyrhynchus - bluntnose jack		X	X			X	X		
Naucrates ductor - pilot fish	X	X	X		X	X	X		
Oligoplites saurus - leatherjacket	X	X	X	X	X				
Selar crumenophthalmus - bigeye scad	X	X	X	X	X	X	X		
Selene setapinnis - Atlantic moonfish	X	X	X	X	X	X			
S. vomer - lookdown	X	X	X	X	X	X			
Serioli dumerilii - greater amberjack	X	X	X		X	X	X	X	
S. fasciata - lesser amberjack	X	X	X		X	X	X		
S. rivoliana - almaco jack	X	X	X			X	X	X	
S. zonata - banded rudderfish	X	X	X		X	X	X		
Trachinotus carolinus - Florida pompano	X	X	X	X	X	X			
T. falcatus - permit	X	X	X	X	X	X			
T. goodei - palometa	X	X	X	X	X				
Trachurus lathami - rough scad	X	X	X		X	X	X	X	
Uraspis secunda - cottonmouth jack	X	X	X			X	X		
Coryphaenidae									
Coryphaena equisetis - pompano dolphin	X	X	X			X	X	X	
C. hippurus - dolphin	X	X	X			X	X	X	
Bramidae									
Brama brama - Atlantic pomfret	X	X						X	X
Brama caribbean - Caribbean pomfret		X	X					X	X
Pteraclis carolinus			X					X	
Lutjanidae									
Etelis oculatus - queen snapper		X	X		X	X			
Lutjanus analis - mutton snapper	X	X	X	X	X	X	X		
L. apodus - schoolmaster									
L. buccanella - blackfin snapper		X	X		X	X	X		
L. campechanus - red snapper				X	X		X		
L. cyanopterus - cubera snapper		X	X			X	X		
L. griseus - gray snapper	X	X	X			X	X		
L. jocu - dog snapper	X	X	X	X	X	X	X		
L. mahogoni - mahogany snapper		X	X	X			X		
L. synagris - lane snapper		X	X	X	X		X		
L. vivanus - silk snapper		X	X				X	X	X
Ocyurus chrysurus - yellowtail snapper	X	X	X			X	X	X	
Pristipomoides aquilonaris - wenchman		X	X				X	X	
Rhomboplites aurorubens - vermilion snapper		X	X			X	X	X	X
Lobotidae									
Lobotes surinamensis - tripletail	X	X	X	X	X	X			
Gerreidae									
Diapterus auratus - Irish pompano		X	X	X	X				
Eucinostomus argenteus - spotfin mojarra	X	X	X	X	X				
E. gula - silver jenny	X	X	X	X	X				
E. lefroyi - mottled mojarra		X	X	X	X				

Table 1 (con't)	Province			Habitat					
	VA	Car	Carib	E	C	OS	R	SE	LS
Haemulidae									
Anisotremus surinamenis - black margate		X	X	X	X				
Haemulon aurolineatum - caesar grunt	X	X	X			X	X		
H. flavolineatum - French grunt		X	X			X	X		
H. plumieri - white grunt	X	X	X			X	X		
H. sciurus - bluestriped grunt		X	X				X		
Orthopristis chrysoptera - pigfish	X	X	X	X	X	X			
Sparidae									
Archosargus probatocephalus - sheepshead	X	X	X	X	X	X			
Calamus bajonado - jolthead porgy	X	X	X			X	X	X	
C. calamus - saucereye porgy		X	X				X		
C. leucosteus - whitebone porgy		X	X		X	X	X		
C. nodosus - knobbed porgy		X	X		X	X	X		
C. penna - sheepshead porgy		X	X				X		
C. proridens - littlehead porgy		X	X			X	X	X	
Diplodus holbrooki - spottail pinfish	X	X	X	X	X	X	X		
Lagodon rhomboides - pinfish	X	X	X	X	X	X	X		
Pagrus pagrus - red porgy	X	X	X			X	X	X	
Stenotomus caprinus - longspine porgy		X	X			X	X		
S. chrysops - scup	X	X		X		X	X		
Sciaenidae									
Bairdiella chrysoura - silver perch	X	X	X	X	X	X			
Cynoscion nebulosus - spotted seatrout	X	X	X	X	X				
C. nothus - silver seatrout	X	X	X	X	X				
C. regalis - weakfish	X	X	X	X	X				
Equetus acuminatus - high-hat		X	X	X	X		X		
E. iwamotoi - black bar		X	X			X	?		
E. lanceolatus - jackknife-fish		X	X		X		X		
E. umbrosus - cubbyu		X	X		X		X		
Larimus fasciatus - banded drum	X	X	X	X	X				
Leiostomus xanthurus - spot	X	X	X	X	X	X			
Menticirrhus americanus - southern kingfish	X	X	X	X	X	X			
M. littoralis - gulf kingfish	X	X	X	X	X	X			
M. saxatilis - northern kingfish	X	X	X	X	X	X			
Micropogonias undulatus - Atlantic croaker	X	X	X	X	X	X			
Pogonias cromis - black drum	X	X	X	X	X				
Sciaenops ocellatus - red drum	X	X	X	X	X				
Stellifer lanceolatus - star drum	X	X	X	X	X				
Umbrina coroides - sand drum	X	X	X				X		
Mullidae									
Mulloidichthys martinicus - yellow goatfish		X	X		X	X	X		
Mullus auratus - red goatfish	X	X	X			X	X		
Pseudupeneus maculatus - spotted goatfish	X	X	X			X	X		
Upeneus parvus - dwarf goatfish		X	X		X	X	X		
Kyphosidae									
Kyphosus incisor - yellow chub	X	X	X		X	X	X		
K. sectatrix - Bermuda chub	X	X	X	X	X	X	X		
Ephippididae									
Chaetodipterus faber - Atlantic spadefish	X	X	X	X	X	X	X		
Chaetodontidae									
Chaetodon aya - bank butterflyfish		X	X				X		
C. capristratus - foureye butterflyfish	X	X	X				X		
C. ocellatus - spotfin butterflyfish	X	X	X	X			X		
C. sedentarius - reef butterflyfish		X	X	X			X		
C. striatus - banded butterflyfish	X	X	X	X			X		
Pomacanthidae									
Holacanthus bermudensis - blue anglefish		X	X	X			X		
H. ciliaris - queen anglefish		X	X				X		
H. tricolor - rock beauth		X	X	X			X		
Pomacanthus arcuatus - gray anglefish	X	X	X	X			X		
P. paru - French anglefish		X	X				X		
Pomacentridae									
Abudefduf saxatilis - sergeant major	X	X	X	X	X		X		
A. taurus - night sergeant		X	X				X		
Chromis enchrysurus - yellowtail reeffish		X	X				X		
C. insolatus - sunshinefish		X	X				X		
C. scotti - purple reeffish		X	X				X		
Microspathodon chrysurus - yellowtail damselfish							X		
Stegastes fuscus - dusky damselfish							X		
S. leucostictus - beaugregory		X	X	X			X		
S. partitus - bicolor damselfish		X	X	X			X		
S. planifrons - threespot damselfish		X	X				X		
S. variabilis - cocoa damselfish			X				X		
Labridae									
Bodianus pulchellus - spotfin hogfish		X	X			X	X		

Table 1 (con't)	Province			Habitat					
	VA	Car	Carib	E	C	OS	R	SE	LS
B. rufus - Spanish hogfish		X	X			X	X		
Clepticus parrai - creole wrasse		X	X				X		
Decodon puellaris - red hogfish		X	X				X		
Halichoeres bivittatus - slippery dick		X	X	X			X		
H. caudalis - painted wrasse		X	X				X		
H. garnoti - yellowhead wrasse		X	X				X		
H. maculipinna - clown wrasse		X	X				X		
H. pictus - rainbow wrasse		X	X				X		
H. poeyi - blackear wrasse		X	X				X		
Hemipteronotus novacula - pearly razorfish		X	X			X	X	X	
Lachnolaimus maximus - hogfish	X	X	X			X	X	X	
Tautoga onitis - tautog	X	X		X	X				
Tautogolabrus adspersus - cunner	X	X		X	X				
Thalassoma bifasciatum - bluehead		X	X				X		
Xyrichtys novacula - pearly razorfish		X	X			X	X	X	
Scaridae									
Nicholsina usta - emerald parrotfish	X	X	X				X		
Scarus coeruleus - blue parrotfish	X	X	X				X		
Sparisoma radians - bucktooth parrotfish		X	X				X		
S. rubripinne - redfin parrotfish	X	X	X				X		
Mugilidae									
Mugil cephalus - striped mullet	X	X	X	X	X				
M. curema - white mullet	X	X	X	X	X				
Sphyraenidae									
Sphyraena barracuda - great barracuda	X	X	X		X	X	X		
S. borealis - northern sennet	X	X	X		X	X			
S. guachancho - guaguanche	X	X	X		X	X			
Polynemidae									
Polydactylus octonemus - Atlantic threadfin	X	X	X			X			
P. virginicus - barbu		X	X			X			
Opistognathidae									
Opistognathus melachasme - yellowmouth jawfish		X	X				X		
Dactyloscopidae									
Dactyloscopus moorei - speckled stargazer		X	X			X			
Uranoscopidae									
Astroscopus guttatus - northern stargazer	X	X	X	X	X	X			
A. y-graecum - southern stargazer	X	X	X	X	X	X			
Kathetostoma albigutta - lancer stargazer		X	X			X		X	
Clinidae									
Starksia ocellata - checkered blenny			X				X		
Blenniidae									
Chasmodes bosquianus - striped blenny	X	X	X	X	X				
Hypleurochilus geminatus - crested blenny		X	X	X					
Hypsoblennius hentzi - feather blenny	X	X	X	X					
H. ionthas - freckled blenny		X	X	X	X				
Ophioblennius atlanticus - redlip blenny		X	X				X		
Parablennius marmoreus - seaweed blenny	X	X	X		X	X	X		
Zoarcidae									
Macrozoarces americanus - ocean pout	X	X				X		X	X
Lycenchelys verrillii - wolf eelpout	X	X				X		X	X
Ammodytidae									
Ammodytes dubius - Northern sand lance	X	X				X			
Callionymidae									
Diplogrammus pauciradiatus - spotted dragonet		X	X			X			
Paradiplogrammus bairdi - lancer dragonet		X	X			X			
Eleotridae									
Dormitator maculatus - fat sleeper		X	X	X	X				
Eleotris pisonis - spinycheek sleeper		X	X	X					
Gobiidae									
Bathygobius soporator - frillfin goby		X	X	X					
Coryphopterus glaucofraenum - gridled goby		X	X				X		
C. punctipectophorus - spotted goby		X	X				X		
Ctenogobius boleosoma - darter goby		X	X	X	X				
C. saepepallens - dash goby		X	X						
C. shufeldti - freshwater goby		X	X	X					
C. smaragdus - emerald goby		X	X	X					
C. stigmaticus - marked goby		X	X	X					
Evermannichthys spongicola - sponge goby		X	X				X		
Evorthodus lyricus - lyre goby	X	X	X	X					
Gnatholepis thompsoni - goldspot goby		X	X				X		
Gobioides broussoneti - violet goby		X	X	X					
G. oceanicus - highfin goby		X	X			X			
Gobiosoma bosci - naked goby	X	X	X	X	X				
G. ginsburgi - seaboard goby	X	X	X	X	X	X			
G. robustum - code goby	X	X	X						

Table 1 (con't)

	Province			Habitat					
	VA	Car	Carib	E	C	OS	R	SE	LS
G. xanthiprora - yellowprow goby		X	X				X		
Ioglossus calliurus - blue goby		X	X				X		
Lythrypnus nesiotes - island goby			X				X		
L. phorellus - convict goby		X	X				X		
L. spilus - bluegold goby		X	X						
Microgobius carri - Seminole goby		X	X				X		
M. thalassinus - green goby	X	X	X	X					
Quisquilius hipoliti - rusty goby		X	X				X		
Microdesmidae									
Microdesmus longipinnis - pink wormfish		X	X	X					
Acanthuridae									
Acanthurus chirurgus - doctorfish	X	X	X				X		
A. coeruleus - blue tang		X	X				X		
Gempylidae									
Lepidocybium flavobrunneum - escolar			X					X	X
Nesiarchus nasutus			X			X			
Promichthys promethius - Bermuda catfish			X					X	X
Ruvettus pretiosus - oilfish		X	X					X	X
Trichiuridae									
Trichiurus lepturus - Atlantic cutlassfish	X	X	X	X	X	X			
Scombridae									
Acanthocybium solanderi - wahoo	X	X	X			X	X	X	
Auxis rochei - bullet mackerel			X					X	
Euthynnus alletteratus - little tunny	X	X	X			X	X	X	
Sarda sarda - Atlantic bonito	X	X	X			X	X	X	
Scomber japonicus - club mackerel	X	X	X		X	X	X		
S. scombrus - Atlantic mackerel	X	X				X		X	
Scomberomorus cavalla - king mackerel	X	X	X		X	X	X	X	
S. maculatus - spanish mackerel	X	X	X		X	X	X	X	
Thunnus alalunga - albacore		X	X			X	X	X	
T. albacares - yellowfin tuna	X	X	X		X	X	X	X	
T. atlanticus - blackfin tuna	X	X	X			X		X	
T. obesus - bigeye tuna	X	X	X			X		X	
T. thynnus - bluefin tuna	X	X	X			X		X	
Istiophoridae									
Istiophorus playpterus - sailfish	X	X	X		X	X	X	X	
Makaira nigricans - blue marlin	X	X	X			X	X	X	
Tetrapturus albidus - white marlin	X	X	X			X	X	X	
T. pfluegeri - longbill spearfish	X	X	X			X	X	X	
T. sp. - hatchet marlin		X	X			X	X	X	
Xiphiidae									
Xiphias gladius - swordfish	X	X	X			X	X	X	X
Stromateidae									
Ariomma bondi - silver-rag	X	X							
Hyperoglyphe perciformis - barrelfish	X	X	X	X	X	X		X	X
Nomeus gronovii - man-of-war fish	X	X	X			X		X	
Peprilus alepidotus - harvestfish	X	X	X	X	X				
P. burti - gulf butterfish		X	X	X	X				
P. triacanthus - butterfish	X	X	X	X	X				
Psenes cyanophrys - freckled driftfish	X	X	X					X	
Scorpaenidae									
Helicolenus dactylopterus - blackbelly rosefish	X	X	X			X		X	X
Neomerinthe hemingwayi - spinycheek scorpionfish	X	X	X			X		X	X
Pontinus rathbuni - highfin scorpionfish	X	X	X				X	X	X
Scorpaena agassizi - longfin scorpionfish		X	X					X	
S. brasiliensis - barbfish	X	X	X		X	X		X	
S. calcarata - smoothhead scorpionfish		X	X		X	X			
S. dispar - hunchback scorpionfish		X	X			X		X	
S. grandicornis - plumed scorpionfish		X	X					X	
S. inermis - mushroom scorpionfish		X	X					X	
S. isthmensis - smoothcheek scorpionfish		X	X		X	X			
S. plumieri - spotted scorpionfish	X	X	X			X			
Scorpaenodes tredecimspinosus - deepreef scorpionfish		X	X			X		X	X
Triglidae									
Bellator brachychir - shortfin searobin		X	X			X		X	X
B. egretta - streamer searobin		X	X					X	X
B. militaris - horned searobin		X	X					X	X
Peristedion gracile - slender searobin	X	X	X					X	X
P. minatum - armored searobin	X	X	X			X		X	X
P. thompsoni - rimspine searobin			X					X	X
P. truncatum			X					X	X
Prionotus alatus - spiny searobin	X	X	X					X	
P. carolinus - northern searobin	X	X	X	X	X	X		X	
P. evolans - striped searobin	X	X	X	X	X	X			

Table 1 (con't)

	Province			Habitat					
	VA	Car	Carib	E	C	OS	R	SE	LS
P. grayae		X	X					X	
P. ophryas - bandtail searobin		X	X		X	X		X	
P. roseus - bluespotted searobin		X	X			X		X	
P. rubio - blackfin searobin		X	X					X	
P. salmonicolor - blackwing searobin		X	X	X	X	X			
P. scitulus - leopard searobin		X	X	X	X	X			
P. sternsi - shortwing searobin		X	X			X		X	
P. tribulus - bighead searobin	X	X	X	X	X	X			
Psychrolutidae									
Cottunculus microps			X						X
Cyclopteridae									
Cyclopterus lumpus - lumpfish	X	X				X		X	
Liparis inquilinus - inquiline snailfish	X	X				X		X	
Paraliparis sp.		X	X					X	X
Dactylopteridae									
Cephalacanthus volitans - flying gurnard	X	X	X	X	X	X			
Bothidae									
Ancylopsetta dilecta - three-eye flounder		X	X		X	X			
A. quadrocellata - ocellated flounder		X	X	X	X	X			
Bothus ocellatus - eye flounder	X	X	X			X			
B. robinsi - twospot flounder	X	X	X			X			
Chascanopsetta lugubris - pelican flounder	X	X						X	
Citharichthys arctifrons - Gulf Stream flounder	X	X	X			X		X	
C. macrops - spotted whiff		X	X		X				
C. spilopterus - bay whiff	X	X	X	X	X	X			
Cyclopsetta fimbriata - spotfin flounder		X	X			X		X	X
Etropus crossotus - fringed flounder	X	X	X	X	X	X			
E. cyclosquamous		X							X
E. microstomus - smallmouth flounder		X	X		X	X			
E. rimosus - gray flounder		X	X		X	X		X	
Gastropsetta frontalis - shrimp flounder		X	X					X	X
Monolene sessilicauda - deepwater flounder		X	X			X		X	X
Paralichthys albigutta - gulf flounder	X	X	X	X	X				
P. dentatus - summer flounder	X	X	X	X	X				
P. lethostigma - southern flounder	X	X	X	X	X				
P. oblongus - fourspot flounder	X	X	X			X		X	X
P. squamilentus - broad flounder		X	X	X	X	X			
Scophthalmus aquosus - windowpane	X	X	X	X	X	X			
Syacium papillosum - dusky flounder		X	X			X			
Pleuronectidae									
Glyptocephalus cynoglossus - witch flounder	X	X				X		X	X
Pseudopleuronectes americanus - winter flounder	X	X	X	X	X				
Soleidae									
Gymnachirus melas - naked sole	X	X	X		X				
Trinectes maculatus - hogchoker	X	X	X	X	X				
Cynoglossidae									
Symphurus civitatus - offshore tonguefish		X	X			X			
S. diomedianus - spottedfin tonguefish		X	X			X			
S. minor - largescale tonguefish		X	X			X			
S. parvus - pygmy tongue fish		X	X			X			
S. plagiusa - blackcheek tonguefish	X	X	X	X	X				
S. pusillus - northern tonguefish	X	X				X			
Triacanthodidae									
Parahollardia lineata - jambeau	X	X	X			X		X	X
Balistidae									
Aluterus heudeloti - dotterel filefish	X	X	X			X			
A. monoceros - unicorn filefish	X	X	X			X		X	X
A. schoepfi - orange filefish	X	X	X	X	X	X			
A. scriptus - scrawled filefish	X	X	X		X	X			
Balistes capriscus - gray triggerfish	X	X	X			X	X	X	X
B. vetula - queen triggerfish	X	X	X			X	X	X	
Cantherhines macrocerus - whitespotted filefish		X	X				X	X	X
C. pullus - orangespotted filefish	X	X	X				X	X	
C. sufflamen - ocean triggerfish		X	X				X	X	
Monacanthus hispidus - planehead filefish	X	X	X	X	X				
M. setifer - pgymy filefish		X	X			X	X	X	X
M. tuckeri - slender filefish		X	X			X	X		
Xanthichthys ringens - sargassum triggerfish		X	X				X		X
Ostraciidae									
Rhinesomus bicaudalis - spotted trunkfish		X	X			X			
R. polygonia - honeycomb cowfish	X	X	X			X			
R. quadricornis - scrawled cowfish	X	X	X		X	X			
R. trigonus - trunkfish	X	X	X			X			
R. triqueter - smooth trunkfish	X	X	X		X	X			
Tetradontidae									

Table 1 (con't)	Province			Habitat					
	VA	Car	Carib	E	C	OS	R	SE	LS
<u>Canthigaster</u> <u>rostrata</u> - sharpnose puffer		X	X			X		X	
<u>Lagocephalus</u> <u>laevigatus</u> - smooth puffer	X	X	X		X	X		X	
<u>L</u>. <u>lagocephalus</u> - oceanic puffer	X	X						X	
<u>Sphoeroides</u> <u>dorsalis</u> - marbled puffer		X	X			X		X	
<u>S</u>. <u>maculatus</u> - northern puffer	X	X	X	X	X	X			
<u>S</u>. <u>spengleri</u> - bandtail puffer		X	X			X			
		X	X			X			
Diodontidae									
<u>Chilomycterus</u> <u>antillarum</u> - web burrfish		X	X			X			
<u>C</u>. <u>schoepfi</u> - striped burrfish	X	X	X	X	X				
<u>Diodon</u> <u>holocanthus</u> - balloonfish		X	X			X	X		
<u>D</u>. <u>hystrix</u> - porcupinefish		X	X			X	X		
Molidae									
<u>Mola</u> <u>lancelota</u> - sharptail mola		X	X	X	X	X			
<u>M</u>. <u>mola</u> - ocean sunfish	X	X	X	X	X	X			

a - anadromous
c - catadromous
Carib = Caribbean
C = Coastal
SE = Shelf edge
R = reef
LS = Lower shelf
Car = Carolina
VA = Virginia
E = Estuarine
OS = Offshore

<u>Definitions</u>

Middle Atlantic Bight (includes Chesapeake Bay subregion):

The Middle Atlantic Bight is that portion of the Atlantic Ocean that extends from off Cape Cod to near Cape Hatteras, affected by discharges or influence from the Chesapeake Bay (Colvocoresses and Musick, 1984).

South Atlantic Bight:

The South Atlantic Bight is that portion of the Atlantic Ocean shelf that extends from Cape Hatteras southward to West Palm Beach, Florida, a point where the Florida current first diverges from the coast and a definite fish faunal break occurs. Its outer edge is bounded and strongly influenced by the Gulf Stream (Atkinson and Menzel, 1985).

Virginian Province:

This is a cold water area, triangular in outline, that has Cape Hatteras near its apex or southern boundary. Its widest portion is northward. It is under heavy influence from the southerly longshore cold Virginian (Chesapeake Bay subregion) coastal current (Gray et al., 1968).

Carolinian Province:

This province extends south from Cape Hatteras and occupies about three-fourths of the continental shelf. Its fauna receives contributions from the Virginian and Caribbean provinces as transports of reverse shore currents from the offshore Gulf Stream and the Caribbean Province (Gray et al., 1968).

Caribbean Province:

This province occupies about one-fourth of the continental shelf, and perhaps part of the continental slope, that lies seaward of the Carolinian Province. It is strongly influenced by the northerly flowing Gulf Stream and its meanders (Bumpus, 1955, 1973; Bumpus and Lauzier, 1965; Bumpus and Pierce, 1955; Rao et al., 1971).

Estuaries:
There are just as many definitions of an estuary (Symposium on the Classification of Brackish Waters, 1958; Barnes, 1964; Caspers, 1967; Lauff, 1967; Schwartz, 1981) as there are types of estuaries (Pritchard, 1952, 1955, 1967; Williams, 1961). Herein, estuaries are considered those river, river mouths, or sound areas which are subject to the combined influence and mixture of down-stream moving freshwater and up-stream moving oceanic water. Middle and South Atlantic Bight estuaries extend from the mainland eastward or southeastward toward the Atlantic Ocean and experience salinity changes from near zero to 35 ppt. Low lying barrier islands separate the estuaries from the sea. Access of estuarine waters to the sea is via a limited number of inlets.

Continental Shelf:
The continental shelf off North Carolina is that area of the sea bed extending seaward from the coastal barrier islands. It has a gradual (0.3 m depth/270 m horizontal distance) descending terrace for about 25.6 km, at the level of Cape Hatteras, and up to 0.3 m/104 km in Long Bay, south of the Cape Fear River (Newton et al., 1971). Depths at the outer limits (edge of the shelf are near 80 m north of Cape Hatteras and 70-90 m or less off the Cape Fear (Struhsaker, 1969). Robins and Ray (1986) portray the shelf extending to 200 m depths. The outer edge of the shelf, especially in Onslow Bay, is characterized by reefs (Chester et al., 1984; Grimes et al., 1982; Huntsman, 1976; Huntsman and Manooch, 1978; Miller and Richards, 1980; Parker et al., 1983; Parker and Ross, 1986; Struhsaker, 1969; Wenner, 1983).

Continental Slope:
The continental slope is that area north of Cape Hatteras where there is a steep shift in the slope bottom from the continental shelf to that of 0.3 m of depth/3.0 m horizontal distance. That area south of Cape Hatteras possesses a more gentle slope of 0.3 m of depth/6 m of horizontal distance. Numerous submarine canyons interdigitate throughout the area, especially north of Cape Hatteras, whereas south of Cape Hatteras a smoother progression of the slope occurs down to the Blake Plateau (Menzies et al., 1973). See physiographic provinces discussion for additional subdivision detail for both the continental shelf and slope areas.

METHODS

Other than literature records, species listed are either on deposit in the University of North Carolina (UNC), Institute of Marine Sciences fish collection or at other national museum repositories. Various capture methods were used to obtain the fishes reported: otter trawls, gill nets, crab pots, tumbler dredges, scallop dredges, dip net, and hook and line. Species identification was facilitated by using a host of regional and local publications. Museum specimens were checked to verify species identity. Doubtful literature records were verified by actual specimen examination.

Physical Features of the Area

Physiographic Provinces

A nearly north-south coastline prevails north of Cape Hatteras while to the south a series of scalloped northeast-southwest bays persist. The reefs Menzies et al. (1966) mention predominate in Raleigh Bay. The abundant reefs of Onslow Bay often occur within 0.15 km of the beach (Parker et al., 1983).

Historically, or by tradition, that area north of Cape Hatteras has usually been considered part of the middle Atlantic, Virginian or Chesapeake Bight (Joseph et al., 1960), while that to the south has been divided physically, chemically, and biologically into two provincial subzones. The inner area, based on faunal occurrence distinctions, is designated the Carolinian Province and the offshore, the Caribbean Province (Cerame-Vivas and Gray, 1966; Gray et al., 1968; Franz and Merrill, 1980a,b; Lee et al., 1985; Menzies et al., 1966; Vernberg and Vernberg, 1970).

Oceanographers, on the other hand, consider the South Atlantic Bight to be broken into two or three north-south flow delineated coastal zones. This distinction is based on currents, flow, seasonality, etc. The zones divide the continental shelf into inner, middle, and outer zones (Atkinson, 1985; Atkinson and Menzel, 1985; Brooks and Bane, 1978, 1983; Pietrafesa et al., 1985). The inner shelf is defined as the area of 0-20 m, the middle shelf 21-40 m, and outer shelf 41-75 m depths. The inner shelf is dominated by tidal currents, river flows, local muds, and interaction with coastal estuaries. The middle shelf is dominated by local wind forming and pressure gradients with northward mean flows. There is some interaction with the coastal environment and the nearby Gulf Stream. The outer shelf is dominated by the Gulf Stream and is subject to turmoil caused by intrusions, warm and cold water eddies, and other seasonal events (Atkinson, 1985; Atkinson and Pietrafesa, 1980; Atkinson et al., 1980; Blanton et al., 1981; Bush et al., 1985; Hofmann et al., 1981; Lee et al., 1985). Pietrafesa et al. (1985) and Tenor (1985) further subdivide these three zones into two subsubzones, one north of Savannah, Georgia, the other southward to Daytona Beach, Florida. Both subsubzones are directly and seasonally influenced by water mass circulation in relation to the Charleston Bump (Brooks and Bane, 1983; McClain and Atkinson, 1985; Pietrafesa and Janowitz, 1979; Pietrafesa et al., 1985).

Cape Hatteras is usually considered a barrier to most northern and southern faunas (Leslie and Stewart, 1986; Magnuson et al., 1980). In most cases this is true, but a province's entity is often broken or ill defined, especially during the winter or summer, when strong northeast or southwest winds prevail. Often what appears to be discharges of sound waters that may act as a barrier is really masses of cold northern water passing south of Cape Hatteras (Mavis, 1970; Stevenson and Pastula, 1971). Likewise, especially during spring months, the Hatteras barrier seems to shift northward to near False Cape or Oregon Inlet and is reinforced by a diverticulum of the Gulf Stream that develops perpendicular to the coast. Within days, annually, the diverticulum may and does extend out from the coast from near False Cape, North Carolina, seaward thereby seemingly dividing the waters and faunas of the middle Western Atlantic into two entities (see U.S. Coast Guard oceanographic aerial isotherm reports or Oceanographic Monthly Summaries, NOAA, National Environmental Satellite Data and Information Service, Washington, D.C.). During such occasions, it is not uncommon to find striped bass, basking sharks, or spiny dogfish north but not south of the diverticulum or barrier. Once the diverticulum dissipates, they resume their usual winter southward movements (November to April) to near Cape Lookout or even as far south as South Carolina. The opposite is true for butterfly fishes, spade fishes, and other tropical species which move north of Cape Hatteras or the Charleston Bump during the spring or summer. During these seasons a strong or weak physiographic deflection or flow past or around the Charleston Bump affects the location, seasonality, and abundance of tropical or other local fishes in North Carolinian waters (e.g., king and Spanish mackerels, marlin, porgies, and many tropical fishes).

Rarely do Carolinian or Caribbean fishes penetrate far northward into the Virginian province during the winter and spring when the Hatteras barrier is the strongest. Conversely, larval or adult fishes are often carried north of Cape Hatteras as Gulf Stream or gyre transports once the Gulf Stream flow eases or is diverted offshore by the primarily southwesterly summer winds.

Bottom Types

Beginning at the high tide mark, most estuaries possess a mud or silty-mud substrate. This bottom type persists throughout most river estuaries and the great sounds north of Cape Lookout

(Pickett and Ingram, 1969). As one approaches the eastern limits of these sounds, the Outer Banks, bottom composition is sandier, especially in the vicinity of inlets (Ingram, 1968; Pilkey et al., 1980). South of Pamlico Sound, Bogue Sound, and most of the short estuaries south of Cape Lookout and of the lower North Carolina coast (white oak, New, Cape Fear, Lockwood Folly, and Shallotte rivers) possess a sandy substrate texture; the adjoining estuaries, however, have substrates of mud overlain with silt or sand (Schwartz et al., 1981).

The continental shelf north of Cape Hatteras has an inshore sandy substrate that changes to mud-sand near the continental slope. Edwards et al. (1962) categorized, during ground fish trawl surveys, the substrate types north of Cape Hatteras. Bond and Meade (1966), Doyle and Maynard (1967), and Pierce (1970) noted sand grain transport southward along the North Carolina coast north of Cape Hatteras. Manheim et al. (1970) commented that considerable amounts of suspended matter escaping from inshore sounds also tend to move longshoreward rather than seaward of North Carolina (Pietrafesa et al., 1985).

South of Cape Hatteras, Newton et al. (1971) categorized continental shelf substrates as grading from sand to mud interspersed with outcrops of coral reefs. Menzies et al. (1966) proposed that the broken substrates of this area were the remains of ancient reefs that existed when the sea level was lower during the last glacial period. Struhsaker (1969) divided the coastal and shelf habitats off North Carolina into five general types: coastal, open shelf, live bottom, shelf edge, and lower shelf; each harboring distinct associations of fishes. His coastal shelf habitat had a smooth sandy-mud substrate out to 14.8-18.5 m; the open shelf had smooth sands from 18.5 to 65.5 m; the shelf edge had a highly broken substrate between 65.5 and 132 m, where sediments were variable, and the lower shelf substrate, between 132 and 185 m, consisted of smooth mud. Parker et al. (1983) noted that the Cape Hatteras to Cape Fear area had substrates composed of 75.6% sand-shell, 11.5% mud, and 14% reefs. The Cape Fear-Cape Canaveral area substrate was composed of 57.9% sand-shell, vegetation 12.3%, and reefs 30%.

Temperature and Salinity Profiles

Within the estuaries and sounds, there are progressions from low salinity inland to full sea water conditions (34 ppt salinity) along the Outer Banks (Schwartz and Chestnut, 1973). The water temperature-salinity profile to the north, especially in the Chesapeake area, is well documented (Edwards et al., 1962; Grosslein, 1969). That area south of Cape Hatteras was well surveyed and documented by the nine U.S. Fish and Wildlife Service vessel cruises of the Theodore N. Gill (Anderson et al., 1961; Moore and Gorsline, 1960). Anderson et al. (1961), Newton et al. (1971), and Wright and Worthington (1970) summarized environmental data over the entire shelf off North Carolina.

Surface conditions, along selected transects across the Gulf Stream, were reported, until discontinued, by the U.S. Oceanographic Office in the publication "Gulf Stream". These water temperature aerial surveillances were monitored by the U.S. Coast Guard Oceanographic Institute. Additional general aspects dealing with water temperature-salinity relationships over the entire area, were reported by Bumpus (1955), Pyle (1962) and Walford and Wicklund (1968). Deep water conditions have been reported by Lee et al. (1985), Schroeder (1963), Worthington and Wright (1970), and Wright and Worthington (1970).

Circulation and Current Patterns

Circulation patterns within the coastal sounds are poorly known (Pietrafesa et al., 1986; Roelofs and Bumpus, 1953). Only in recent years has any effort been made to understand the circulation of Pamlico Sound (Pietrafesa et al., 1986). Surface shelf water currents are better known (Atkinson, 1985). Subsurface currents are only now being resolved (Atkinson, 1985). To the north of Cape Hatteras, Norcross and Harrison (1967), and Norcross and Stanley (1967) comment on the southerly longshore current from the lower Chesapeake Bay area. Vernberg and Vernberg (1970) vividly describe the dynamic contact of the northerly flowing Gulf Stream, with its relatively warm waters, with the southerly flowing colder waters of the Virginian coastal current, and both water masses bending to the east and flowing away from the continent. South of Cape Hatteras, an inshore current component is characterized by water with seasonal changes in temperature and salinity whereas offshore the Gulf Stream has environmental parameters which vary slightly (Atkinson, 1985; Cerame-Vivas and Gray, 1966; Menzies et al., 1966; Wells and Gray, 1960). Stefansson et al. (1971) documented the shelf water conditions off North Carolina. Offshore meanders of the Gulf Stream and its effect or intrusion on or into the continental shelf were noted by Blanton (1971) and Webster (1961), while those along the slope were documented by Amos et al. (1971) and Rowe and Menzies (1968). Subsurface currents south of Hatteras or gyres off the Gulf Stream may flow northerly or southerly, depending on the strength and influence of the Gulf Stream, on or offshore winds (Bumpus, 1955; Bumpus and Pierce, 1955; Gray and Cerame-Vivas, 1963; Wells and Gray, 1960), and intrusions from excess runoff inland.

Early Fish and Faunal Studies

Most early studies dealing with the fishes of North Carolina and the adjacent areas were simply species occurrence records or local faunal observations. This was true of Catesby (1771), Earll (1887), Fowler (1945), Gill (1861, 1873, 1878), Jordan (1887a, b), Jordan and Evermann (1896-1900), Jordan and Gilbert (1879, 1883), Lawson (1709), McDonald (1887), Pratt (1917), Radcliffe (1914), and Storer (1846). Pratt listed 352 species for the area. The Beaufort area fish fauna was ably documented by such workers as: Gudger (1905, 1910, 1912a, b, 1913a, b), Hildebrand (1916, 1917, 1941), Hildebrand and Cable (1930, 1934, 1938), Jenkins (1885, 1887), Nichols and Firth (1939), Pearse (1936) and Tagatz and Dudley (1961). As offshore trawlers became available and the fisheries moved out of the estuaries and away from a dependence on the pound net, gill net and haul seine fisheries of the sounds and beaches, such action expanded the known shelf fish fauna out to depths of about 74 m (see Coles, 1910, 1913; McGlone, 1908; Powell, 1950; Radcliffe, 1914; Roelofs, 1951; Taylor, 1951; Woodward, 1956). Brown and McCoy (1969), Wolff (1972) and others reviewed the scrap or trash fisheries incidental to the shrimp fishery operations and added occurrences of other odd or stray fishes. Cummins et al. (1962), Powell (1950) and Roelofs (1953) noted the faunas and fishery potentials further offshore. Edwards et al. (1962) and Grosslein (1969) noted the shelf fishes north of Cape Hatteras during various ground fish surveys. Buller (1951), Bullis and Thompson (1965) and Nesbit and Neville (1953) reported on the fisheries south of Cape Hatteras. Pearse and Williams (1951) documented the fishes of the nearshore reefs. Goode and Bean (1896) and Schroeder (1940) commented on several deep-sea fishes while Grey (1956) studied the fishes below 2000 m.

Recent Efforts

Concentrated explorations of the North Carolina continental shelf and slope did not begin in earnest until 1950 when federal research vessels sampled the area (Buller, 1951; Bullis and Thompson, 1965; Clark and Brown, 1977; Cummins et al., 1962; Edwards et al., 1962; Grosslein, 1969; Struhsaker, 1969). Since then the composition of various substrate fish communities have been reported in a series of trawl reports by Colvocoresses and Musick (1984) for the adjacent Middle Atlantic Bight or off South Carolina (Sedberry and Van Dolah, 1984; Wenner, 1983; Wenner et al., 1980, etc.). Wenner (1983) explored the faunal composition of trawl catches for inshore sponge-coral habitats in the South Atlantic Bight. Presently most bottom sampling is accomplished by trawling, primarily during the months of May-November, for shrimp in inshore waters of less than 40 m, offshore from November-April for flounders in 150-200+ m off Ocracoke, North Carolina, and north of Cape Hatteras, and in 55-100 m for gray trout and Atlantic sturgeon in November-April near Cape Lookout and Oregon Inlet. Other winter efforts in Raleigh and Onslow Bays center around a crab pot fishery for black sea bass, *C. striatus*. Shrimp trawling with flat nets is limited to depths of less than 40 m. That fishery captures a number of small young stages of mostly inshore fishes. Occasionally trawlers from northern states or North Carolina engage in deep offshore winter December-March catches of sea bass or flounder. Longline and hook and line fishing in deep water are also winter or year-round fishing pursuits. Bottom fishing beyond 95 m exists primarily as a summer hook and line sport or head boat fishery out of Oregon Inlet, Hatteras, Ocracoke, Morehead City, Carolina Beach, and Southport, North Carolina. Depths of up to 1100 m are so fished, preference being for snappers, groupers, porgies and sea basses, when not trolling for amberjacks, king mackerel, dolphin (Coryphaena), billfishes and tunas.

Faunal Components

General

Ten of the 149 families, comprising 202 of the 686 known species of fishes, dominate the total fish fauna treated in Table 2. This assemblage accounts for 29.4% of the fishes listed. They are members of the families: sea basses (Serranidae, with 33 representative species), jacks (Carangidae, 26), gobies (Gobiidae, 25), left-eyed flounders (Bothidae, 22), drums (Sciaenidae, 18), sea robins (Triglidae, 18), wrasses (Labridae, 15), sharks (Carcharhinidae, 16), herrings (Clupeidae, 15), and snappers (Lutjanidae, 14). Two families, the sharks (Schwartz, 1989) and herrings, possess mostly pelagic representatives, two families possess fishes common to reef habitats (wrasses and snappers), while the remaining six families have fishes usually associated with the near bottom or benthos. About 18.5% of the fishes listed in Table 2 can be referred to as typically northern faunal components, i.e. those that generally range north of Cape Hatteras in the area dominated by cooler water masses of the Virginian Province or Middle Atlantic and Chesapeake Bight subregion. Some 81.5% of the pelagic, demersal and benthic fish fauna off North Carolina is composed of southern representations - those which usually occur or occupy the continental shelf slope or Gulf Stream areas south of Cape Hatteras in areas where they encounter waters with temperate or warm temperatures.

Members of each faunal component have been found to be seasonally dependent and associated with, to a large degree, wind and water mass movements and water temperatures, either north or south of Cape Hatteras. Examples of northern elements moving southward are tautog, cunner and blackline rosefish, and occasionally striped bass, all occur or move during winter and spring months often as far south as Cape Lookout or Cape Fear, North Carolina. As offshore waters cool, dense populations of the more northerly spiny dogfish (Squalus acanthias), smooth dogfish (Mustelus canis) along with basking sharks (Cetorhinus maximus), move south to off Wilmington, North Carolina or South Carolina (Bearden, 1965) before retreating in April northward, as warm water temperatures develop in the spring. More northerly fishes, such as cod and northern tilefish, penetrate south to Cape Hatteras but rarely move south of the Cape during December-March.

Table 2. Analysis of the fishes frequenting North Carolina and adjacent estuarine and marine waters to depths of 600 m by faunal composition, physiographic provinces, depth distribution, habitat preference, type of fish and type of movement.

	NUMBER	PERCENT TOTAL
FAMILIES	149	----
SPECIES	686	----
FAUNAL COMPONENT		
Northern	127	18.5
Southern	559	81.5
PHYSIOGRAPHIC PROVINCE OCCUPIED		
Virginia	127	18.5
Carolinian	281	41.0
Caribbean	278	40.5
DEPTH DISTRIBUTION		
Estuaries	44	6.4
Shelf 200 m	518	75.5
Deep Ocean	124	18.1
HABITAT PREFERENCE		
Pelagic	173	25.2
Benthic	513	74.8
mud	151	29.4
sand	242	47.2
reef	119	23.2
sponge	1	0.2
TYPE OF FISH		
Resident	100	14.7
Migrant	518	75.5
Estuarine dependent	216	--
Unknown	67	9.8
TYPE MIGRANT		
Local Short Distant	45	6.6
North - South	419	61.1
Onshore - Offshore	72	10.5
Freshwater Intruder	38	5.5
Vertical	14	2.0
Unknown	98	14.3

Distributions of southern fishes, to the north of Cape Hatteras, are influenced greatly by the strength of winter winds forcing cold northern waters toward, or summer southwesterlies away from Hatteras. Other influencing factors include the narrowness of the shelf off Hatteras, the ecological barrier that often develops near False Cape, and the drift, meanders, eddies and strength of the Gulf Stream as it passes, from the south, over the shelf off Hatteras. Larval fishes, especially, are carried, wind dependent, northward by the Gulf Stream or ashore in wind slicks that develop during various seasons.

Many southern fishes have their northern abundance limits near Cape Hatteras: sand tilefish (*Malacanthus plumieri*), naked sole (*Gymnachirus melas*), sand perch (*Diplectrum formosum*), yellowmouth grouper (*Mycteroperca interstitialis*), etc. (Table 1). Others move northward along the coast to near False Cape or into Chesapeake Bay or other northern areas, only when wind and water temperatures permit. Examples of this type of movement are the crevalle jack (*Caranx hippos*), spotfin butterflyfish (*Chaetodon ocellatus*), gag (*Mycteroperca microlepis*), etc. Most strong swimming fishes are oblivious of any physical or ecological faunal barrier near Cape Hatteras or False Cape and move north or south of the Cape with each seasonal water temperature warming or cooling. Fishes exhibiting such movement are: black drum (*Pogonias chromis*), red drum (*Scianops ocellatus*), striped searobin (*Prionotus evolans*), northern searobin (*Prionotus carolinas*), northern puffer (*Sphoeroides maculatus*), pigfish (*Orthopristis chrysoptera*), pinfish (*Lagodon rhomboides*), inshore lizardfish (*Synodus foetans*), gag (*Mycteroperca microlepis*), cownose ray (*Rhinoptera bonasus*), bullnose ray (*Myliobatis freminvillei*), and tunas, marlins, dolphin fishes, and sturgeons (*Acipenser oxyrhynchus*). Additional members of each northern or southern faunal component are also added or restricted by the effects of inshore intrusions of deep offshore waters. Examples are great white sharks (*Carcharodon carcharias*), long and shortnose lancetfishes (*Alepisaurus* spp.), many deep water sharks (*Etmopterus* spp.), rays (*Rajidae*), searobins (*Peristedion* spp.), ratfishes (*Macrouridae*), etc. Transatlantic or south Atlantic additions also increase the faunal list, e.g., *Evermanella balboa*, *Gephyroberyx darwini*.

Physiographic Province Occupied

Accepting the premise that three physiographic provinces, viz. Virginian, Carolinian and Caribbean (as defined by Cerame-Vivas and Gray, 1966), exist in that portion of the Atlantic Ocean off the Carolinas, the breakdown of pelagic, demersal and benthic fishes favors a preponderance of southern fish representatives. The Virginian province contributes about 18.5% of the fishes compared to 81.5% from provinces to the south (Table 2). Dividing the area south of Hatteras into two provinces, Carolinian and Caribbean, a preponderance of shelf species (41.0%) occupy the Carolinian province (Table 2). The Caribbean province (by nature of its designation, Cerame-Vivas and Gray, 1966) may prove to harbor an equal or greater number of species (40.5%); only further exploration and sampling will refine the true picture. The fish composition of the Caribbean province is poorly known because few scientific excursions have taken place in the area, many difficulties are encountered when working the rough bottom terrain (see Struhsaker, 1969), and few ships are adequately equipped to readily sample the extreme depths of the area. Once these obstacles are surmounted, and as data and accessibility to the area become possible, many more species will be authenticated and added as members of this province and to Table 2.

Spatial Distribution by Habitat

Estuaries

The term estuaries includes the great shallow sounds of North Carolina. These are: Albemarle, Currituck, Croatan, Pamlico, Core and Back, to the north of Cape Lookout. Southwest of Cape Lookout small elongate sounds persist: Bogue, Stump, Topsail, Middle, Masonboro and Myrtle. The great sounds, usually wider sounds, usually wider mouths of coastal rivers, are protected from the sea by low lying barrier islands known as the Outer Banks. These shallow sounds are subject, throughout all parts of the year, to much wind and wave action. Southwest winds predominate during the warmer April-November months and cooler northwest or northeast winds prevail during the winter months. Waters at their western limits are brownish from the tannic acids of the entering slow sluggish coastal streams. *Spartina* marshes abound along most western sound shores. Eastward in each sound the bottom texture may shift abruptly to sand. Much tidal and current action may prevail at the few inlets, Oregon, Hatteras, Ocracoke and Drum (now closing after being reopened) north of Cape Lookout, which are opened or closed by the restless sea outside.

The small sounds southwest of Cape Lookout are usually short inshore embayments and are usually associated with a nearby inlet and/or short estuary (i.e., Lockwood Folly, Shallotte rivers, etc.). Few have major contributing freshwater tributaries. Some 12 inlets connect these sounds with the sea, the largest being Beaufort Inlet, 12.8 km west of Cape Lookout. Environmental conditions are similar to that of the great sounds. Only the Cape Fear River estuary dominates the southwestern part of the state (Schwartz et al., 1981).

Estuaries, or sound habitats, serve as a nursery area for most if not all of the species in Table 1, during some stage of their lives (Schwartz et al., 1981; Weinstein, 1979). A number of species, such as gobies, blennies, clingfish and oyster toadfish, are usually associated with oyster reefs, be they natural or cultivated by man. Pipefishes, sea horses, and a host of other species comprise the resident fishes of this habitat. A seasonal influx of local fishes such as drums (Sciaenidae), flounders, kingfish (Menticirrhus, known locally as sea mullets), searobins and stingrays, enter the sounds most as larvae in early spring and scatter throughout the area, at first as far as the innermost limits of the estuaries and then as they grow, into nearby marsh or open water areas. Adults of most species (Table 1), especially drums, flounders, kingfish, sea trout, sharks and stingrays (Myliobatis, Dasyatis and Rhinoptera), enter and utilize the area for growth and sometimes reproduction. Sharks, rays and skates also abound or pass through the area; the latter as they move about feeding on mollusks (oysters, hard clams), or pass up or down the coast (Schwartz, 1989). Stingrays prefer sandier habitats where they can hide or mine up hard clams and a host of mollusks and invertebrates as food. Cooling winter water temperatures in September-October drive most of the pelagic, demersal and benthic fishes offshore to winter over or spawn, leaving the sounds to such resident species as young pinfish, pigfish, and, in Albemarle Sound, striped bass and white perch. Cusk-eels (Ophidion sp.) remain throughout the year usually buried in the mud-sandy substrates, being most active at night. Others such as young gray snappers (Lutjanus griseus) remain and hide near piers, shells or in cans in order to overwinter in the cold inshore or estuarine waters.

Coastal Habitat

Beyond the barrier island (Outer Banks) and along the entire length of the North Carolina coast lies an oceanic area with a gradually sloping beach and bottom that extends to a depth of 110 m. Few rock jetties (mostly at inlets) exist. Some of the offshore reefs penetrate within 0.4 to 0.8 km of the beach.

The coastal habitat, in the surf zone, possesses such fishes as smooth puffer, kingfishes (Menticirrhus), gray trout, clearnose skates, spiny dogfish, smooth and sharpnose sharks, stingrays, inshore lizard fish, spot, croakers, porgies (Stenotomus chrysops, S. caprinus), silver perch, red drum, and a host of searobins. Usually young life stages are encountered in the surf zone but in March-May and September-November adults of all species also occur there and may be caught by using gill nets, hook and line, stop nets, and beach haul seines as they pass along the coast or out to sea to spawn.

In the spring, one finds huge schools of red drum moving northward along the coast to enter Ocracoke Inlet and Pamlico Sound. Most sciaenids, by April, are moving from the coastal habitat into estuarine habitats. Late stragglers of the spiny dogfish and smooth dogfish sharks retreat offshore or further to the north to apparently escape the gradually warming waters.

Summer finds the coastal habitat teeming or nearly devoid of most demersal and benthic fishes. While bluefish and a host of pelagic fishes persist in the water column above, the inshore bottom waters gradually become so warm that benthic forms, except for sharks, seem to either move into deeper "cooler" offshore waters or move elsewhere along the coast. Shrimping prevails as the primary summer-fall fishery and is often considered to have deleterious effects on the early life stages of many species of fishes.

In the fall (following cold snaps locally referred to as mullet blows), one finds most fishes migrating out of the sounds or estuaries in September-October to move south or offshore into nearby shelf waters to spend the winter. In this the season dense and large schools of gray trout, silver perch, kingfish (Menticirrhus), croakers, spot and mullets (Mugil sp.), support the haul seine, gill net, or trawl fisheries. North of Cape Hatteras the flounder season begins, often in the surf zone where haul seine crews are active, and slowly moves offshore, as the winter prolongs, to 150 m depths by March and April when capture is by trawl. While flounders support a vast trawl industry in the shelf area north and south of Cape Hatteras, large schools of gray trout provide a winter fishery near Cape Lookout. Sea bass potting or hook and line efforts prevail during the extremes of the winter off Morehead City, Wrightsville Beach, Southport and deep water areas to the south.

Open Shelf Habitat

North of Cape Hatteras the open shelf habitat is a thin narrow north-south zone while south of Cape Hatteras it is broader, often 16 km wide. Herein one finds numerous offshore reefs (Menzies et al., 1966; Struhsaker, 1969) as well as many shipwrecks (Newton et al., 1971). The reefs and shelf abound seasonally with pelagic species such as wrasses, damselfishes, sharks, sea bass (three species of Centropristis), sand perch, pigfish, snappers and porgies. Additionally, this habitat usually has a sandy substrate with some mud. As a result the benthic open areas harbor sparse fish populations other than a variety of pelagic species: tunas, marlins, anchovies, jacks, etc. A portion of the habitat in Onslow Bay is rougher and one generally experiences damaged gear when fishing in that area, hence it is avoided and left to the pelagic fishes.

Many, if not most, of the coastal habitat fishes can be found, season dependent, at some portion of the year in the open shelf or slope habitat. Spring finds large schools of gray trout, flounder, silver perch, searobins, whiting and spotted hake off Cape Hatteras and Cape Lookout. The same is true south of Cape Hatteras where sea bass and, cyclically, smooth puffer also abound and add to the species diversity.

During summer months stingrays, skates, sharks, sea basses, eels and many tropical fishes enter and utilize the shelf area. The scallop fishery (Cummins et al., 1962; Schwartz and Porter, 1977) often harbors, in water ±160 m, more than 111 species of fishes (e.g., goatfishes, flounders, sand perch, wrasses, etc.). This fishery persists, in years of good scallop set, until over exploited or if weather conditions permit between April and October. Many pelagic fishes are also present and contribute to the hook and line fishery of this habitat.

The fall months reveal that many flounders and porgies abound off North Carolina and many other species are either moving north and south, depending on the faunal component to which they belong. During the winter months of December-March, rough seas over the shelf harbor dense schools of drums, puffers, goosefish (Lophius americanus), spiny dogfish, etc. Few but the hardy sport, hook and line, commercial or sea bass potter fishermen venture forth. Perhaps many more species occupy this habitat, but this information must await better sampling methods by larger seaworthy ships.

Reef Habitat

Newton et al. (1971) and Parker and Ross (1986) noted many coral rock or shipwreck reefs abounding throughout the reef habitat that exists as outcrops of the open shelf habitat. These reefs may be simple ridges (Menzies et al., 1966; Struhsaker, 1969) or have complicated configurations (Newton et al., 1971; Parker et al., 1983). Sparids, groupers (mostly Epinephelus and Mycteroperca), snappers, tilefishes (Lopholatilus to the north and Caulolatilus and Malacanthus from Hatteras south), scorpion fishes, sea basses, squirrelfishes, damselfishes, butterflyfishes, wrasses, triggerfishes, puffers and searobins abound on these reefs. Many reefs, especially those off Cape Hatteras, Morehead City and Wrightsville Beach, are potted for sea bass during the winter.

Whether north-south, inshore-offshore, or resident movements are exhibited by most fishes occupying the offshore reef habitats of 23-152 m remains presently unresolved (Parker and Ross, 1986). Head boats (with 50-150 people aboard) can and often do fish a reef for several days before the catch drops off or changes (Chester et al., 1984; Huntsman, 1976). This suggests only some movement may occur. Whether recruitment occurs from populations farther offshore or the Gulf Stream is unknown (Miller and Richards, 1980). The grayline tilefish, Caulolatilus spp., seems to occur from April to November and probably simply moves in or offshore (although they live in burrows, Able et al., 1982) with the season, at least it so appears from hook and line catches in July-September. There also seems to be a north-south movement as well as resident characteristic for some of the reef inhabitants, as evidenced by head and commercial snapper fishing boat catches from March-November or December (weather permitting). Snappers, groupers, porgies and some tropical fishes seem to remain on the reef during all seasons.

The snappers (red, vermilion and silk) supported an active hook and line fishery in 1951-55 and again in recent years (Huntsman, 1976). Snapper fishermen from Virginia, North Carolina, and even Florida (Tampa) fish the reefs from Hatteras southward during July-September and can each amass 900 kg catches of groupers and snappers during trips of less than a week of fishing. They prefer to fish for vermilion and red snappers, which bring the highest prices, as compared to groupers and porgies, and have recently concentrated their efforts on the snowy grouper, once populations of other reef fishes became scarcer and smaller in size. A depth preference seems to prevail for each snapper. The red snapper occurs in 46-91 m waters, while the vermilion snapper is caught in 64-128 m waters over sand or reefs (Grimes et al., 1982). Red and vermilion snappers are found primarily over reefs while the vermilion snapper occurs in the water column off the reef. The silk snapper may be found over reefs throughout the area. Mass mortalities of reef fishes occurred in 1957-58 and 1976-77 when many species were killed by sudden or late spring cold weather that lowered water temperatures and persisted for extended periods of time. This could account for the lack of or slow build-up of various snappers to the fishery.

Shelf Edge Habitat

The shelf edge habitat is a transition zone between the inshore habitats, the reefs, and the slope leading to the abyssal plain. Its features are varied, being a narrow strip north of Hatteras while that to the south is often a few kilometers wide. It has a jagged broken bottom over which many groupers, snappers and porgies abound. Currents are often strong, set on shore and influenced by the nearby Gulf Stream (Blanton, 1971). Because of its configuration, little scientific sampling has been or can be safely performed. The true species picture remains blurred except for that brought in by head boat or party boat fishermen.

Lower Shelf Habitat

The lower shelf slope is steep, north of Hatteras, or gradual, south of Cape Lookout. A muddy bottom prevails over which macrurids, brotulids, and gadids have been taken. Little is known of this habitat or its inhabitants other than many pelagic fishes utilize the open ocean water column. Some fishes, such as hatchetfishes, make vertical migrations following diurnal concentrations of planktonic foods. Few vessels are capable of sampling these waters or depths. Fishes often outswim sampling trawl gear in the pelagic habitat zone or the dense mud substrates cause substantial loss of gear when attempts are made to sample its benthic fauna.

Epipelagic Zone

This zone represents near and offshore waters, from the surface to depths of 200 m. About 90% of the fishes associated or found in waters of North Carolina occur within this water mass during some aspect of their lives. This may include pelagic larval and adult stages of pelagic fishes that feed or migrate through (e.g., bluefish, marlins, sharks, etc.) or spawn in the area. The early life stages of many species (at best 90% of the fauna) are also found in the surface waters or utilize the entire water column for breeding, feeding, etc. (e.g., malacanthids, stromateids, coryphaenids, gobiids, etc.). Many species, are carried as adults or larvae by northward of Gulf Stream currents from the south into waters off North Carolina to populate the offshore reefs (e.g., groupers, snappers, damselfishes, butterflyfishes, etc.). Thus, the epipelagic zone is a highly dynamic and complicated physiographic zone that is subject to hurricane perturbation (Kirby-Smith and Ustach, 1986) and where species abundance and variety change constantly as a result of the interplay of many ecological, biological or seasonal factors.

Mesopelagic Zone

This water zone, occurring from depths of 200 to 1000 m, overlaps the continental slope area, where at present about 10% of the known fish fauna thrives. Here one finds oceanic pelagic fishes, the vertical migrants (lantern fishes, snipe eels, lancetfishes, and a host of deepwater fishes), as well as the truly benthic deepwater fishes (i.e., catsharks, rattails, etc.).

Overall Observations and Conclusions

North Carolina's estuaries, shelf and slope waters contain a wide diversity of fishes, about many of which we know virtually little in relation to their biology, life history or existence needs. While much remains to be learned about this fauna, some information is at hand that causes concern. We have already witnessed the effects of freshwater inflow on our sounds and how that phenomenon affects the survival of about 100 species of freshwater and marine fishes (Schwartz, 1981). More importantly, we are only now becoming cognizant of the great influences of these impacts when coupled with changes in land use practices. Their high nutrient loads of domestic pollution, pesticides, herbicides and heavy metals, often seriously affect the survival and utilization of our sounds by young and juvenile fishes (Davis et al., 1985; Rulifson, 1985). Increased domestic pollution is affecting many local or migrant fishes as they increasingly exhibit sores and a variety of diseases not known for shallow water estuarine, sound and near shore water fishes. Fish kills resulting from diseases have seriously affected white perch, flounders, gray trout, spot, croakers and menhaden, fishes that are important to sport and commercial fisheries alike. Nutrients from city sewage or phosphate operations are chemically enhancing our sound and near shore waters so that algae blooms have been increasing and reoccurring with alarming frequency. Algae blooms, in turn, often cause severe oxygen depletion and subsequent death of shallow water fishes.

Near and offshore fishes have also been affected by man in other ways. Increased overfishing, whether by sport, commercial or foreign efforts, artificial reef construction and mining explorations, etc. are affecting many species of fishes causing serious declines that are precipitating state and federal management regulations (e.g., groupers, snappers, Spanish and king mackerels, striped bass, all of the shads, sturgeons, marlins, and possibly tunas and sharks). While efforts to create offshore reefs in order to enhance or create sport fishing havens abound for waters up to 40 m deep, these efforts are often unplanned, misdirected or unsubstantiated by scientific study. While artificial reefs will increase fish abundance or aggregation of such fishes as flounders, sea basses, jacks, groupers, snappers, etc. in an area (Carlisle et al., 1964; Turner et al., 1969), their effectiveness will ultimately depend on the type of reef, its position, the environment, fishing pressure placed on the reef and sound scientific research and management of the reef (Sheehy, 1982; Stone, 1982; Walton, 1982).

Efforts to carry man's pollutants offshore as a means of easing inshore problems should be viewed dimly and with caution for the offshore fishes will be subject to diseases over a far greater portion of the open sea. Offshore mining efforts for phosphates or oil should be approached cautiously for mishaps may affect the fish faunas north and south of North Carolina, as oil spills or drill muds and sediment will be carried about by the Gulf Stream or onshore, along-shore, etc. water mass movements.

Man must come to grips with the fact that the ocean's fish faunas and resources are finite. We must quickly learn more about each species and how it interacts with its habitat or how it is affected or enhanced by man. We must learn to manage important food or commercial species and how to conserve the environment so all can enjoy the fishes of the area. An overall approach of study, management and use should be used in relation to the fishes frequenting North Carolina's waters. Fishes certainly do not recognize arbitrary state boundaries or laws but do rapidly recognize natural and ecological effects, boundaries or barriers.

The day of unrestricted usage of the fishes of the area is over, no longer can any one species be decimated in the name of sport or commercial fishing. Our last frontier, the ocean, should not be decimated or used as a dumping ground to the detriment of its fish inhabitants, they are too varied, too unique and necessary for man's enjoyment, use and survival.

Acknowledgements

The information distilled herein would not have been possible without the concerted efforts of many over the years. The efforts of some, in particular, stand out and merit thanks. The cruises of the R/V OREGON, COMBAT, SILVER BAY, ALBATROS IV of the National Marine Science Fisheries contributed a wealth of specimens and information. Efforts by the M/V Ensign of C. Davis, Edith M of O. Purifoy, The UNC Institute of Marine Sciences' vessels R/V MACHAPUNGA and CAPRICORN, captained over the years by J. Wegener, T. Kellum and O. Lewis, were local active participants. Sport fishermen such as T. Talton, R. Talton, G. Bedsworth and head boats Danco and Captain Stacey I and III added much. Commercial fishermen such as E. Turnage, W. Fulcher, O. Davis, R. Jones and T.B. Smith supplied many specimens and were instrumental in furnishing historical and up-to-date changes that occurred in many fisheries. J. Sterling, E. Bayer, J. Gilligan, M. Street, F. Holland of the North Carolina Marine Fisheries vessel R/V DAN MOORE provided many deep water specimens. Duke University and the vessels R/V EASTWARD and CAPE HATTERAS made facilities available to work in waters 2000 m deep. Their personnel G. Newton, J. Newton, E. Nelson and C. Olsen were extremely helpful during such endeavors. The labor of many Institute of Marine Sciences staff, especially G. Safrit and J. Purifoy, and students added much to our sampling and curating the thousands of specimens brought to our attention. To the many unsung sports, commercial, party boat, and head boat fishermen plying the waters off North Carolina, too numerous to list in detail, goes my grateful thanks for without their support and constant supply of information and specimens much would still be lacking from this report. The curators of several museums, N.C. Natural History Museum, U.S. National Museum, Grice Marine Laboratory, SC, etc., graciously permitted checks of specimens deposited in their care. Dr. D. McAllister, National Museum of Canada, Ottawa and Dr. W. Hamlett, Medical College of Ohio, Toledo, reviewed the manuscript and provided helpful comments on the text and species list. B. Bright typed the manuscript; Jane Garner typed Table 1.

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BEHAVIORAL AND ECOLOGICAL ASPECTS OF REEF ASSOCIATED FISHES: APPLICATION TO AN ARTIFICIAL REEF TECHNOLOGY IN NORTH CAROLINA

David G. Lindquist

Dept. of Biological Science, University of North Carolina
Wilmington, North Carolina 28403-3297

ABSTRACT

There has been very little scientific basis for the selection or location of artificial reef materials in North Carolina. The application of scientific principles to artificial reef building has suffered from a lack of thorough understanding of the "mechanics" of reef function through experimentation and documentation.

The North Carolina continental shelf south of Cape Hatteras can be broken down into three physiographic zones for reef fishes: coastal, midshelf, and outer shelf (including shelf break area). Reef associated fishes can also be divided into three behavioral groups: benthic species, reef hovering (semi-pelagic) species and pelagic species.

Benthic species depend most heavily on the reef itself for space in which to refuge, feed, and reproduce. Reef hovering species are less closely tied to the reef physically and behaviorally; they are less dependent on the reef to provide their total necessary resources. Pelagic species are the least dependent upon the reef but, ironically, are among the most sought-after reef associated sportfishes.

Reef builders should maximize returns on artificial reefs by carefully designing and locating reefs to take advantage of specific ecological and behavioral tendencies of the target species and their preferred forage species.

Index words: reefs, reef fishes, North Carolina,
artificial reefs, behavior, ecology

INTRODUCTION

North Carolina's artificial reef building history indicates that artificial reefs have been constructed with materials of opportunity (e.g. derelict vessels, train cars, tires, concrete rubble, scrap metal, etc.). Although some of these materials have been used successfully as reef materials and this use has resulted in the establishment of long-term productive sportfishing locations, other materials have not resulted in successful reefs. For example, tires have failed to stay in position during winter storms and have washed ashore onto public beaches. Scrap metal has quickly oxidized and the structures have collapsed or have been silted in or sanded over, resulting in extremely short-lived reefs. Moreover, the selection of in extremely short-lived reefs. Moreover, the selection of locations for artificial reefs has had a haphazard history. Reef siting decisions have been based on meeting minimum U. S. Coast Guard navigation criteria with local and state political influence playing an even larger role. In practice, artificial reefs have been located where they are most accessible to the sport fishing enthusiast.

As a result of North Carolina's opportunistic artificial reef building history, there has been very little scientific basis for the selection or location of artificial reef materials in North Carolina. Further hampering the application of scientific principles to artificial reef building has been a lack of a thorough understanding of the "mechanics" of reef function through experimentation and documentation (Bohnsack and Sutherland, 1985). It is my purpose in this paper to attempt to examine some pertinent behavioral and ecological aspects of North Carolina's reef associated fishes in order to arrive at an improved set of criteria to use in the selection of artificial reef materials and the siting of these materials in North Carolina's coastal waters.

Overview of North Carolina's Reef Associated Fishes

Ecological Groupings

The North Carolina continental shelf south of Cape Hatteras can be conveniently and somewhat arbitrarily broken down into three physiographic zones for reef fishes: coastal, midshelf, and outer shelf (including shelf break area). The coastal zone extends from the shoreline to depths of approximately 25 m, the midshelf from 25 m to 50 m, and the outer shelf from 50 m to 125 m. The species associated with these three zones are reasonably well documented (Table 1) except for the outer shelf zone which has received the least attention (Huntsman, 1976; Grimes et al., 1982; Lindquist et al., 1985; Miller and Richards, 1980; Parker and Ross, 1986; Powles and Barans, 1980; Sedberry and Van Dolah, 1984; Strusaker, 1969).

Typically during the warm season, the coastal zone consists of a mixture of temperate and tropical fish species. As one moves offshore to the midshelf zone the temperate species gradually drop out. The outer shelf zone consists of tropical species more typical of the Caribbean Sea. During the cold season, the tropical species shift their distributions seaward toward the warmer Gulf Stream waters leaving behind the temperate species in the coastal zone. Some reef associated species also exhibit well documented north-south shifts in distribution corresponding to preferred water temperatures. For example, warm water species migrate northward in the spring as water temperatures increase and conversely in the fall; cool water species extend their ranges southward in winter and retreat northward in the spring.

Table 1. Representative indicator fish species for coastal, midshelf, and outer shelf reef zones for the North Carolina continental shelf south of Cape Hatteras

Scientific Name	Common Name
Coastal Species	
Centropristis striata	black sea bass
Orthopristis chrysoptera	pigfish
Stenotomus chrysops	scup
Pomacentrus variabilis	cocoa damselfish
Tautoga onitis	tautog
Hypleurochilus geminatus	crested blenny
Monacanthus hispidus	planehead filefish
Midshelf Species	
Centropristis ocyurus	bank sea bass
Mycteroperca microlepis	gag
Haemulon aurolineatum	tomtate
Haemulon plumieri	white grunt
Diplodus holbrooki	spottail pinfish
Chromis enchrysurus	yellowtail reeffish
Chromis scotti	purple reeffish
Sphyraena barracuda	barracuda
Halichoeres maculipinna	clown wrasse
Parablennius marmoratus	seaweed blenny
Balistes capriscus	gray triggerfish
Outer Shelf Fishes	
Holocentrus ascensionis	squirrelfish
Anthias nicholsi	yellowfin bass
Epinephelus drummondhayi	speckled hind
Epinephelus niveatus	snowy grouper
Hemanthias vivanus	red barbier
Serranus phoebe	tattler
Pristigenys alta	short bigeye
Caulolatilus microps	blueline tilefish
Lutjanus vivanus	silk snapper
Chaetodon aya	bank butterflyfish
Bodianus pulchellus	spotfin hogfish
Lachnolaimus maximus	hogfish

Behavioral Groupings

Reef associated fishes can also be conveniently and somewhat arbitrarily divided into three groups depending on their degree of behavioral association with the reef. The degree of association of fish species with the reef and their instinctive swimming behavior relative to the reef will vary from species to species and from larvae to adult within the same species. This degree of association with the reef has been termed "reefiness" (Nakamura, 1985). These three behavioral groups are: the benthic species, the reef hovering (semi-pelagic) species, and the pelagic species (Table 2).

Benthic species are most closely associated with the reef. These species are normally in physical contact with reef surfaces as they take up residence within holes, crevices or other small openings in the reef. Reef hovering species, as their name implies, station themselves just above the reef in the water column. These species tend to form loose aggregations to well coordinated schools depending upon the species. Reef hovering species are both visually and auditorially oriented to the reef. Reef hovering species usually stay in close proximity of the reef except for some species that depart the reef at night to forage over adjacent sand bottom. These species seldom come in direct physical contact with the reef during the day. Pelagic species tend to swim in well coordinated schools in the middle to the upper portions of the water column over the reef. Pelagic species may also come very near to the reef surface (often in search of prey) but rarely, if ever, come in direct physical contact with the reef. These species tend to be wide ranging and may roam from one reef area to the next during short periods of time (days).

Behavioral and Ecological Aspects

Benthic Species

Since these are the species that are most closely and physically associated with the reef, I would therefore argue that it is this group that depends most heavily on the reef itself for space in which to refuge, feed, and reproduce.

In order to accommodate a diversity of benthic reef species and their refuge requirements, a reef should have a variety of crevices, holes, and other heterogeneous irregularities at the surface. Since crevice seeking fishes often sit or hover at the entrance of the refuge, crevices need not be too deep. Crevices or holes that are too deep and blind-ended are not conducive to fish occupation because the space may become stagnant and devoid of water mixing and oxygenation. Also, openings on the reef should not be more than 2 m in diameter since fishes tend to be short sighted and apparently have difficulty resolving objects more than 1 m apart (Nakamura, 1985).

Table 2. Representative reef associated fishes belonging to the benthic, hovering, and pelagic behavioral groups for the North Carolina continental shelf.

Scientific name	Common name
Benthic Species	
Holocentrus ascensionis	squirrelfish
Centropristis striata	black sea bass
Epinephelus drummondhayi	speckled hind
Epinephelus niveatus	snowy grouper
Mycteroperca microlepis	gag
Serranus phoebe	tattler
Pristigenys alta	short bigeye
Caulolatilus microps	blueline tilefish
Hypleurochilus geminatus	crested blenny
Hovering (Semi-Pelagic) Species	
Anthias nicholsi	yellowfin bass
Haemulon aurolineatum	tomtate
Haemulon plumieri	white grunt
Orthopristis chrysoptera	pigfish
Diplodus holbrooki	spottail pinfish
Stenotomus chrysops	scup
Rhomboplites aurorubens	vermilion snapper
Decapterus punctatus	round scad
Sphyraena barracuda	barracuda
Pelagic Species	
Eugomphodus taurus	sand tiger shark
Pomatomus saltatrix	bluefish
Caranx hippos	crevalle jack
Seriola dumerili	greater amberjack
Rachycentron canadum	cobia
Scomberomorus cavalla	king mackerel
Scomberomorus maculatus	Spanish mackerel

Since virtually all of North Carolina's reef associated species, including the benthic reef species, have pelagic larval stages, the reef surface should offer a variety of small holes or crevices that can accommodate the very small (ca. 5-10 mm) post-larval stages that will settle out of the plankton and take refuge in the reef surface irregularities. However, these smaller holes are certainly less important than the larger holes in the reef since reefs eventually become encrusted with fouling organisms and thus small holes will be obliterated by algae and invertebrates. These fouling organisms will then provide the necessary shelter for the smaller fishes.

In my opinion, the most important, but least understood factor in producing more fishes is the attractiveness of the reef to the young of the reef associated fishes. These small fishes may encounter reefs more or less haphazardly as a result of nearshore currents sweeping the larvae around. However, some young fishes may even be able to select a particularly suitable reef in lieu of another less desirable one (larvae may not settle-out until they encounter suitable substrate). As different species of juvenile fishes settle and grow on the reef, the need for a greater variety and density of shelters increases. Thus, if reef complexity is high then a greater variety and abundance of reef fishes could be accommodated.

The availability of suitable refuges is also important for the successful reproduction of those benthic reef species that usually attach their eggs inside of a cave or crevice on the reef. These reef fishes are known as demersal spawners which characteristically involves the preparation of a nest on or adjacent to the reef and parental care of the eggs during a short incubation period (ca. one week). Most demersal spawners are also territorial during nest preparation, courtship (if any), and actual spawning. The amount of territory defended (usually by the male) varies from species to species and individual to individual and is often related to the size of the individual fish.

The newly hatched larvae of demersal spawners are unusually well developed and planktonic feeding begins within the first 24 hours (Thresher, 1984). Moreover, the larvae of the demersal spawners tend to spend less time in the plankton and are therefore dispersed over shorter distances away from the reef (Thresher, 1984). Although this dispersal distance is highly variable and, in most cases either unknown or unpredictable, the implication here is that artificial reefs should be located in a fashion that is compatible with the dispersal patterns of the demersal spawners.

The trophic requirements of the benthic species are reasonably well known, at least in general terms. Their feeding habits are, as might be expected, tied very close to reef surface and, in many cases, benthic species feed directly on the organisms (algae and encrusting invertebrates) attached to the reef. If the surface of the reef encourages the encrustation of algae and invertebrates, then additional food will be available for picking, nibbling, and browsing fishes. Thus, these fishes have added food for growth and will increase their weights as a result of added surface area that the artificial reef provides. Reef surfaces should be arranged in a variety of orientations so that a heterogeneous assemblage of fouling organisms results.

It should also be kept in mind that some benthic species will also feed off-reef to a significant extent. These species will feed on various types of invertebrates that inhabit the sand substrate surrounding the reef. However, most of the off-reef feeding by reef associated fishes is done by the reef hovering species. This phenomenon and its implications for reef siting will be discussed more fully in the following section.

Benthic species will also use the shade produced by overhanging structure on the reef as a visual advantage both during predatory behavior and as a mechanism to avoid becoming prey for other predators. This advantage is apparently caused by two interacting phenomena (Helfman, 1981): 1) a sunlit viewer has difficulty seeing a shaded object (prey protection in shade); and 2) veiling brightness which tends to scatter relatively bright light into the viewers eyes is reduced in the shade. Therefore, the result seems to be that shade may be attractive to fishes because the overhanging structure tends to reduce both the background light (and hence contrast) and the backscattered (veiling) brightness. Hence, a shaded fish has a better view of approaching objects and, at the same time, is more difficult to be seen (Helfman, 1981).

Reef Hovering Species

Since these fishes are less closely tied to the reef physically and behaviorally, they are less dependent on the reef to provide their total necessary resources. These species are most dependent on the reef for a place to orient to for cover and protection against predators. Reef hovering species tend to form aggregations that vary in their cohesiveness. Some species form coordinated schools that tend to circle around the reef or orient into the prevailing current. Schooling species that hover in the lower to middle part of the water column tend to be diurnal zooplankton feeders (e.g. round scad). Aggregating species, on the other hand, hover just over the surface of the reef in large numbers and tend to be nocturnal foragers over adjacent sand substrates (e.g. grunts). Other hovering species roam in small groups or as individuals in search of food on soft or hard substrates (e.g. porgies).

These reef hovering species form a large portion of the fish biomass on reefs and are the numerically dominant forage species for larger predators. Two of these species, the southern porgy and the tomtate, account for almost 80% of the demersal fishes associated with the hard bottom habitats between Cape Hatteras and Cape Canaveral, Florida (Sedberry and Van Dolah, 1984). These two species also feed, to a significant degree, on soft bottom organisms. The obvious consequence here is that these numerically dominant species are using food resources that are not tied to the reef itself and that a significant amount of energy in the form of forage fish biomass is being imported to the reef from external sources. The implication is that future reef siting and reef management zone decisions should take this consequence into account as data on soft bottom benthic productivity become available.

The reef hovering species are by-in-large, if not exclusively, pelagic spawners. Pelagic spawners release their eggs into the water column above the reef and the eggs are normally slightly buoyant and become a part of the plankton. Despite the fact that the eggs are not attached to the reef, reef hovering pelagic spawners may still require space or territory on the reef for courtship behavior. Pelagically spawned eggs hatch sooner than demersally spawned eggs and usually spend a longer period of time in the plankton. Thus, their larvae are dispersed farther from the reef. One exception appears to be the larva of the reef hovering cubbyu (Family Sciaenidae). The cubbyu has a benthic larval stage that may find its way back to the reef sooner than other larvae of pelagic spawners (Powles and Burgess, 1978).

Since reef hovering species are not in direct contact with the reef and do not depend upon a refuge to help maintain their relative position on the reef as the benthic species do, they must maintain their relative position on the reef by hovering in place or simply milling about an area of the reef. Energetically, it would be more efficient if these hovering species could do so while expending the least amount of effort. This can be accomplished if these fishes take advantage of the currents that impinge upon and are shed from the reef surface. These localized currents are known as shed eddies, current vortices or vortex shedding (Lindquist and Pietrafesa, 1987; Nakamura, 1985).

When current speeds are low and shed eddy production is minimal, hovering species tend to spread out over the reef and throughout the water column. On particularly calm days, hovering species such as round scad will gather at the surface of the water to feed in the zooplankton-rich neuston layer. These dense schools of hovering fishes at the surface are obvious to the surface observer and have been termed "the fisherman's boils" because fisherman have described these areas as "boiling" with fish and seabirds. However, as minimum current speeds are reached to begin causing vortex shedding about the reef structure, the hovering species begin gathering close to the reef. Most of the hovering fishes gather slightly upcurrent of the reef in a small shed eddy or current reversal caused by the laminar currents impinging directly on the front surface of the reef and being reflected by the reef for a short distance. In this position, the fish are given a small boost from behind while still maintaining a position facing directly into the current. This position is particularly advantageous for the round scad, which is a diurnal zooplanktivore (Hales, 1987), because less energy is expended maintaining position, the fish can face directly into the laminar currents that bring zooplankton into the reef, and food that is missed on the first pass will be kicked back by the current reversal making it possible to get a second chance to feed. This phenomenon is somewhat analogous to bow wake riding in porpoises.

The implication here for artificial reef builders is to structure and orient a reef so as to maximize current shedding. General current patterns of an area should be studied and structural members of a reef should be designed so that laminar currents can best be intercepted. By knowing the current vectors and speed, the minimum width and orientation of individual reef structural members can be computed in order to trigger vortex shedding (Nakamura, 1985). Shed eddy currents also produce very low frequency sounds which are hypothesized to be attractive to fishes. The implications of this phenomenon will be discussed under the pelagic species in the following section.

Pelagic Species

These species are the least dependent upon the reef but, ironically, are among the most sought-after reef associated sportfishes. Pelagic species often associate with reefs because reefs offer an abundance of concentrated forage fishes for them to feed on. Reefs, as passive visual attractors, may also form a central location from which pelagic species will roam widely for food (Brock, 1985).

Pelagic species do not appear to depend on the reef for a place to spawn. As might be expected, these species are pelagic spawners that release their eggs into the water column. Very little is known about spawning behavior in the pelagic species, but it is assumed that eggs are released well away from reefs and in most cases, well offshore. Pelagic species do not appear to become associated with reefs until they reach the size of small adults.

As mentioned in the previous section, reefs may be attractive to fishes because of the very low frequency sounds that are produced by shed eddies (Nakamura, 1985). Since water is a very good conductor of sound and fish can perceive such sounds through their acoustico-lateralis system, the implication is that reefs should be constructed so as to maximize shed eddy production and therefore the attractiveness of the reef to the wide ranging and highly sought after pelagic species. By increasing the vertical height of a reef, two things can be accomplished: 1) shed eddy production can be increased; and 2) the reef's passive visual effect can be enhanced for these water column species.

SUMMARY

The North Carolina continental shelf south of Cape Hatteras can be broken down into three physiographic zones for reef fishes: coastal, midshelf, and outer shelf (including shelf break area). Reef associated fishes can also be divided into three behavioral groups: benthic species, reef hovering (semi-pelagic) species and pelagic species. Benthic species depend most heavily on the reef itself for space in which to refuge, feed, and reproduce. Reef hovering species are less closely tied to the reef physically and behaviorally; they are less dependent on the reef to provide their total necessary resources. Pelagic species are the least dependent upon the reef but, ironically, are among the most sought-after reef associated sportfishes. Reef builders should maximize returns on artificial reefs by carefully designing and locating reefs to take advantage of specific ecological and behavioral tendencies of the target species and their preferred forage species.

ACKNOWLEDGMENTS

I thank Dr. Robert Y. George, symposium convener, for the opportunity to make this presentation to the Coastal Oceanography Symposium. I was supported as a Marine Research Associate at the University of North Carolina at Wilmington during the preparation of this paper.

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STATUS OF REEF FISH STOCKS OFF NORTH CAROLINA AND SOUTH CAROLINA AS REVEALED BY HEADBOAT CATCH STATISTICS

Eugene R. Huntsman and Peggy W. Willis
Beaufort Laboratory, Beaufort, North Carolina

ABSTRACT

A series of annual estimates of headboat catches and of size samples from those catches allowed investigation of trends in mean weight, catch, and catch per unit effort of the reef species (red porgy _Pagrus pagrus_, vermilion snapper _Rhomboplites aurorubens_, red snapper _Lutjanus campechanus_, white grunt _Haemulon plumieri_, gag _Mycteroperca microlepis_, scamp _M. phenax_, speckled hind _Epinephelus drummondhayi_, snowy grouper _E. niveatus_, black sea bass _Centropristis striata_, gray triggerfish _Balistes capriscus_) important to catches from the outer continental shelf off North Carolina and South Carolina. While catch per unit effort is usually the preferred index of stock abundance, in this investigation total catch is as useful because angling effort has been remarkably constant. Both catch and catch per unit effort may have underestimated declines in abundance because fishing power of headboats, which is related to speed and electronic fish-finding aids, has increased. Other factors complicating interpretation of the catch sequence were shifting of principal target species by vessel operators in response to differential changes in abundance, and shifting of fishing to more inshore areas as the expensive-to-reach offshore grounds became heavily exploited by commercial operators. Despite complications, important trends were evident. Mean weight per individual decreased in almost all parts of the region for eight of ten species studied (black sea bass, red porgy, vermilion snapper, gag, scamp, speckled hind, snowy grouper, and red snapper). Mean sizes for some species in 1985 were 25% of sizes in the early 1970's, and were reduced by 50% for other species. For red porgy, gag, speckled hind, and snowy grouper the mean size in 1985 equaled the minimum size needed to produce a reasonable yield per recruit. In one subarea or more, catch per unit effort in numbers decreased for red porgy, white grunt, speckled hind, and snowy grouper. Numerous explanations are available for these changes, but for red porgy off South Carolina and for speckled hind throughout the region, impaired recruitment resulting from fishing appeared to be a likely cause.

Finally, a few species (especially Warsaw grouper) became so uncommon that analyses of catches was impossible and special protection may be warranted.

INTRODUCTION

In this paper, we examine the status of reef fish stocks in the waters of the outer continental shelf off North Carolina and

South Carolina from 35°N (Cape Hatteras) south to 32°N (Savannah). For evidence we use several indices of stock status derived from catches of reef fishes made by anglers fishing with hook and line from headboats. (Headboats are for hire recreational fishing vessels which usually carry 15 or more anglers and charge on a per person, thus per "head", basis.) These data limit the application of conclusions to only those grounds used by headboats but these grounds constitute a substantial (>90%) fraction of the continental shelf (Chester et al., 1984) and support much of the commercial reef fishery as well. Our goals are to determine if interpretable trends in the fishery have occurred, to determine if these are man-induced, and if possible, to suggest options for managing depleted or misused species. This presentation is different from most in this symposium in that it discusses not only the natural oceanographic system but also anthropogenic changes in that system.

Reef fish are widespread (Tester et al., 1983) and numerous on the outer continental shelf and upper slope off the Carolinas. On the order of three hundred species (Struhsaker, 1969; Huntsman, 1976; Grimes et al., 1982; Chester et al., 1984; Parker and Ross, 1986) representing every major family of western Atlantic reef fishes occur on reefs off the Carolinas. The larger species support recreational and commercial fisheries currently producing over 1500 mt annually in North Carolina alone (Dixon and Huntsman, unpublished data; Mercer et al., 1986). The species can be fairly readily assigned to several communities usually related to depth (which is highly correlated with the nature of bottom topography and mean annual temperature) and latitude (Struhsaker, 1969; Grimes et al., 1982; Miller and Richards, 1980; Chester et al., 1984; Huntsman and Waters, 1987).

Occupancy of the outer shelf by reef fishes is allowed by the interaction of two aspects of the physical environment: (1) existence of substantial areas of exposed bed rock and rock ledges on the shelf and (2) water that is generally warm (or at least not too cold) the year around. Off the Carolinas, hard bottom supporting growth of large epibenthic sponges, soft corals, and some hard corals constitutes 13% of the zone between 27 and 101 m depths from Cape Hatteras to Cape Fear and 23% from Cape Fear to Cape Canaveral. Live bottom, as it is commonly known, with over 1 m of vertical relief, constitutes 1.4 percent of the bottom from Cape Hatteras to Cape Fear and 7% from Cape Fear to Cape Canaveral (Parker et al., 1983). The evidence from studies of fishes and other forms (South Carolina Marine Resources Research Laboratory, 1982, Cerame-Vivas and Grey, 1966) suggests that a biologically accurate depiction of the Caribbean Sea would feature a long narrow peninsula of that ocean extending north along the outer continental shelf of the southeastern U.S. to Cape Hatteras.

MATERIALS AND METHODS

Species for Study

Of the approximately 300 reef fishes occurring on the continental shelf, about 100 appear in headboat catches, perhaps forty are relatively common, and about six (red porgy Pagrus pagrus, vermilion snapper Rhomboplites aurorubens, white grunt Haemulon plumieri, black sea bass Centropristis striata, a grouper - gag Mycteroperca microlepis, and gray triggerfish Balistes capriscus) provide most of the catch. We have selected 10 species for analysis; the six mentioned above because of their importance to the magnitude of the catch and four others (the groupers: speckled hind Epinephelus drummondhayi, snowy grouper E. niveatus, scamp Mycteroperca phenax; and red snapper Lutjanus campechanus) that are either important as trophies because they are (or were) often large or because they were once much more abundant in the catch, or both.

Providing the second greatest weight (160 mt) to the headboat catch, red porgy are medium sized (to 6 kg, usually 1 kg) sparids distributed in warm waters of the Atlantic off North America, Europe, North Africa, and South America to depths of about 200 m. Red porgy feed largely on crabs, school on or near reefs, and off the Carolinas are most abundant from 40 to 100 m. Several porgies of the largely tropical genus Calamus and the scup Stenotomus chrysops (also S. caprinus) (at 20-50 m) occur with red porgy but even in aggregate provide less than 10% of the catch afforded by Pagrus.

The Serranidae, sea basses, provide five of ten selected species including the black sea bass, the species providing the greatest number and weight to the catch. Distributed off the southeastern U.S. on rocky areas from 20 to 60 m from Cape Hatteras to Cape Canaveral and in the northeastern Gulf of Mexico the black sea bass is a cool water reef fish averaging less than 0.5 kg but occasionally reaching 3. The other four serranids, the scamp, the gag, the speckled hind and snowy grouper are groupers, members of the subfamily Epinephelinae. More than a dozen groupers, usually large (5-20 kg, some to 200 kg) inhabit the region and many of these range into the Caribbean as far as South America. The gag growing to 30 kg, is the most abundant grouper of the region and with the scamp, which attains 20 kg and is our most valued grouper for food, occupies reefs from 20 to 85 m and often occurs in aggregations of 10 to 40 individuals. The speckled hind, living on reefs from 35 to 120 m along the U.S. South Atlantic and Gulf of Mexico coasts and along central America, is usually solitary, feeds mostly on crabs, and can reach over 25 kg. The largest individual ever measured weighed 29.1 kg and was taken off Morehead City, North Carolina. The snowy grouper, also a crab eater, weighs up to 20 kg and occurs in aggregations on rocky outcrops from 100 to 300 m, principally from Cape Hatteras to

Key West.

Snappers, Lutjanidae, include the third most abundant species, vermilion snapper, and the most prized trophy, red snapper. Vermilion snapper to 650 mm total length (TL) and weighing to 2.8 kg, school on reefs from 40 to 140 m and feed in midwater on squid, crab larvae, copepods and other small organisms. Red snapper are moderately common off the Carolinas but are much more abundant off Daytona Beach, FL or in the northern and, especially, western Gulf of Mexico. Nonetheless their size, often 0.75 to 0.90 m and greater than 5 kg, is generally greater off the Carolinas than elsewhere. Recreational fishermen usually do not distinguish between, and equally prize, red snappers and their similar, less common, but close relatives silk snapper *Lutjanus vivanus* and blackfin snapper *L. buccanella*. We discuss here only the true red snapper which occurs throughout the region as individuals or in small schools on reefs from 40 to 100 m and eat primarily fish.

White grunt, usually about 0.5 kg each and the fourth most important species (by weight) in the headboat catch, occur in schools on reefs at 25 to 60 m depths, principally south of Cape Lookout. Although ten species of *Haemulon* occur in the tropical western Atlantic as far north as the Florida Keys, only two, the white grunt and the abundant but small (about 0.1 kg) tomtate *Haemulon aurolineatum*, are regular off the Carolinas.

The gray triggerfish is included in our analysis because anglers have learned to appreciate it only recently and the species might potentially support greater catches. Weighing to 5 kg, gray triggerfish were avoided by vessel operators and discarded by anglers prior to the 1970's when the high quality of its white flesh became known and led to a change in angler attitude. Off west Africa the species apparently greatly expanded its population in response to the reduction, by fishing, of other species (Pierre Freon, Pers. Comm.). The potential for a similar expansion on our shelf is unknown.

Indices of Stock Status

This presentation is based on examination for each species of three fishery-dependent indices of stock status: total catch, catch per unit effort, and mean weight per individual. A decline, or increase, in total catch is often the most obvious clue to a change in stock status, but is simultaneously often the most fallible. Changes in total catch can indicate changes in population abundance or merely reflect changes in the fishing activity directed at that species, or most pernicious of all, changes in the catchability coefficient of the species (from Ricker, 1957). In a multispecies fishery, differential focus of vessel operators on one species versus another will alter the catch of a species even though abundance has not changed. Operators may shift interest for many reasons. In the 1970's increases in fuel costs, reduction in outer shelf fish abundance perhaps resulting from commercial fishing, or both, prompted many operators to reduce the distance traveled to find fish. In consequence the catch of outer shelf species, like blueline tilefish, Caulolatilus microps, declined while that of nearshore species, such as black sea bass and white grunt increased. A more subtle factor changing total catch of one species can result from increase in availability or vulnerability of another species. Given that reef fish are usually contagiously distributed by species, and that operators search until they find a "school" of any of several acceptable species, one can see that increases in the availability of one species will decrease the time spent searching for, the probability of encountering, and total catch, of another, - even though the population of the second species remains unchanged.

The adjustment of total catch to account for the amount of fishing activity can provide an improved index of stock abundance, but in multispecies fisheries some problems remain. In the ideal case each unit of fishing activity (usually a combination measure of the amount of gear and of the amount of time the gear is deployed, such as an hour of trawling, a day's fishing of a meter of gill net, or, in our case, an angler day (Table 1) - a "standard" day of four hours of fishing, exclusive of transit time, for a hook and line angler on a headboat) removes exactly the same proportion of the population, and total effort is directly and linearly proportional to the total catch (in numbers), and the catches per unit of activity are directly comparable over time. (Under these conditions catch per unit of activity is, in the strictest use of fishery terminology, catch per unit of effort, CPUE). We assume catch per angler day is CPUE. While the data we present on catch per angler day probably provide more meaningful comparisons than do those among total annual catches, the effects of changes in species preferences of operators or of their fishing zones, or in the relative abundances of species, will prevent straightforward interpretation of the CPUE series.

Interpretation of our third measure of stock status, mean weight per individual, is, of the three, subject to the least ambiguity. Within the limits of our sampling the mean weight clearly represents the population on the grounds frequented by headboats and available to hook and line.

Grounds available to headboats include virtually the entire continental shelf off the Carolinas (Tester et al., 1983). However, there have been shifts in concentration of fishing activity from the extreme outer shelf where the individuals of wide ranging species (like red porgy) are large, to the mid-and inner shelf where the fish are smaller and younger (probably as a result of greater accessibility and more intense fishing) with consequent changes in mean weight. For species like snowy grouper or black sea bass which are restricted to certain portions of the shelf shifts in location of fishing have little effect on mean weight. Not all fish of most species are vulnerable to the gear employed. The generally large hooks (6/0 to 9/0) exclude smaller individuals. But this bias is not unusual nor does it interfere with our comparisons. Virtually no sampling gear employed by either scientists or fishermen is without bias. As long as the distribution of hook sizes employed in the fishery has remained about the same over time (and our observations support this belief), our comparisons are valid.

Table 1. Total Angler Days

Year	Cape Lookout	Cape Fear	Cape Romain Inshore	Cape Romain Offshore
1972	5,234	5,425	5,086	3,244
1973	22,735	15,943	-	20,837
1974	16,287	15,760	39,248	13,136
1975	12,448	18,777	47,797	13,428
1976	10,598	19,727	41,191	19,127
1977	9,343	13,317	49,805	20,105
1978	10,697	15,335	53,552	13,910
1979	13,190	13,300	41,466	15,469
1980	15,150	8,564	50,655	13,589
1981	13,164	8,512	47,144	11,246
1982	17,455	9,482	-	67,519
1983	17,039	6,814	44,405	21,308
1984	18,742	10,123	49,109	18,204
1985	20,129	11,215	44,607	21,393

Mean size is probably the simplest of measures that might be used as a clue to stock status. Size dispersion, which can result from the same data used to calculate mean size and can be converted to age dispersion and mortality rates, is a substantially more sensitive, and useful measure. But analyses of size dispersion are relatively complex. For the initial appraisal desired in this discussion mean size is sufficiently sensitive especially when used with the catch and CPUE. One of the most pronounced responses to increased fishing mortality (F) is the elimination of larger, older, fish from the populations, with a resulting reduction in mean size. Rapid or large reductions in mean fish size often indicate excessive exploitation of the stock. Thus, change in mean size is an easily measured "early warning" device.

Source of Data

There are two conceivable sources of data for assessments of fish stocks: (1) statistically-based surveys conducted at sea to provide data on stock abundance, distribution, and mean size of individuals and (2) surveys of commercial or recreational catches from which to derive the same information. The former is preferred because such so-called fishery independent surveys can be designed to avoid biases caused by gear or geographic distribution of fishing effort. However, fishery independent surveys for reef fish of the U.S. south Atlantic are not currently practicable. Gear which allows rapid and inexpensive surveys of reef fish populations has not been developed. The only gear which dependably takes reef fish from all habitat (including high relief ledges) is that used in the commercial and recreational fisheries, hook and line. Because large variance is associated with hook and line samples, sample sizes (numbers of stations, hours of fishing, etc.) must be extremely large. As a result, adequate fishery independent surveys are currently too expensive to be conducted with the funds available and current assessments must be based on the results of existing reef fisheries. While the "sampling" conducted by fishermen presents problems (inadequate or improper geographic and temporal distribution of sampling effort, gear and techniques with substantial biases towards or against certain sizes or species of fish), it has two great advantages, immense sample sizes (in terms of stations occupied) and low cost. For the investment of a few hours of labor, biologists with a minimal output for gear and record systems and none at all for expensive vessel time, can take advantage of thousands of hours of sampling by proficient samplers. As long as the biases of the sampling are known (or suspected), useful results ensue.

The Fishery Studied

The information for these analyses results from dockside sampling of the headboat fishery of the Carolinas. The headboat fishery was chosen instead of other recreational fisheries, or the commercial fishery, for several reasons. A principal one was that at the inception of this work in 1972, the headboat fishery took the only significant catch of reef fishes (other than black sea bass) off the Carolinas. Few private recreational anglers owned the vessels and electronic instruments necessary for reef fishing, charter vessels concentrated on pelagic fishes, and commercial reef fishing for other than black sea bass was infrequent. Not until 1976 did substantial commercial fishing begin.

A secondary but pragmatic reason for studying the headboat fishery is that its catches are easily and inexpensively observed at dockside. Headboats, in general, use but one dock and adhere to a relatively inflexible schedule. Thus, sampling of catches is efficiently scheduled. Further, the area of fishing is tightly circumscribed to that part of the shelf within a few hours run from the inlet used so that the catches are readily attributed to a given fishing area. Commercial vessels may, and do, make cruises of several days and dock when and where ever convenient, even several days and several states away from the trip origin. Obtaining samples from a commercial catch and ascribing the catch's origin to a particular area can be very difficult. As a consequence of the facts that: (1) the National Marine Fisheries Service Laboratory at Beaufort was at the limit of its resources in studying the headboat fishery and could not afford to study the commercial fishery too; (2) the commercial fishery was more difficult to sample; and (3) there was a general disinterest in reef fisheries with consequent inattention to statistics of the commercial fishery until several years after the initiation of a reef fishery management plan. There were few useful data on the size of the commercial catch, size of individual fish in it or the species composition until approximately 1985. Thus, the data series for the commercial fishery is too short to be useful, and the data from headboat catches since 1972 constitute the best available basis for stock assessment.

Methods of Studying the Headboat Fishery

The catches of the headboat fishery of North Carolina and South Carolina are described using data obtained from measuring fish at dockside and from a system of logbooks. Dockside sampling provides data on fish size (length and weight) and biological materials for studies of growth, diet and reproduction of reef species. Samplers contact each vessel every 7-10 unloadings, and approximately 10,000 individual fish (Table 2) from Carolina headboats are weighed each year. The log books, maintained by a crew member, provide the number of each species taken each day, the associated number of anglers, the location of fishing, the length (in time) of the trips, and associated information. The crew members are paid to keep the records. The total catch in number is the sum of the daily catches. While designed to be a census, our scheme is imperfect and records for some trips do not exist. We usually correct for missing catch data (for full details see Dixon and Huntsman, unpublished data) by multiplying the catch per unit effort for each species (by vessel) for trips with log book records by the total effort in angler days (usually known) applied by that vessel. Total catch in weight is computed by multiplying the number of each species taken by the mean weight of that species for various time and area strata. Strata are summed to obtain yearly totals.

For the purposes of this discussion the fishing areas are defined:

Cape Lookout - From the middle of Raleigh Bay (35°N) southwest to the middle of Onslow Bay (34.2°N)

Table 2. Sample Sizes for Mean Weight by Species and Year.

Red Porgy	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985
Cape Lookout	678	780	669	440	553	431	438	367	527	344	631	955	990	795
Cape Fear	1250	1563	803	381	612	431	192	62	196	151	378	277	369	388
Cape Romain Inshore	84	1093	481	448	129	240	267	90	65	116	268	78	57	43
Cape Romain Offshore	2189	1429	1592	899	583	953	321	229	540	379	1066	773	995	480
Vermilion Snapper														
Cape Lookout	161	196	286	342	251	117	179	238	300	165	544	672	349	564
Cape Fear	592	124	241	295	191	27	27	5	12	9	47	192	143	252
Cape Romain Inshore	197	111	324	276	31	15	97	4	3	31	205	54	44	70
Cape Romain Offshore	147	139	390	326	147	198	122	48	168	106	481	533	1473	557
White Grunt														
Cape Lookout	213	252	187	362	295	216	151	79	139	96	212	270	453	55
Cape Fear	1179	85	534	364	611	339	197	76	331	169	433	374	427	52
Cape Romain Inshore	26	324	141	239	27	33	22	46	21	122	187	45	19	25
Cape Romain Offshore	691	84	68	32	61	113	45	43	59	138	182	238	296	15
Red Snapper														
Cape Lookout	11	21	18	28	61	34	35	6	8	16	27	38	37	153
Cape Fear	9	-	8	24	50	16	12	1	10	1	3	12	11	17
Cape Romain Inshore	3	5	21	63	11	19	15	1	4	3	1	2	3	14
Cape Romain Offshore	27	15	45	17	28	57	22	7	10	-	5	22	97	37
Gag														
Cape Lookout	32	58	38	82	95	101	69	66	108	70	145	207	460	248
Cape Fear	86	68	56	74	119	133	91	26	56	23	86	74	46	111
Cape Romain Inshore	1	39	6	20	3	11	4	6	1	-	4	20	7	4
Cape Romain Offshore	32	69	40	31	21	24	19	8	8	1	11	47	76	41

Table 2 (cont)

Scamp	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985
Cape Lookout	5	10	33	19	13	40	29	51	58	15	57	64	87	75
Cape Fear	139	188	175	272	760	297	187	62	22	5	88	91	92	67
Cape Romain Inshore	1	107	45	52	10	24	20	3	-	4	10	4	2	11
Cape Romain Offshore	230	58	120	66	41	47	3	17	12	5	21	99	144	12
Speckled Hind														
Cape Lookout	2	47	21	21	17	24	10	10	11	1	11	13	17	33
Cape Fear	32	44	17	47	18	2	3	-	4	-	1	-	2	1
Cape Romain Inshore	1	86	7	19	7	1	15	-	1	1	-	4	-	4
Cape Romain Offshore	106	94	126	60	50	117	73	11	13	3	15	56	74	44
Snowy Grouper														
Cape Lookout	60	238	79	12	127	84	11	24	5	6	3	13	2	31
Cape Fear	-	-	-	12	-	-	-	-	1	-	-	-	-	-
Cape Romain Inshore	-	2	-	2	-	-	-	-	2	-	-	-	-	-
Cape Romain Offshore	7	4	145	93	71	19	13	22	37	14	18	52	32	25
Gray Triggerfish														
Cape Lookout	22	92	57	86	68	145	184	159	123	33	112	217	132	294
Cape Fear	26	23	22	49	24	31	15	7	12	2	9	10	11	6
Cape Romain Inshore	4	4	47	86	16	29	49	9	1	7	28	5	3	10
Cape Romain Offshore	60	1	174	57	87	261	96	23	93	32	72	98	183	85
Black Sea Bass														
Cape Lookout	-	-	205	156	250	129	238	119	362	304	403	392	452	622
Cape Fear	-	-	271	65	62	308	187	75	420	230	467	709	398	372
Cape Romain Inshore	-	1	622	740	112	2008	808	694	1078	1608	1200	1782	1989	1977
Cape Romain Offshore	-	-	25	58	33	187	147	207	66	112	175	229	607	175

Cape Fear -	From mid Onslow Bay (34.2°N) southwest to the waters immediately south of Cape Fear (33.8°N)
Cape Romain -	From the southern boundary of the Cape Fear region (33.8°N) southwest to Savannah, Georgia (32°N) (Figure 1).

Although the reef community extends northward to the waters off Cape Hatteras headboat fishing in offshore waters there has been too infrequent to provide data for this paper.

Fishing in the Cape Lookout and Cape Fear districts extended from depths of 40 to 120 m.

The Cape Romain District is divided into two depth zones, (inshore: 30 m to 50 m, and offshore: 50 m to 200 m), because the broad shelf results in fishing trips with such large differences in catches that separate strata are warranted. The other two areas were divided into inshore and offshore strata also. But the Federal prohibition against revealing data aggregated for fewer than three economic entities prevents reporting the outcome of fishing in the Cape Lookout and Cape Fear areas by inshore-offshore subdivisions for some years (thus, for purposes of comparison, for all years).

RESULTS

Red Porgy

Total Catch

Catches in numbers of red porgy (Figure 2) by district present a mixed pattern. For Cape Lookout there has been a slight increase. For Cape Romain, offshore catches seem to fluctuate greatly without evidence of increase or decrease. But in both the Cape Fear and adjacent Cape Romain inshore area a downward trend is clear. For both areas 1985 catches are less than 20% of those in 1974.

Catch Per Unit of Effort

Except in the Cape Lookout area, catch per angler day (CPUE) of red porgy (Figure 3) in both numbers and weight have shown marked declines. By number CPUE for the Cape Fear District in 1985 (1.14) is only 17% of that in 1973 (6.78). Similarly CPUE for Cape Romain offshore in 1985 (3.63) is only 40% of that in 1972 (9.1), and even for inshore Cape Romain, where red porgy are not as abundant, the CPUE (numbers) for 1985 (0.09) is only 10% of that for 1972 (0.91). CPUE-weight (Figure 4) patterns are similar, but declines are more pronounced because mean weight, as well as apparent abundance has declined.

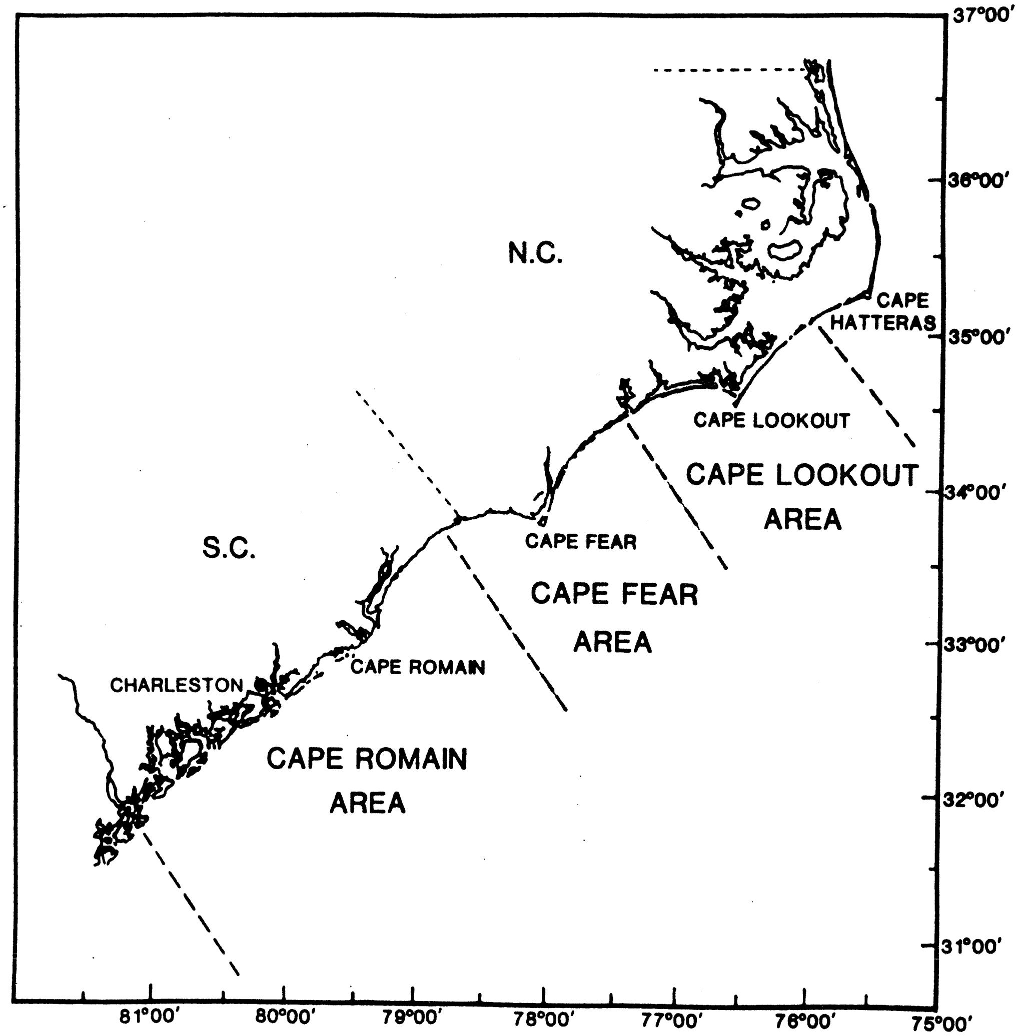

Figure 1. Fishing areas of headboats in the Atlantic Ocean off North Carolina and South Carolina.

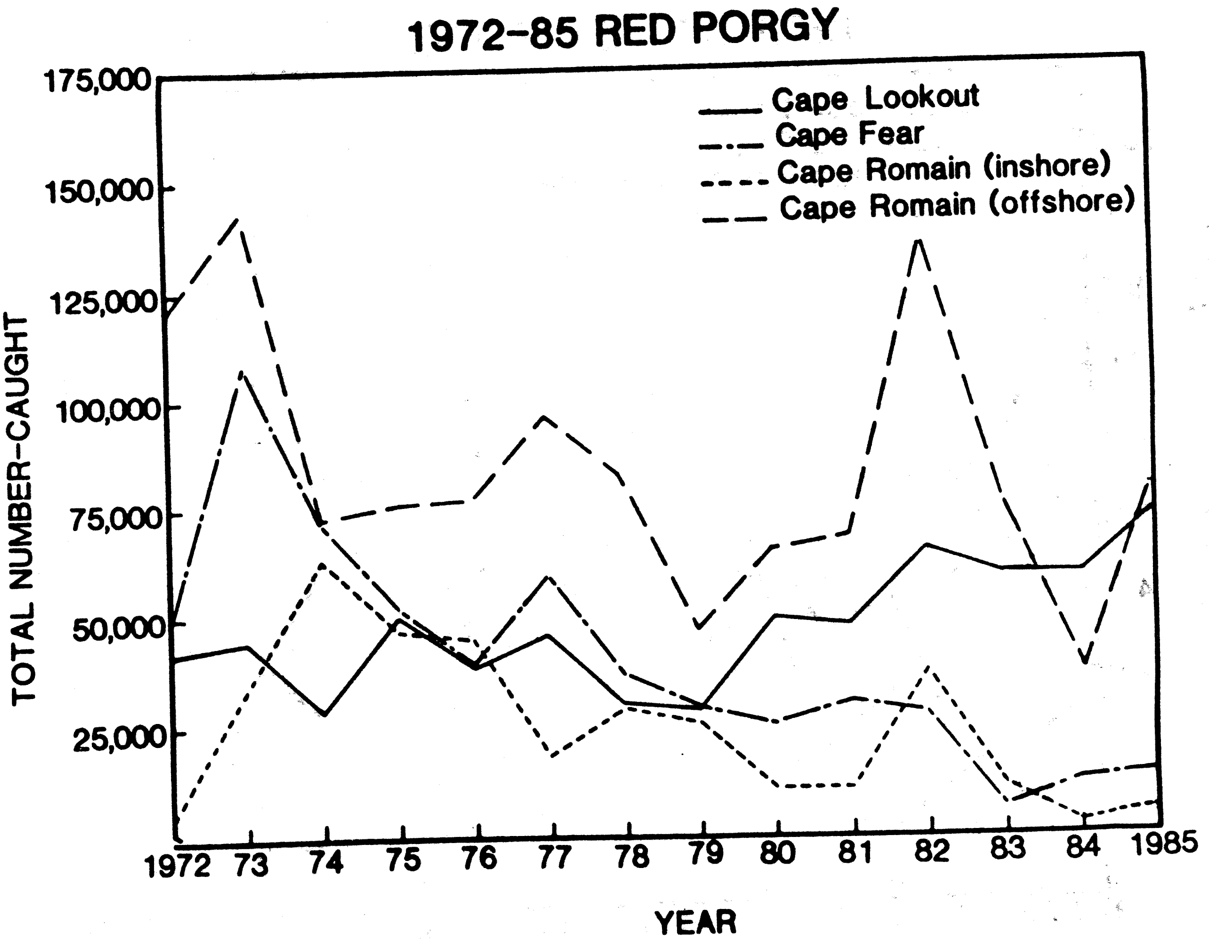

Figure 2. Red porgy total number caught - 1972-85.

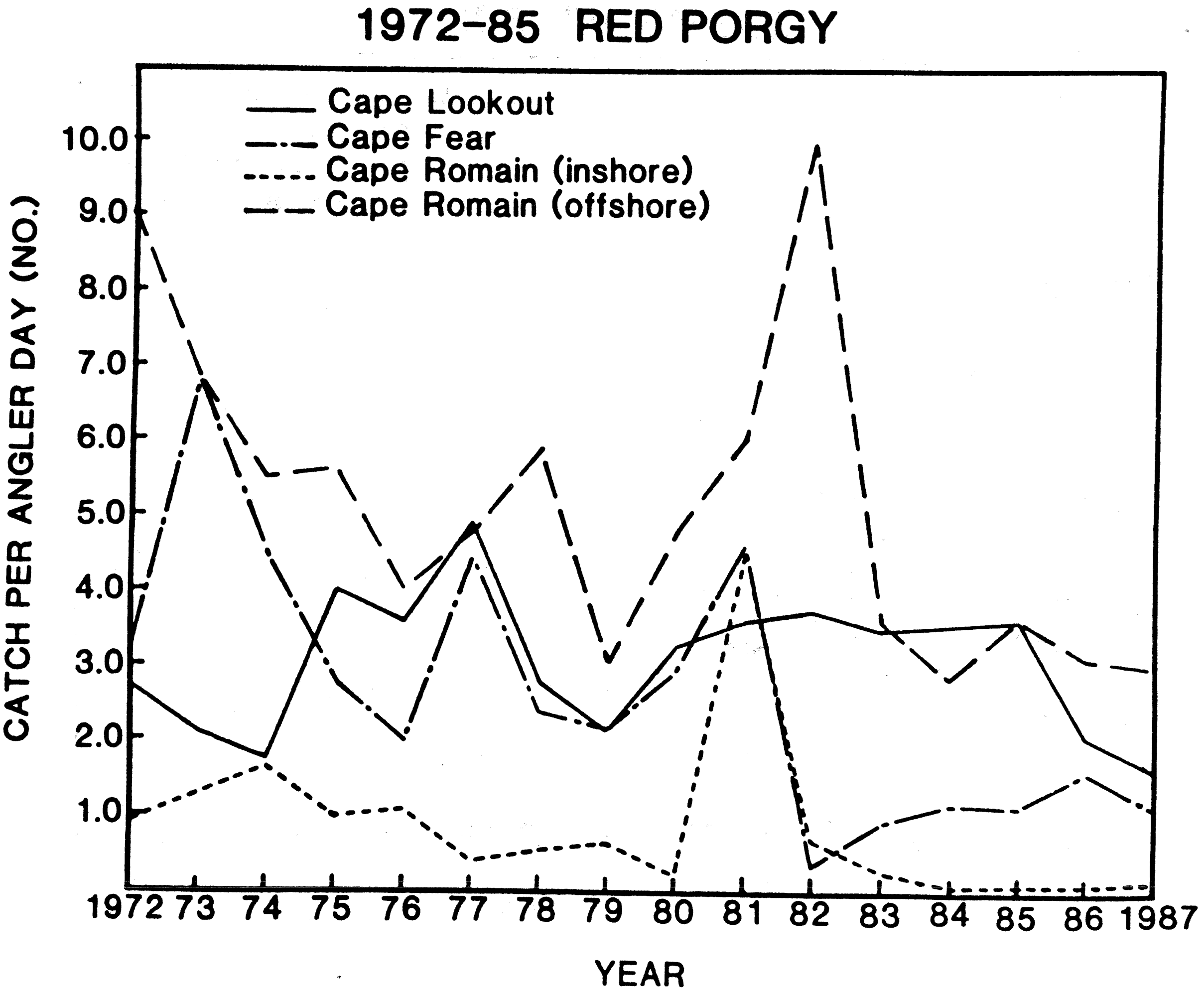

Figure 3. Red porgy catch per angler day in numbers - 1972-85.

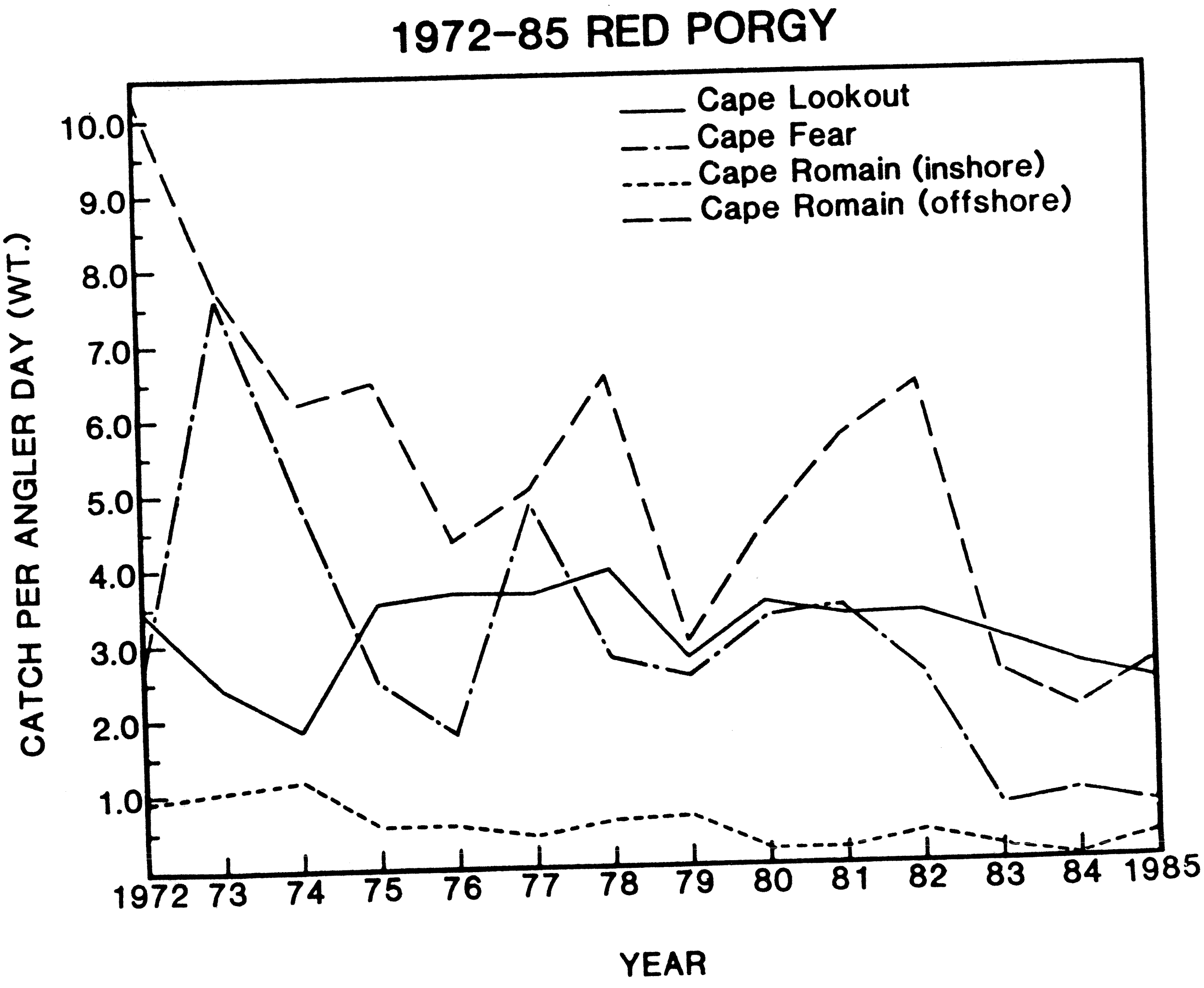

Figure 4. Red porgy catch per angler day in weight - 1972-85.

Mean Weight

In all areas there has been a marked decrease in mean weight from 1972 to 1985 (Figure 5) despite a brief upward trend for Cape Lookout, Cape Fear and Cape Romain (inshore) in the late 1970's. For the Cape Lookout, Cape Fear, Cape Romain inshore, and Cape Romain offshore districts 1985 mean weights are 52, 52, 58 and 64% of the 1972 values.

SUMMARY

Red porgy throughout much of the region appear dramatically reduced in both abundance and size. While the mid-70's shift in fishing area might explain the decline in the CPUE (numbers) for the Cape Romain offshore and Cape Fear areas, it does not correlate with the continual decline in mean weight for all areas. A more robust explanation is that superposition of a growing commercial fishery on the headboat fishery has caused the reduction in porgy size and, probably numbers. The current mean size of red porgy (about 650 g and 364 mm) is essentially equal to the size at first entry to the fishery which maximizes yield per recruit (Manooch and Huntsman, 1979; Huntsman et al., 1983). Capturing red porgy at this mean size is likely deleterious to yield per recruit.

Vermilion Snapper

Total Catch

Catch patterns are confusing (Figure 6). Catches for Cape Romain offshore and Cape Lookout districts rose substantially especially in the 1980's, while catches for Cape Fear and Cape Romain Inshore dropped by 1985 to less than half the level of the early 1970's. A reasonable, but unproven, explanation of these patterns is that in response to fuel price increases, decreased overall CPUE offshore, or both, vessels of the Cape Romain Inshore and Cape Fear (which has a large component of inshore vessels) regions shifted fishing grounds inshore from the area of peak vermilion snapper concentrations, while Cape Romain offshore and Cape Lookout (which has a large component of offshore vessels) region vessels in response to the same stimulus shifted from deeper water to the prime vermilion snapper grounds. Perhaps increased catches resulted from greater attention to vermilion snapper as larger species became scarce. Other explanations relating to shifts in distribution of the population are possible but equally unprovable.

Catch Per Unit of Effort

Catch per unit of effort mimics catch (Figures 7 and 8).

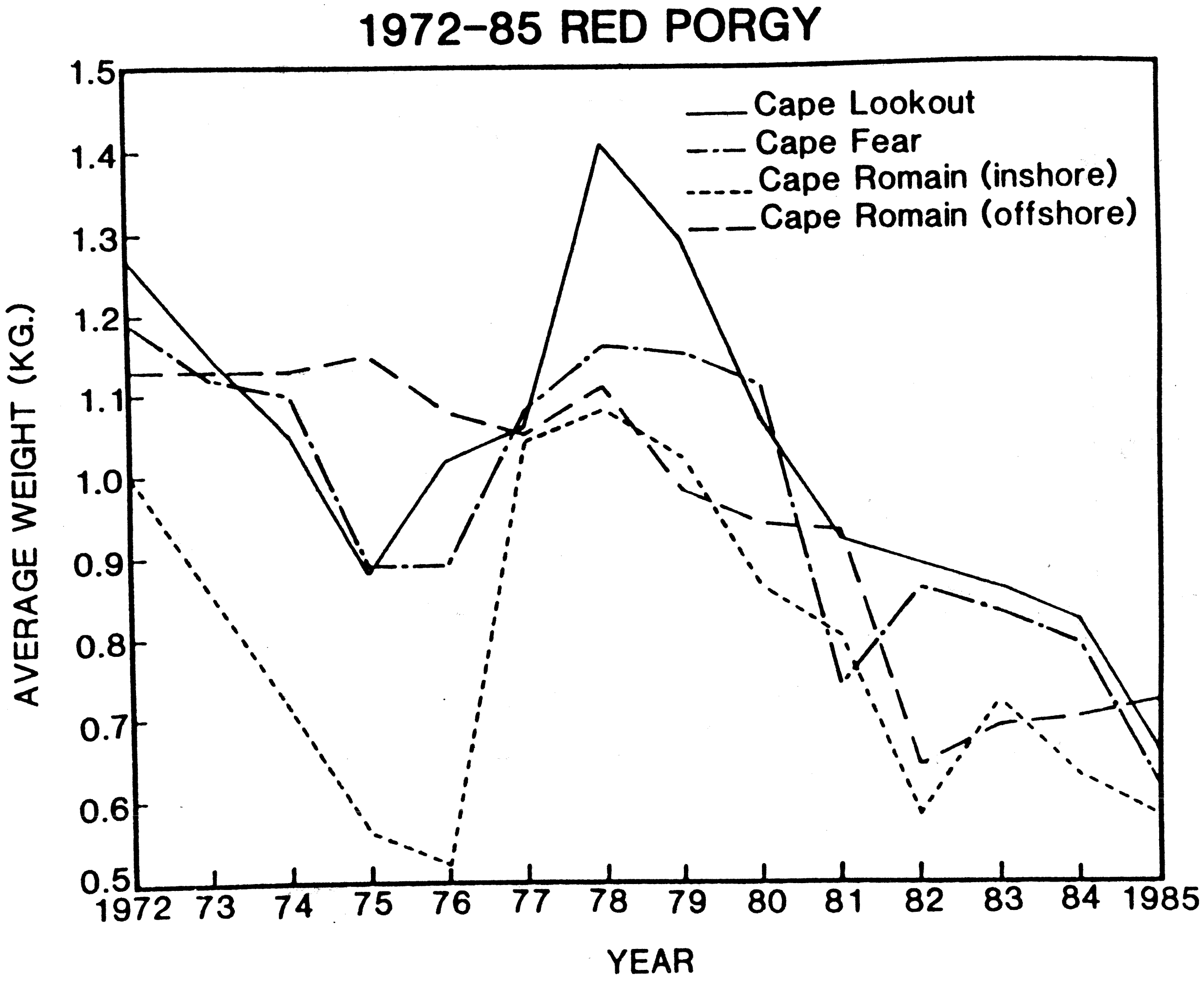

Figure 5. Red porgy average weight - 1972-85.

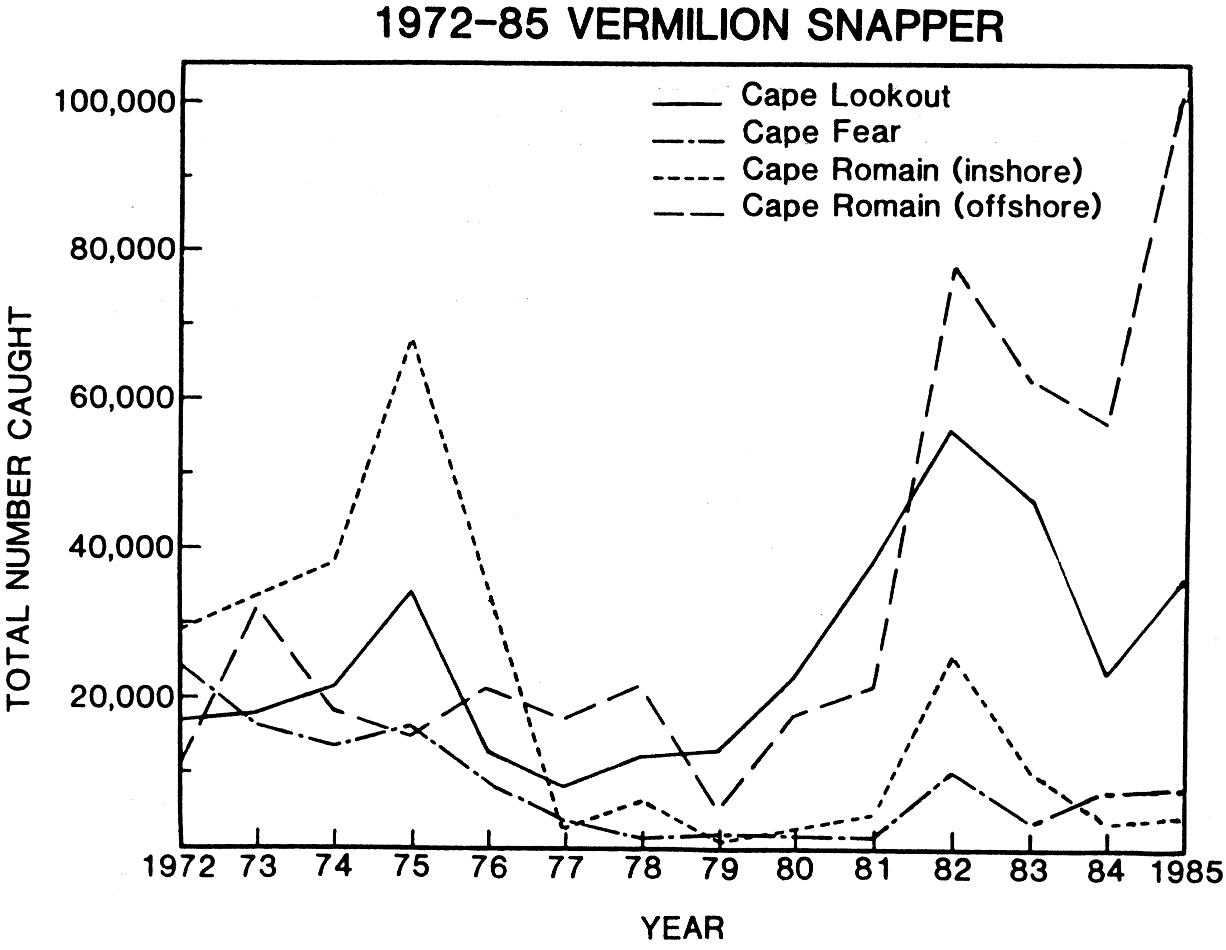

Figure 6. Vermilion snapper total number caught - 1972-85.

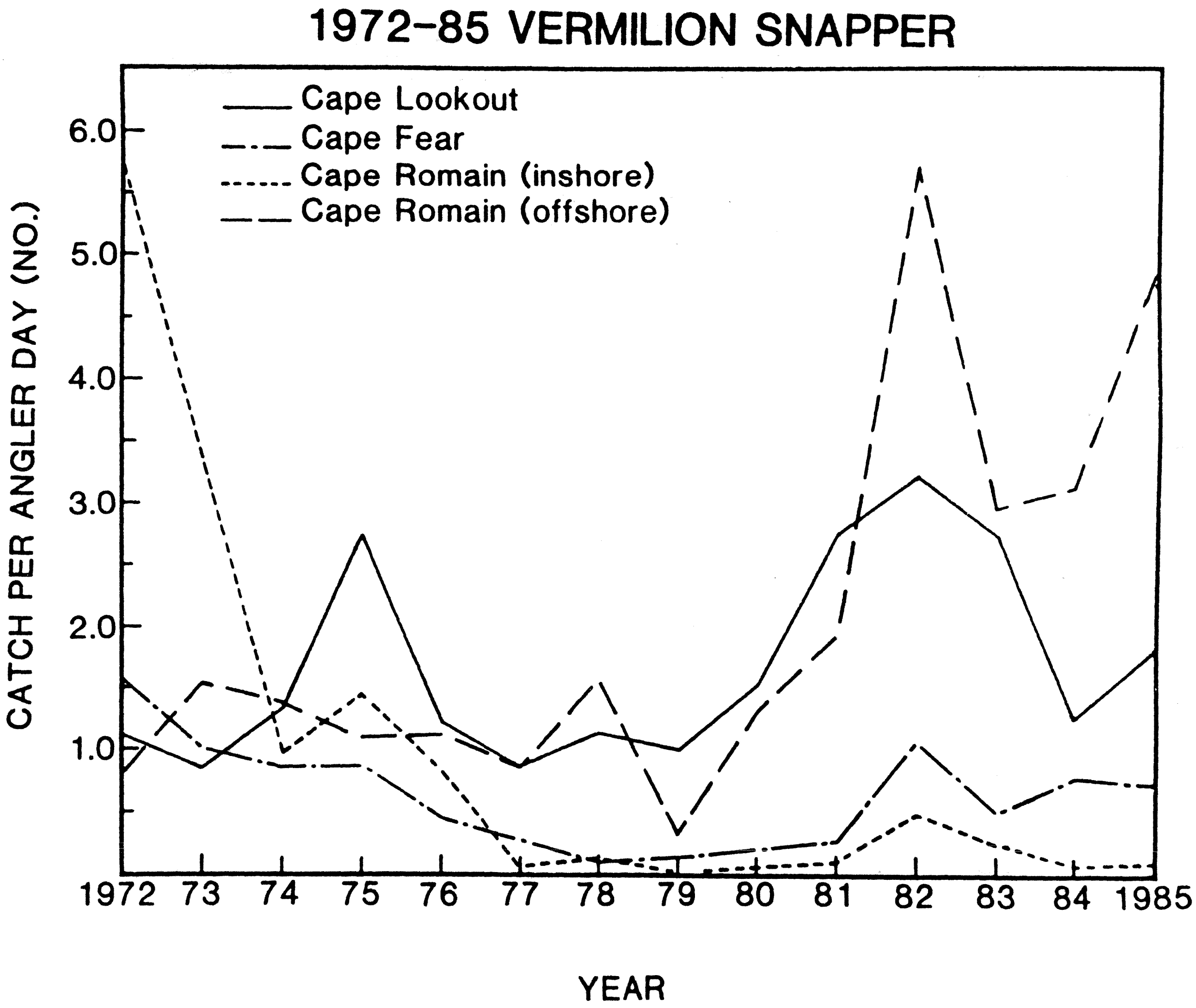

Figure 7. Vermilion snapper catch per angler day in numbers - 1972-85.

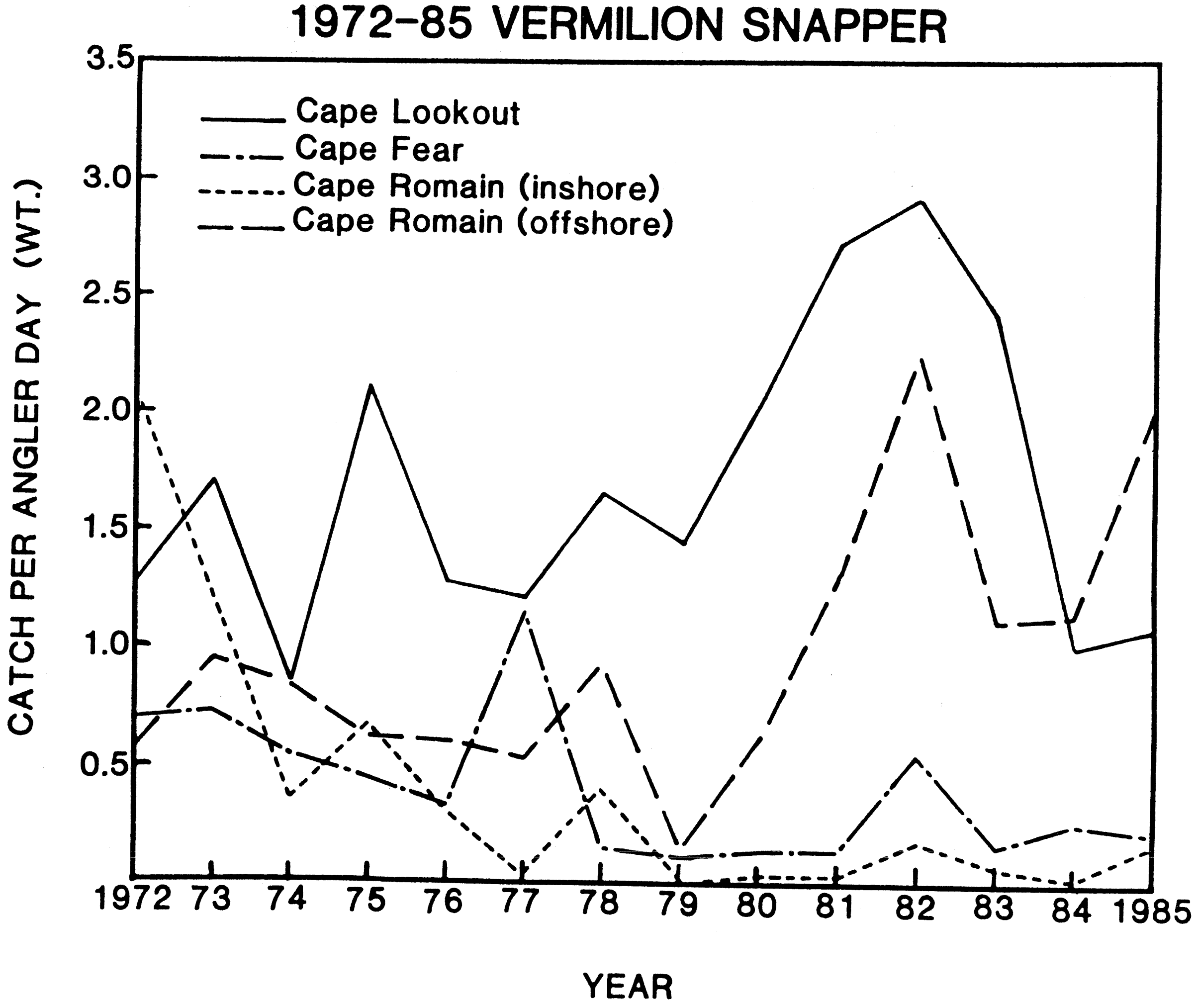

Figure 8. Vermilion snapper catch per angler day in weight- 1972-85.

Mean Weight

No obvious trend in mean weight (Figure 9) exists for the two Cape Romain districts. But for Cape Lookout and Cape Fear mean weights have dropped steadily since 1978, from 1.5 to 0.7 kg (54% decline, Cape Lookout) and from 1.7 to 0.4 kg (76%, Cape Fear).

SUMMARY

It is difficult to reconcile changes in mean weight with changes in catch and CPUE, especially for the Cape Lookout area. While the steep, post 1978 decline in mean weight might suggest a negative response to fishing, the increase in catch and CPUE suggests an expanding population. Cape Romain offshore area catches are up dramatically suggesting population expansion. There mean weight is essentially the same or only slightly lower in 1983 than in 1976. Similarly confusing patterns exist for the other areas. Possible explanations include: (1) a large increase in recruitment with many small fish becoming available to the catch and a resultant lowering or mean size or (2) a shift in operator emphasis toward a long existing population of small vermilion snapper as large species became more scarce. The average vermilion snapper taken in all districts is probably substantially larger than the size at entry to the fishery needed to maximize yield per recruit. This observation is, of course, not equivalent to one that the best age at entry occurs. But it does indicate that there is not a blatantly obvious case of growth overfishing (the situation in which efficiency of harvest, in terms of weight per recruit, is impaired by excess fishing pressure or capture of fish that are too young).

White Grunt

Total Catch

It is difficult to discern an interpretable pattern in catches of white grunt (Figure 10). Only for the Cape Fear region does an unambiguous trend (down from 60,000 fish in 1972 to 18,000 in 1987) exist. Catches for Cape Romain offshore and for Cape Lookout are substantially larger in the 1980's than in the 1970's (20,000 - 30,000 fish vs 5,000 - 10,000). That Cape Romain inshore vessels apparently took extraordinary numbers of white grunt in the early 1970's (from 20,000 to >100,000 fish) but have landed <20,000 annually since 1976, probably results again from the inshore shift of vessel activity off the principal grunt grounds but might suggest impaired recruitment, and perhaps overfishing.

Catch Per Unit of Effort

Patterns of CPUE approximate those of total catch (Figures 11 and 12).

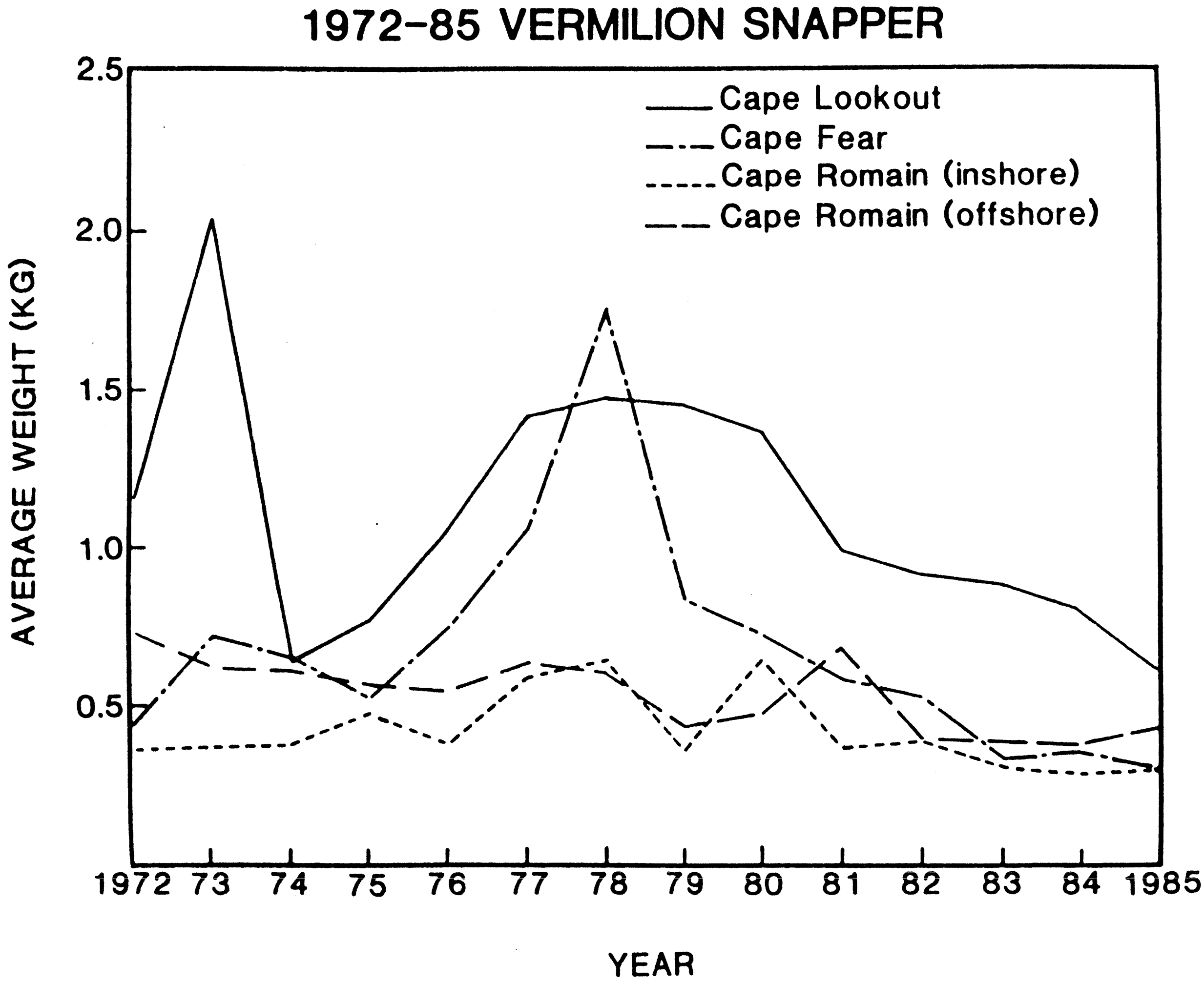

Figure 9. Vermilion snapper average weight - 1972-85.

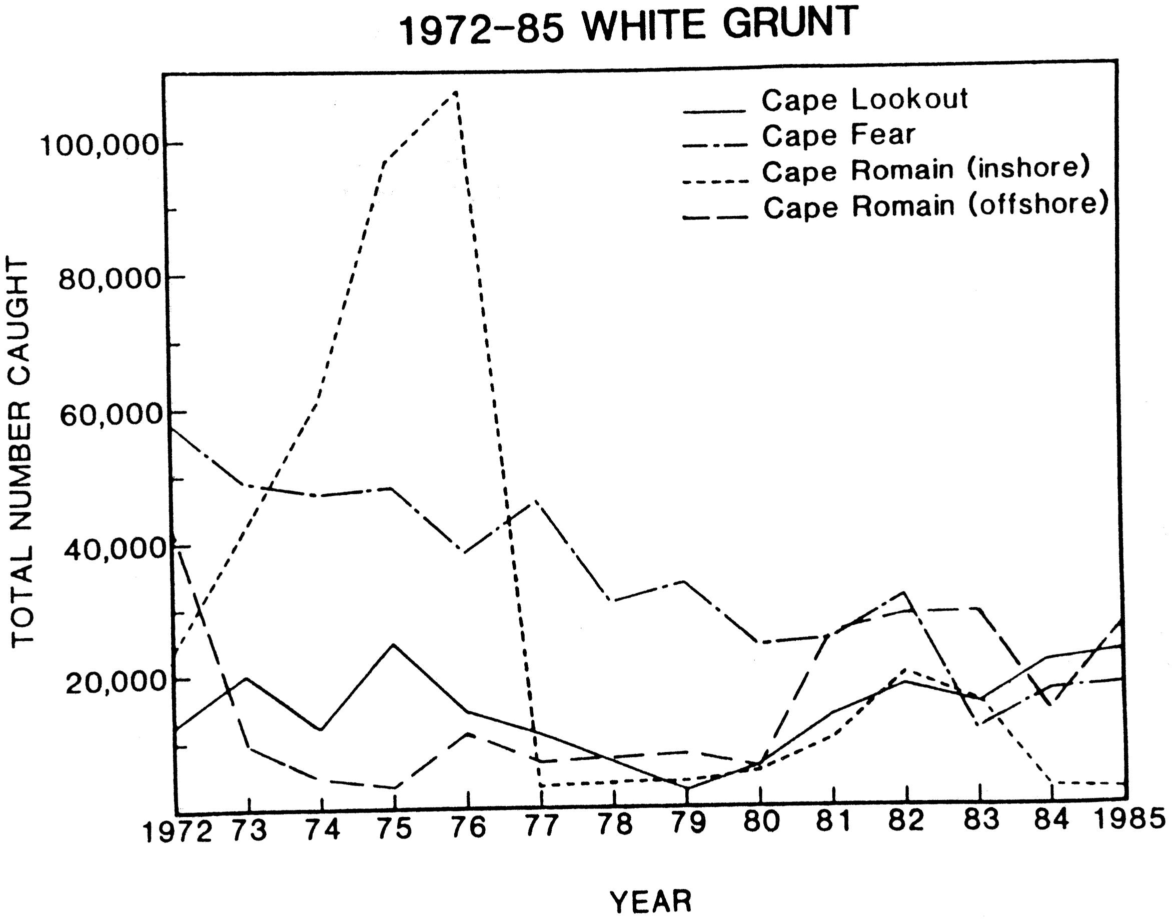

Figure 10. White grunt total number caught - 1972-85.

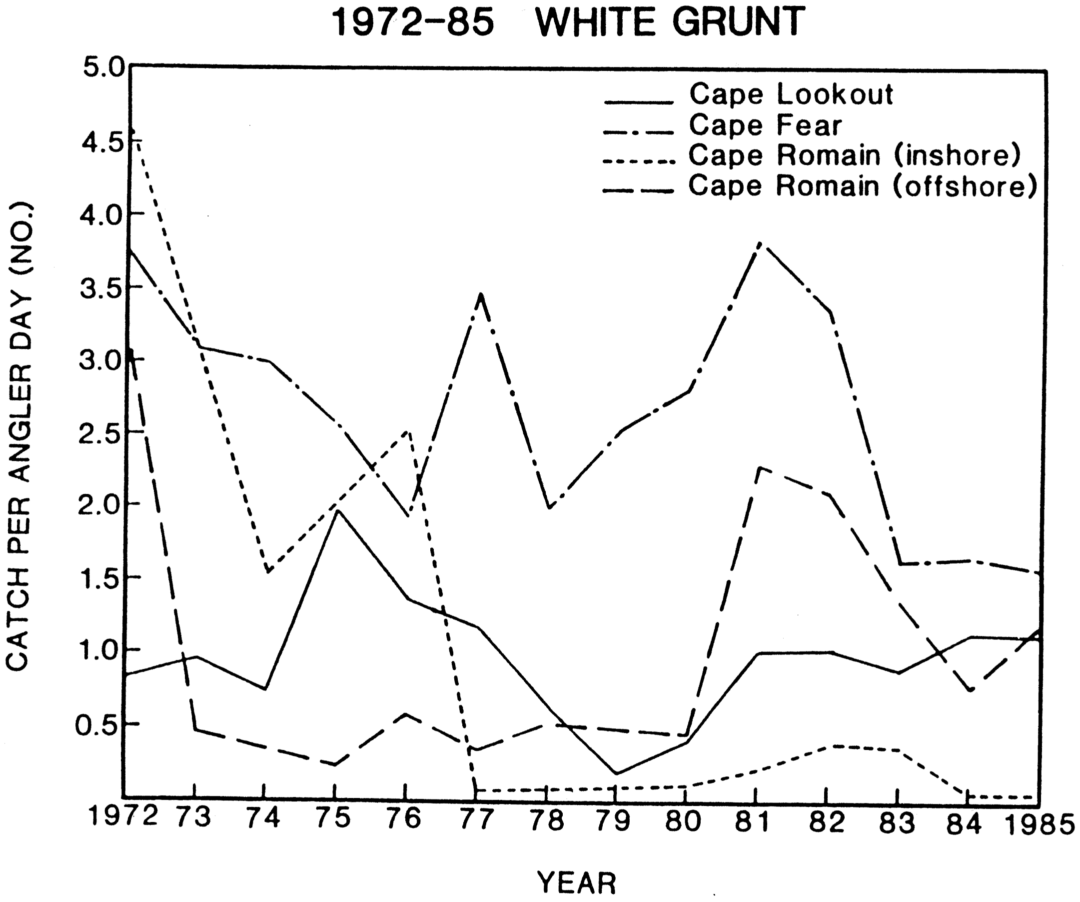

Figure 11. White grunt catch per angler day in numbers- 1972-85.

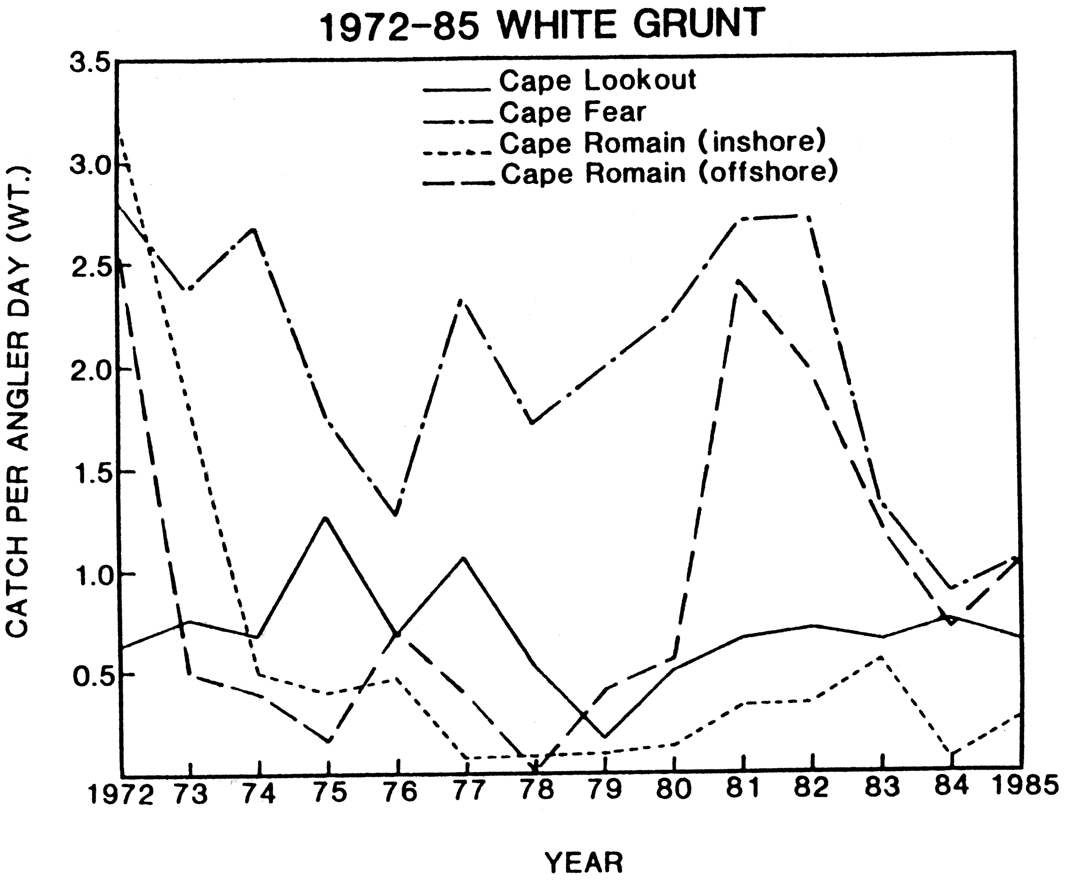

Figure 12. White grunt catch per angler day in weight - 1972-85.

Mean Weight

Overall, white grunt appear larger off South Carolina than North Carolina but since 1974 no trend in mean weight appears (Figure 13). Importantly, white grunt from the Cape Romain inshore area have averaged 1.6 kg (the largest average yet) as recently as 1983.

Summary - No substantial trend in white grunt populations appears. Fish of the size currently harvested exceed the minimum necessary to produce a maximal yield per recruit.

Red Snapper

Total Catch

By district total catch has remained relatively small (around 500 - 2000 fish/district/year) with the exception of an extraordinary catch of 8297 for the Cape Lookout district in 1985 (Figure 14). No substantial trends exist.

Catch Per Unit of Effort

CPUE patterns mimic those of total catch (Figures 15 and 16).

Mean Weight

Despite the usual confusing variability, there appears to be an important decline in red snapper size for all districts (Figure 17). Averaging between 7 and 9 kg in 1972 mean weights of red snapper in 1985 were only on the order of 2-3 kg.

Summary

While no evidence for impaired recruitment of red snapper exists in these data, it is clear that mortality has increased sufficiently to lower mean weights to only one third (or less) of their 1972 values.

Gag

Total Catch

No substantial trends in total catch appear (Figure 18). At present an equal or greater number of gag are being taken in the Cape Lookout, and Cape Romain Inshore and Offshore districts as in the mid 1970's. Cape Lookout catches were lower from 1975-1980 than earlier or later. Catches for the Cape Fear district are down to about 500 fish per year compared to 1000 to 1500 in the 1970's.

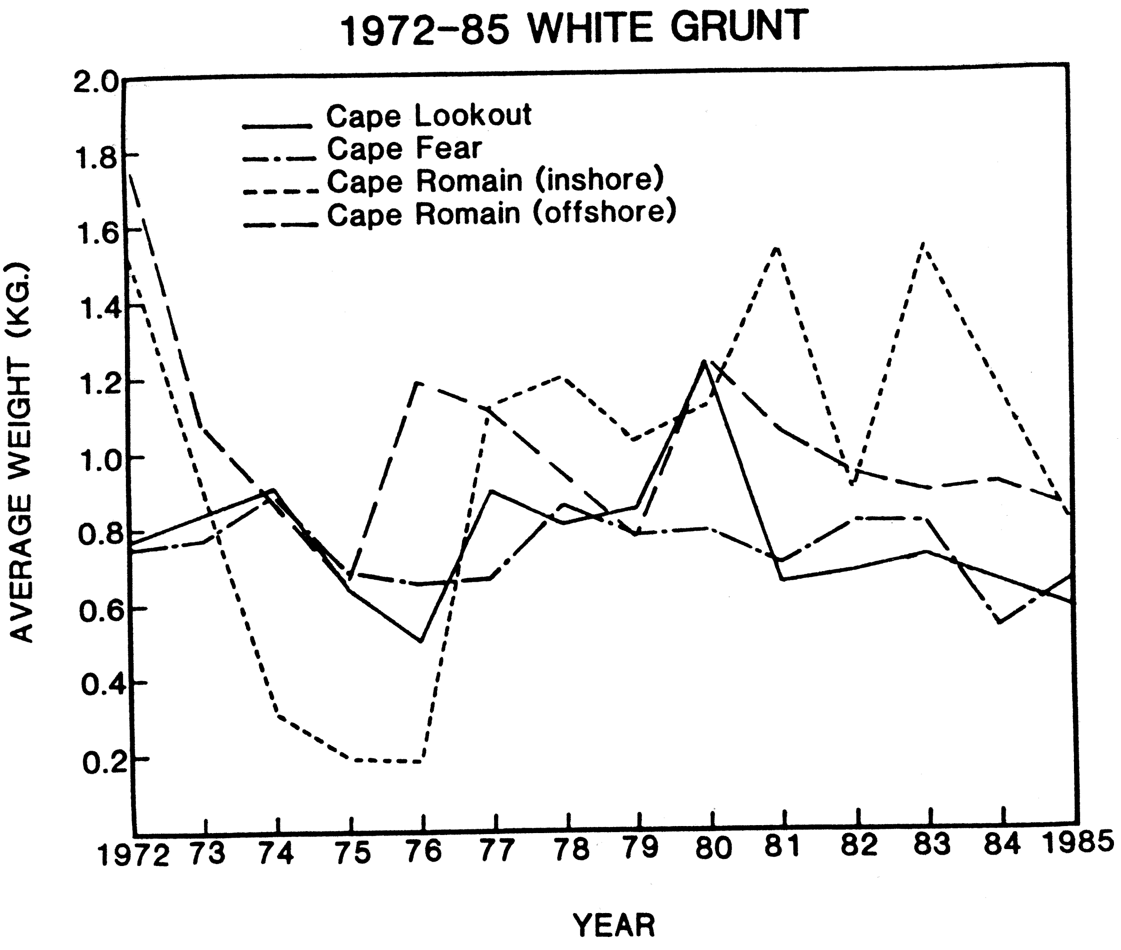

Figure 13. White grunt average weight - 1972-85.

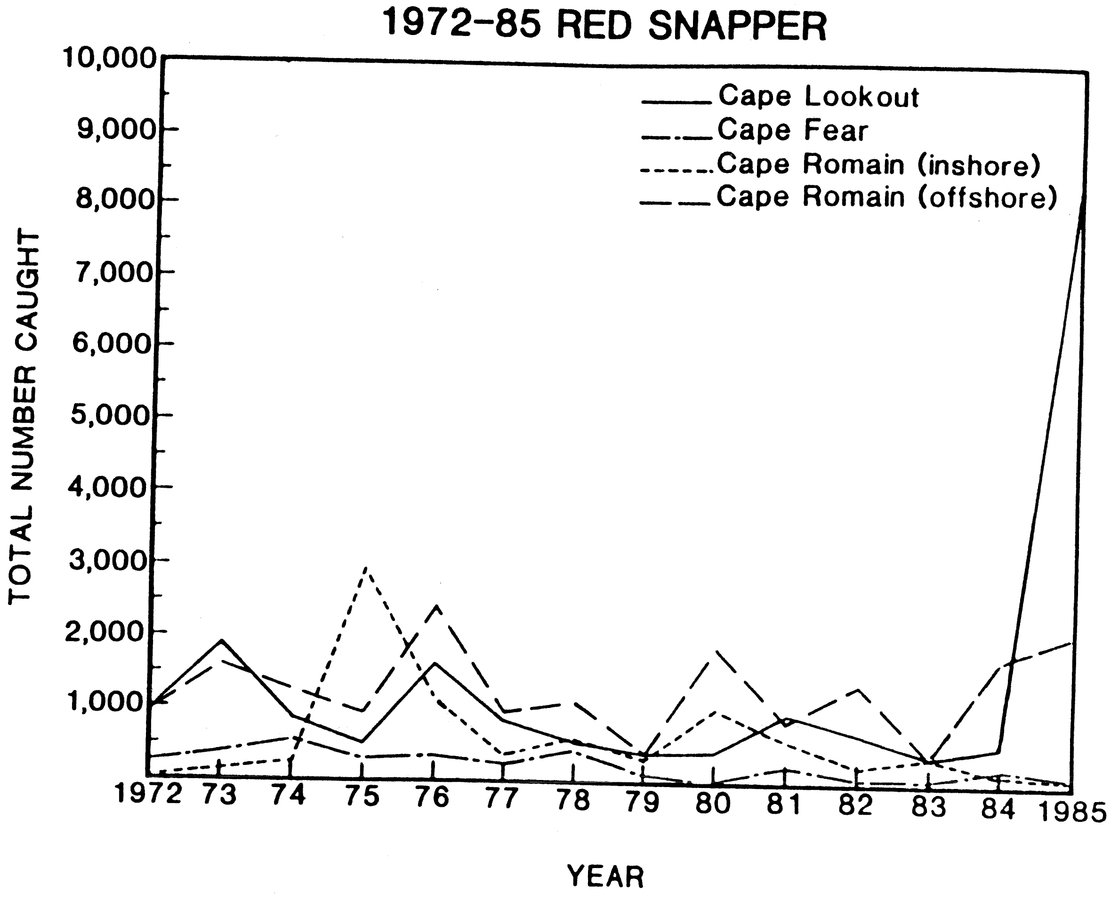

Figure 14. Red snapper total number caught - 1972-85.

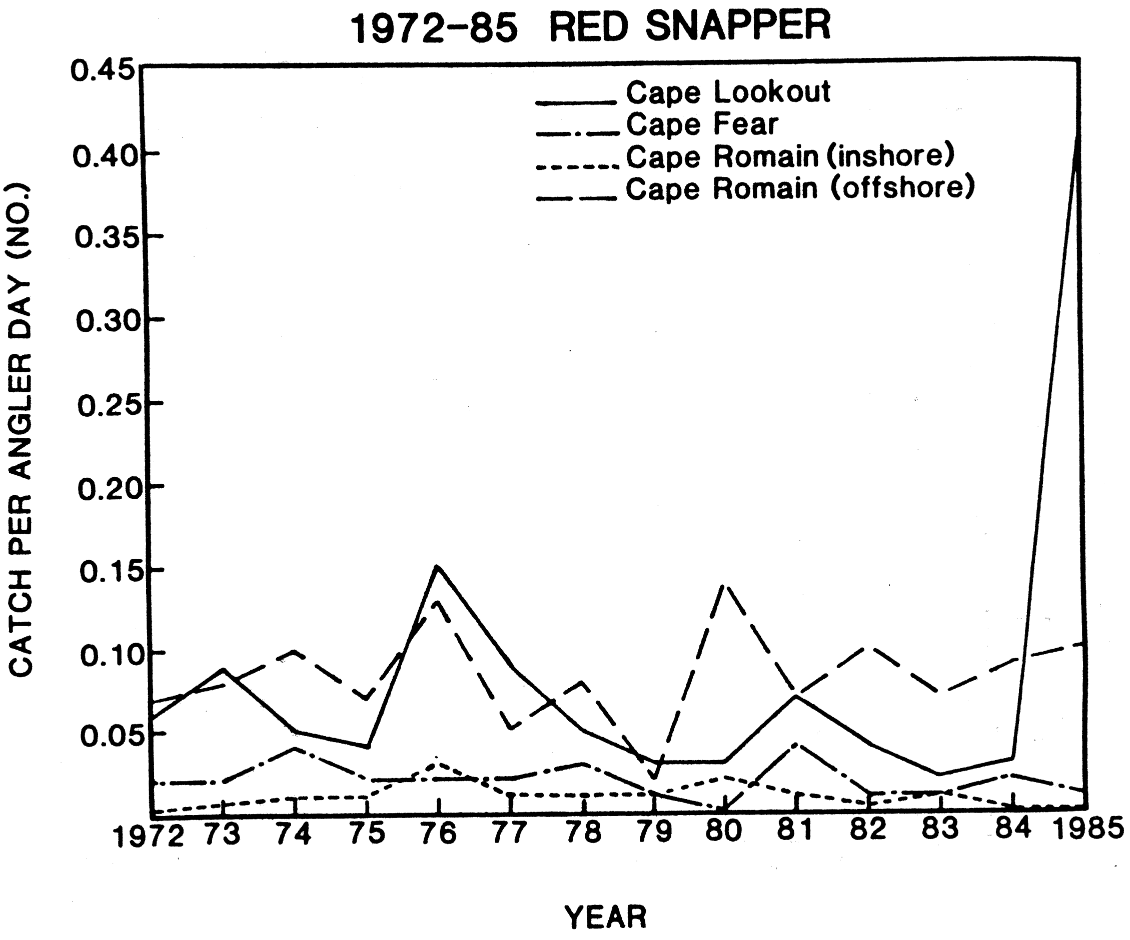

Figure 15. Red snapper total catch per angler day in numbers - 1972-85.

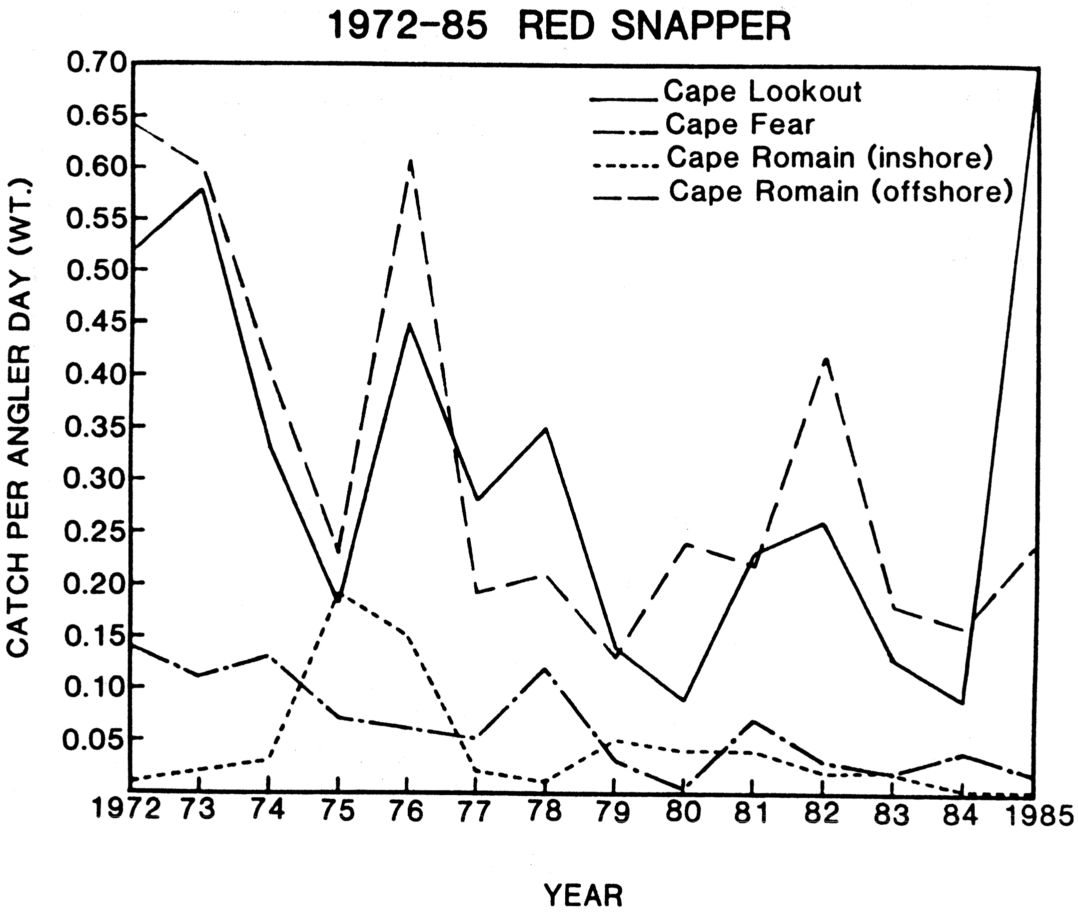

Figure 16. Red snapper catch per angler day in weight - 1972-85.

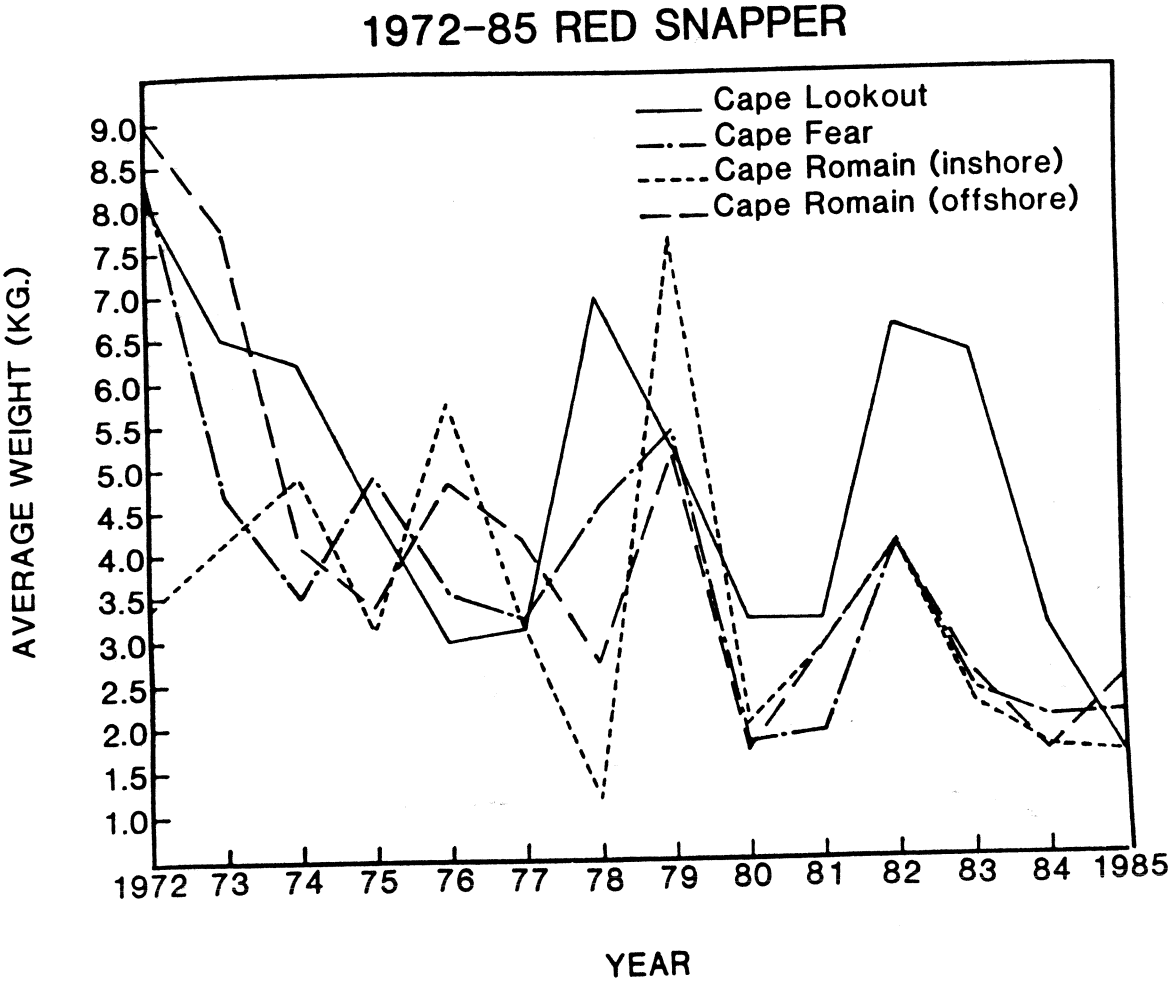

Figure 17. Gag average weight - 1972-85.

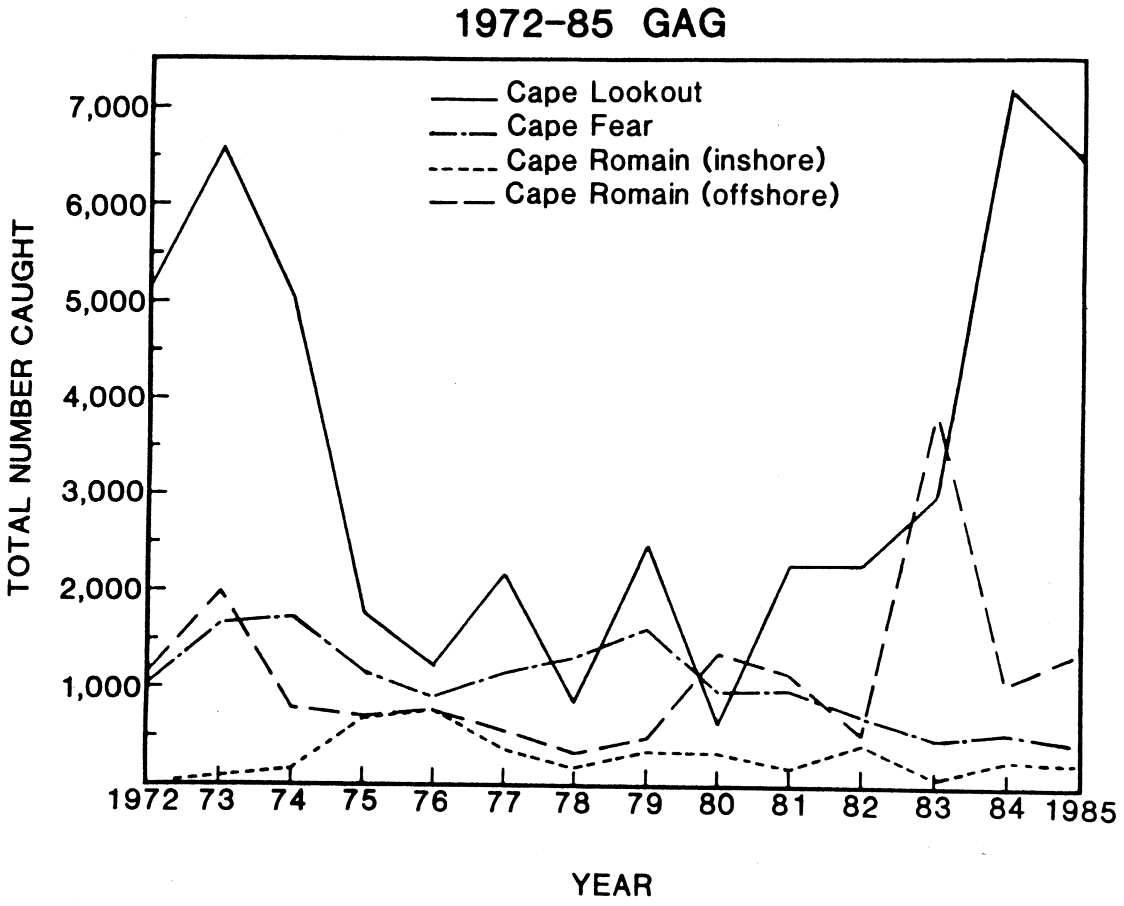

Figure 18. Gag total number caught - 1972-85.

Catch Per Unit Effort

Adjusting total catch for the effort exerted removes most of the few trends evident in the catch data (Figures 19 and 20). For all but the Cape Lookout district catch rates appear to be about the same as they have been for a decade or more, less than 0.1 gag per angler day. A slight decline since 1981 for the Cape Fear region may be of significance. Most extraordinary is the doubling of catch rate for Cape Lookout since 1976-1981 (from about 0.1 to 0.3 gag per angler day). The upturn may not represent a change in the population but instead a shift in fishing area and technique. Anchoring to fish, instead of drifting, produces greater catches of gag and was begun in the late 1970's in the Cape Lookout area. Replacement of older vessels with those faster and better equipped may have allowed the increase. And again effort has been shifted from the outer to the mid-shelf, the most productive for gag.

Mean Weight

Patterns of mean weight change (Figure 21) and are much clearer than catch trends. Despite considerable annual variability mean weights have trended generally downward from 1972 to 1985 for all areas, (although in 1985 weights for Cape Lookout increased to the levels of the late 1970's ≈ 7.5 kg). In the early 1970's, gag averaged 8-12 kg and now average about 3 kg. Some decrease might be attributed to change in fishing area, but the most likely cause is fishing.

Summary

As with red snapper there is little evidence for impaired recruitment of gag, but there is a substantial suggestion of growth overfishing. A mean size of 3 kg is just at or below the size at first capture that allows a good return of yield per recruit. Harvesting fish at this small size represents a substantial departure from what is usually considered good management.

Scamp

Total Catch

Patterns of scamp catches vary by area (Figure 22). Cape Lookout and Cape Romain Inshore catches show no substantial trend and range from about 400 to 1400 fish annually with the Cape Lookout catch rising slightly from 1980 to 1985, and the Cape Romain Inshore catch trending downward to about 100 fish from about 1982 to 1985. Both Cape Romain offshore and especially, Cape Fear produced large catches (around 8000-9000 fish) in the early 1970's and catches for both areas diminished greatly by 1980 to 1000 fish or less. Catches for Cape Romain offshore increased from 1983 to 1985 to about 4000 fish but Cape

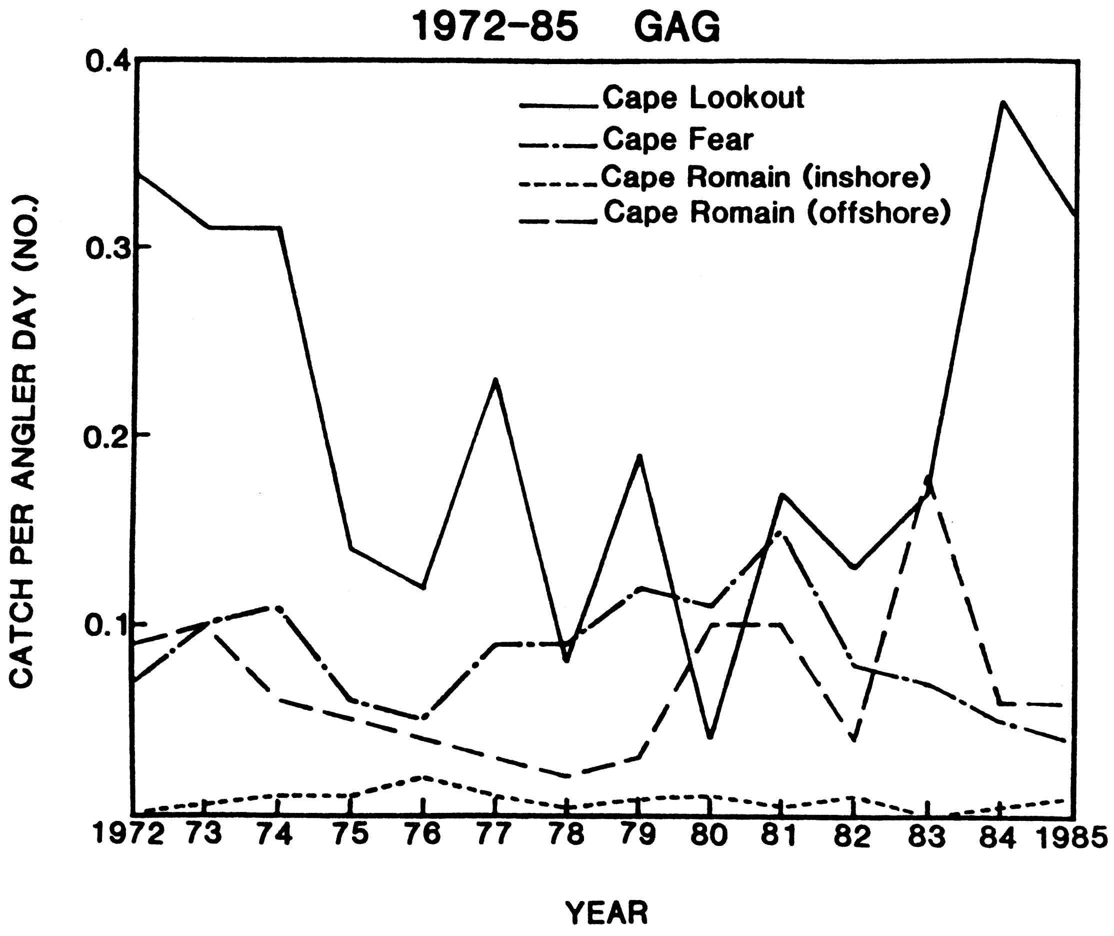

Figure 19. Gag catch per angler day in numbers - 1972-85.

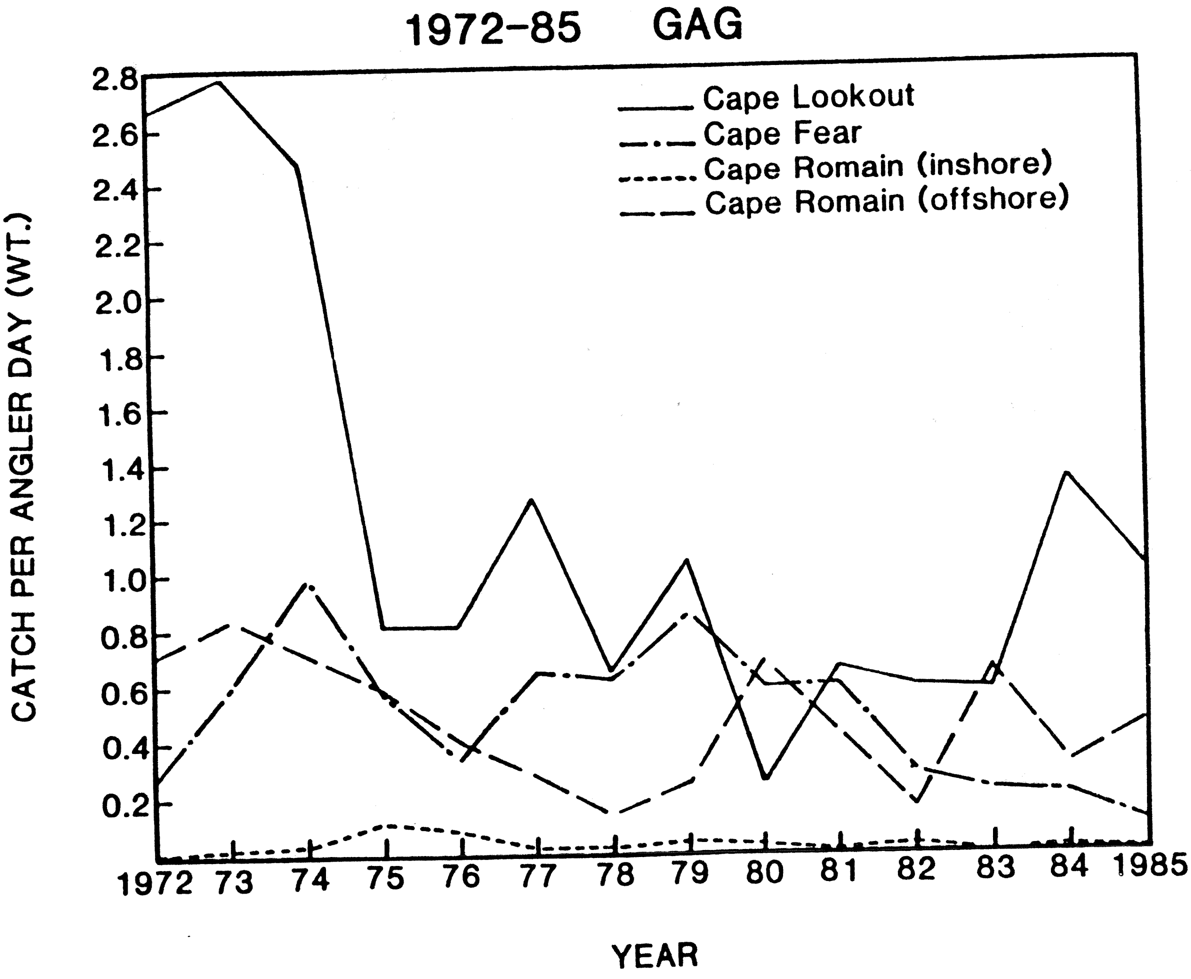

Figure 20. Gag catch per angler day in weight - 1972-85.

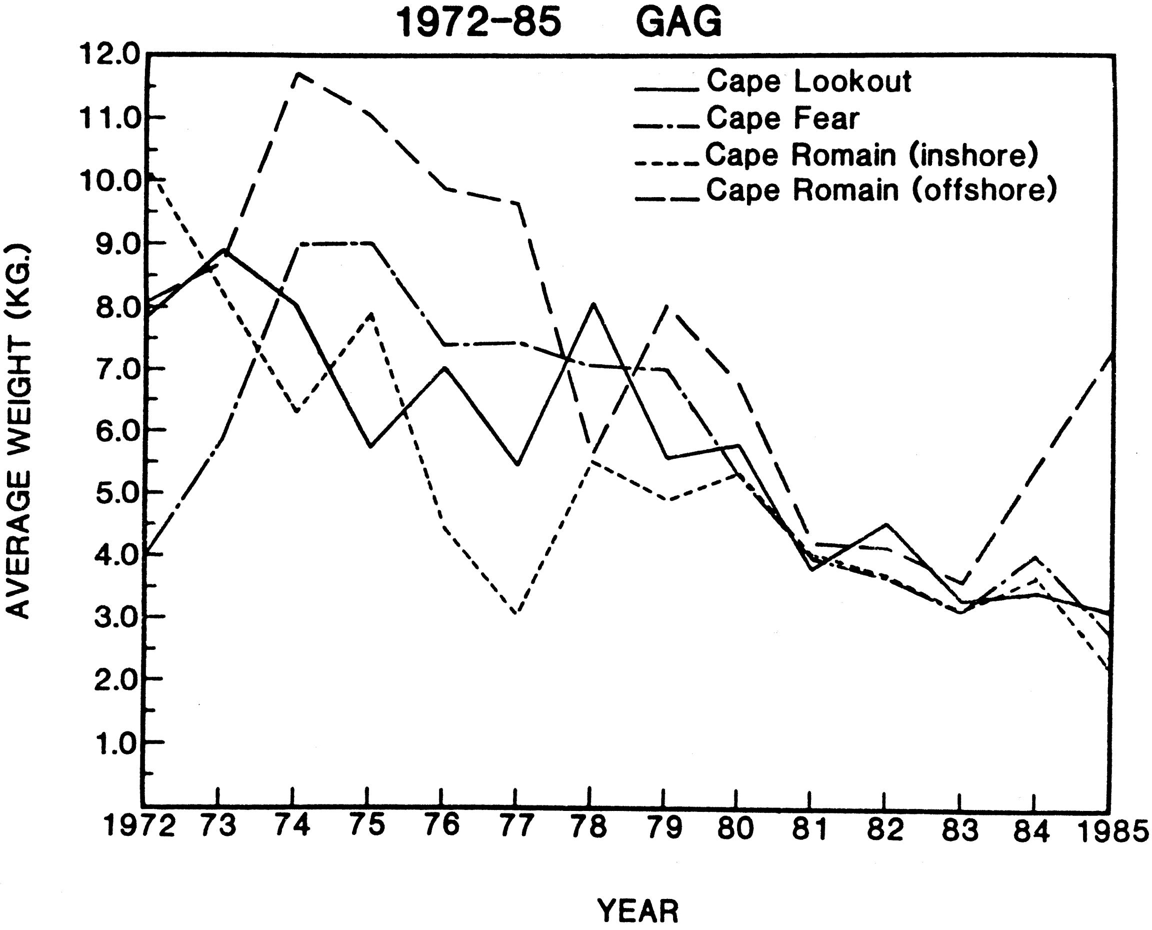

Figure 21. Gag average weight - 1972-85.

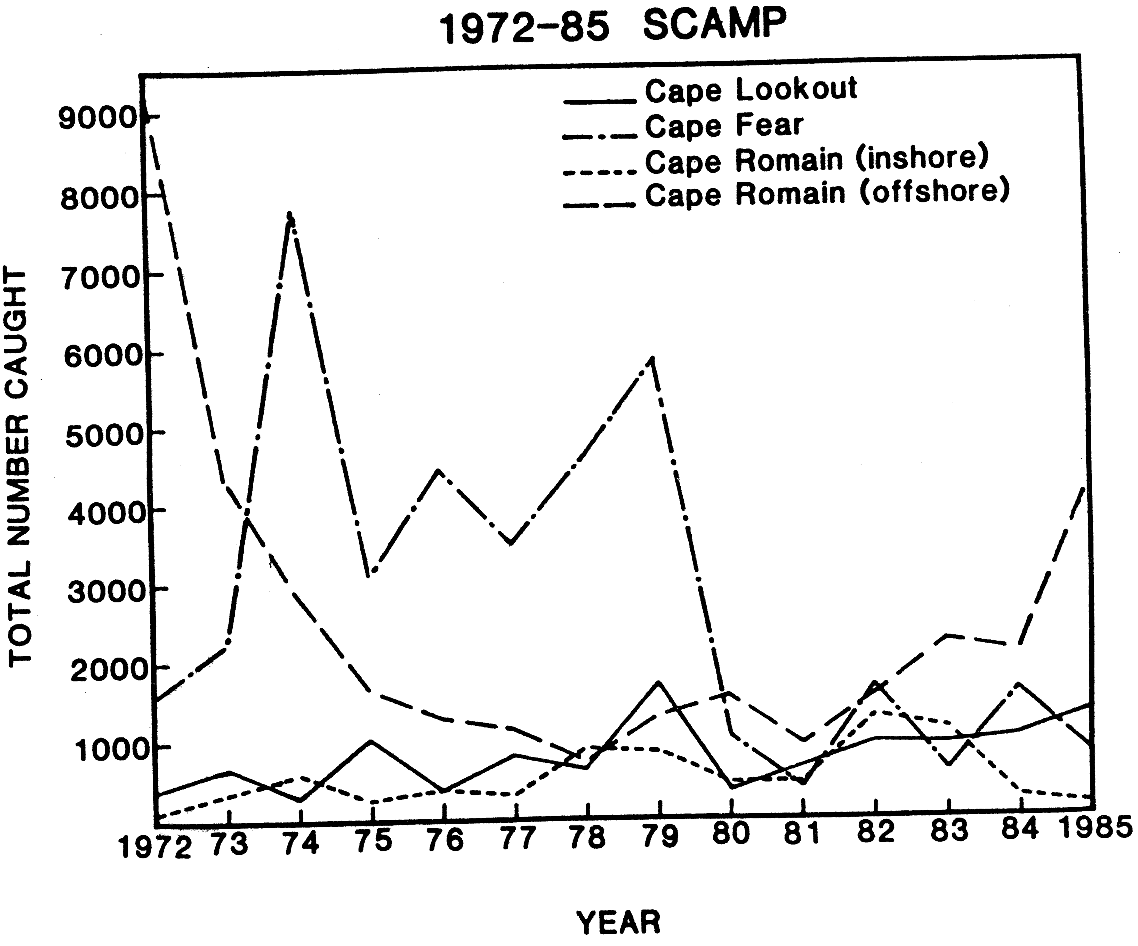

Figure 22. Scamp total number caught - 1972-85.

Fear landings remained low.

Catch Per Unit of Effort

Patterns of CPUE (Figures 23 and 24) mimic those of catch.

Mean Weight

Similar to those of the congeneric gag, mean weights of scamp (Figure 25) have trended generally downward for all areas since the early 1970's and are now around 2.5 kg, half or less of those of the earlier period (4.5 -7.0 kg). Also like those of the gag, mean weights of scamp have become more similar between areas.

Summary

Scamp have been most abundant in the Cape Fear region. Probably the larger catches of scamp made by Cape Romain offshore vessels in the early 1970's also came from the near vicinity of Cape Fear. Fishing on the traditional scamp grounds by Cape Fear vessels continues and may even be more intense now than earlier, but their scamp catches remain low. We believe that the population has been reduced and may have insufficient recruitment. The recent upturn in Cape Romain catches probably results from addition in the Charleston area of long-range offshore vessels that run to areas not previously exploited by headboats or from more intense fishing on the mid-shelf now that snowy grouper populations on the deep shelf are reduced. The diminution of scamp mean size for all areas also raises concern. While the mean size remains above the size at first capture that produces an acceptable yield per recruit, incident age at first capture may be too small.

Speckled Hind

Total Catch

For districts other than Cape Romain Offshore speckled hind are now an incidental catch (about 100 fish per year). While never extremely common, they formerly (early 1970's) appeared regularly in catches of all districts (Figure 26).

The speckled hind were and are more abundant off South Carolina, and the Cape Romain offshore catches in the mid 1980's have rebounded from a low catch of about 600 in 1981 to about 2500, the level of the mid 1970's. Perhaps addition of new long range vessels to the fleet at Charleston is generating this catch by fishing on grounds not previously used heavily by headboats. Populations on the traditional grounds to the north in the Cape Romain Offshore district may be as depleted as those off North Carolina.

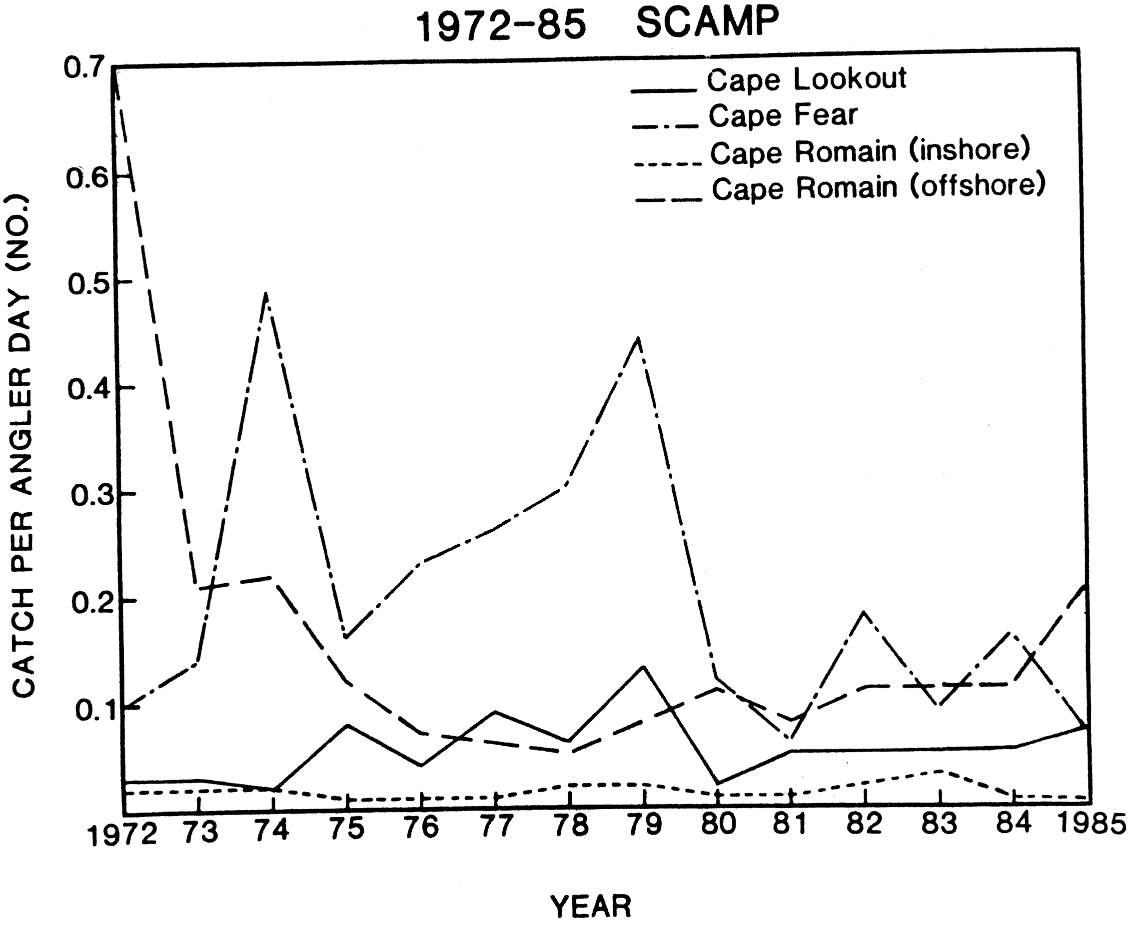

Figure 23. Scamp catch per angler day in numbers - 1972-85.

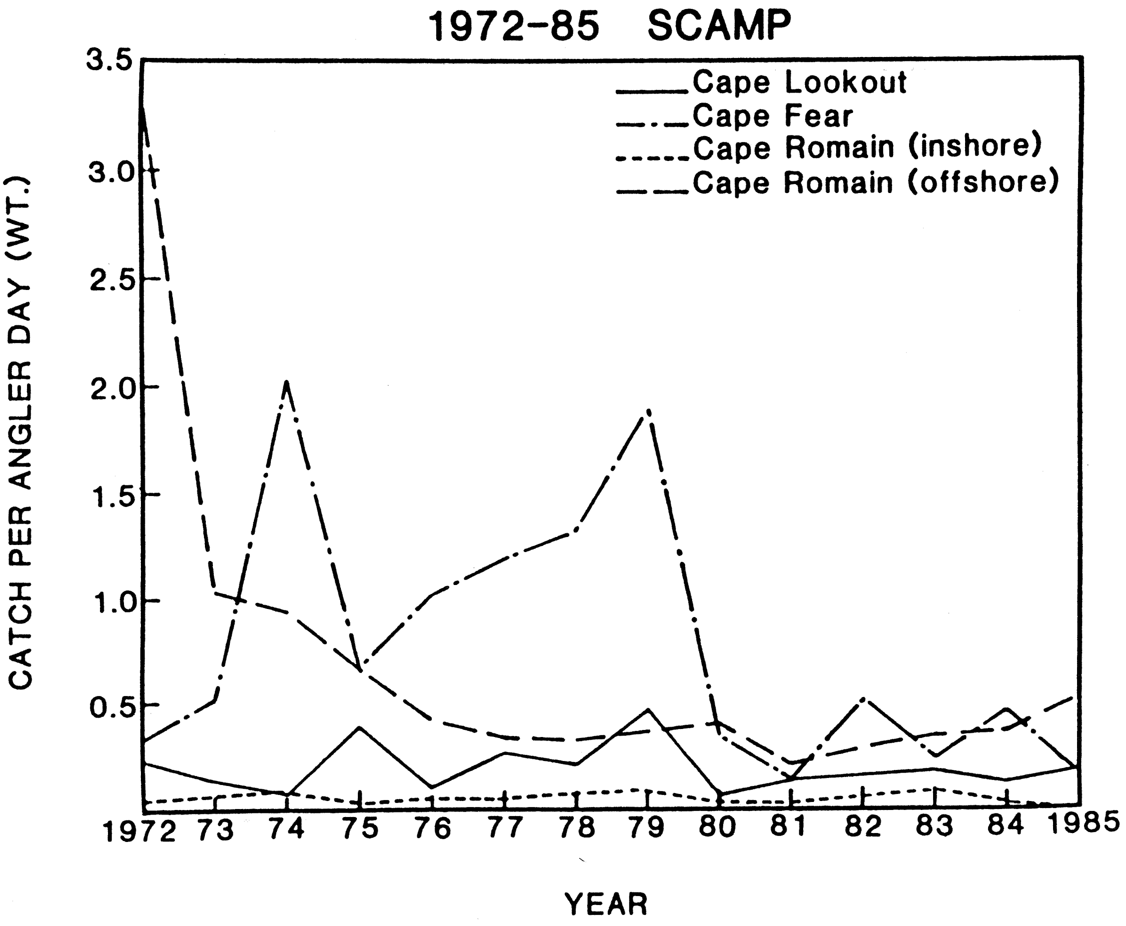

Figure 24. Scamp catch per angler day in weight - 1972-85.

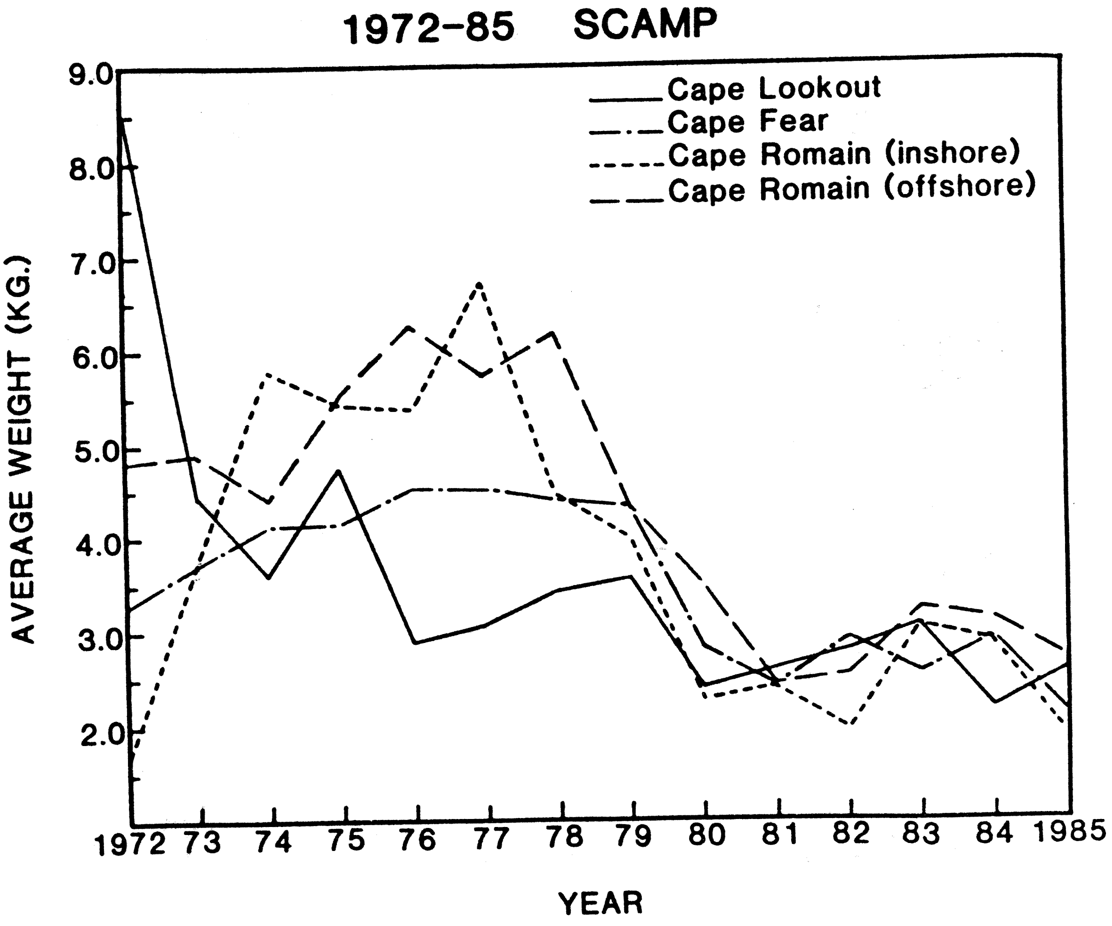

Figure 25. Scamp average weight - 1972-85.

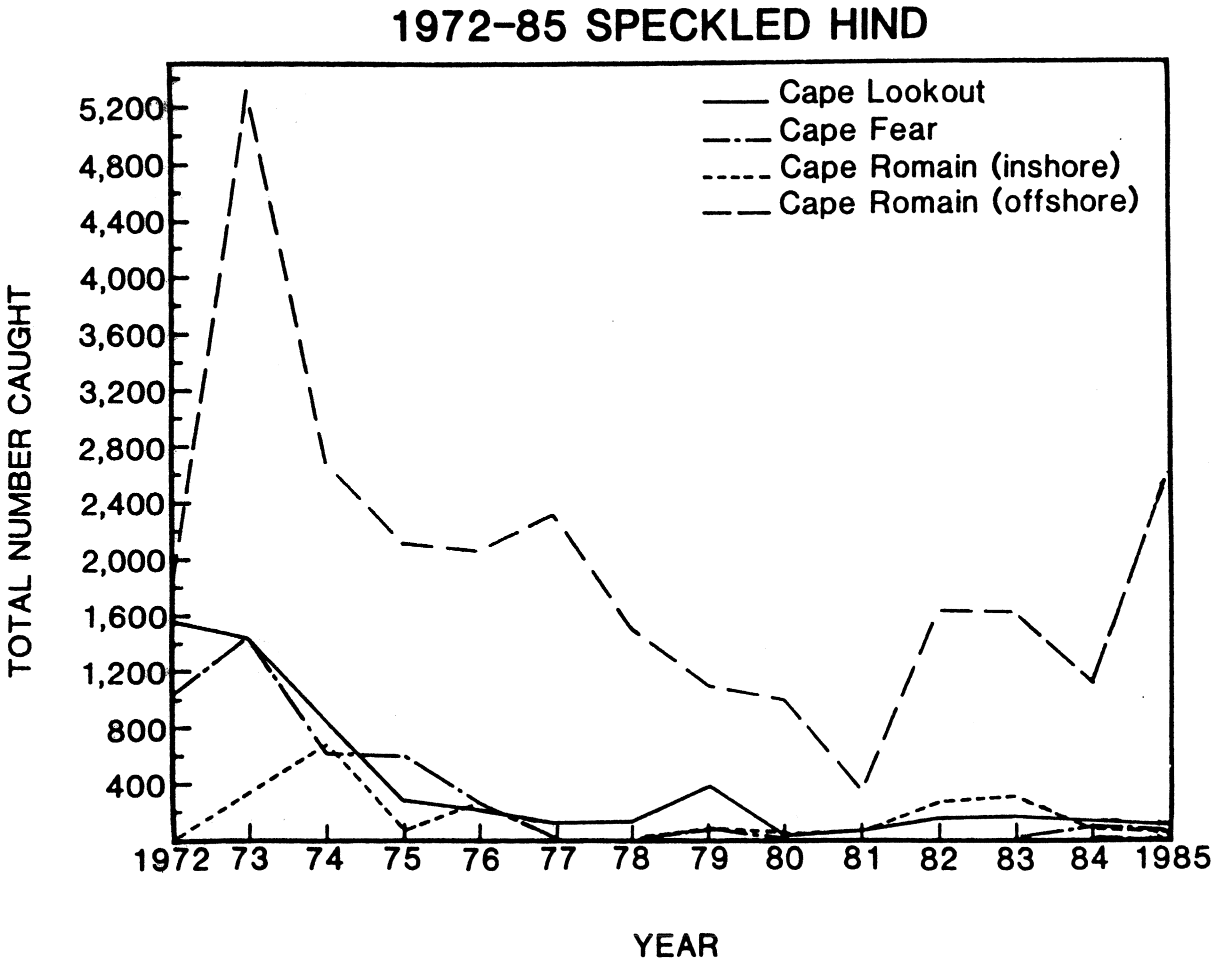

Figure 26. Speckled hind total number caught - 1972-85.

Catch Per Unit Effort

Trends in catch per unit effort largely mimic catch trends (Figures 27 and 28).

Mean Weight

Mean weight of speckled hind fluctuated more erratically than mean weight of any other species examined, (except its congener, snowy grouper), but nonetheless decreased by more than 50% from peak values for all areas (Figure 29). Part of the variability is, of course, attributable to small sample sizes resulting from small catches. For Cape Lookout the decrease (5.4 to 1.0 kg) has been over 80%. Interestingly, the Cape Fear inshore mean weight increased from 1972 to 1976. New vessels in the Cape Fear area during that period increased the take of larger speckled hind. The greatest mean weight by district (for Cape Fear, 2 kg) in 1985 is now equivalent to the size at entry to the fishery that maximizes yield per recruit (Huntsman, et al., 1983). Harvest is now probably too great to allow maximum yield.

Summary

The rarity of speckled hind is illustrated by catch rates that never exceeded 0.25 fish per angler day and except for the Cape Romain Offshore district they never exceeded 0.10. In contrast red porgy catch rates were as high as 10 per angler day and rarely were less than 1.0 for the poorest producing district. Speckled hind were generally large, apparently aggressive and solitary, predators that were often among the first fish taken at each episode of fishing a live-bottom reef. The consequence of the behavior of this relatively rare high-order predator appears to have been its rapid removal from Carolina (especially North Carolina) reefs accessible to headboats. Certainly off the Carolinas the animal was at the northern limit of its range, and might have been expected to be rare and easily reduced. But other reef species remain abundant despite reaching their range limits off North Carolina. And despite being at the limits of its distribution, the speckled hind produced its largest known specimen (1096 mm, total length; 29.0 kg) off North Carolina.

The speckled hind was a significant trophy. Today as a rare animal of only modest size the species no longer provides the angler gratification and incentive for headboat patronage that it did prior to the mid 1970's.

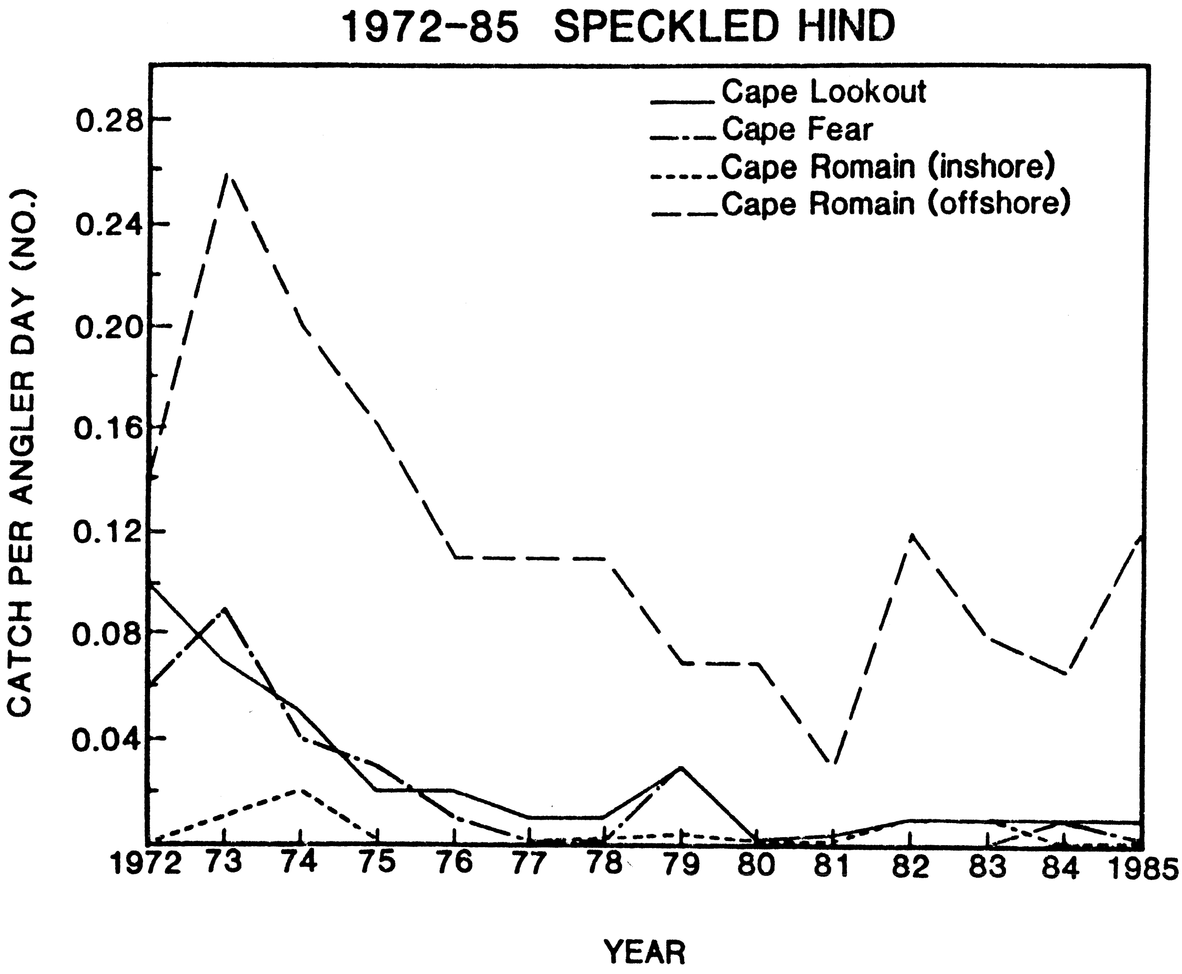

Figure 27. Speckled hind catch per angler day in numbers-1972-85.

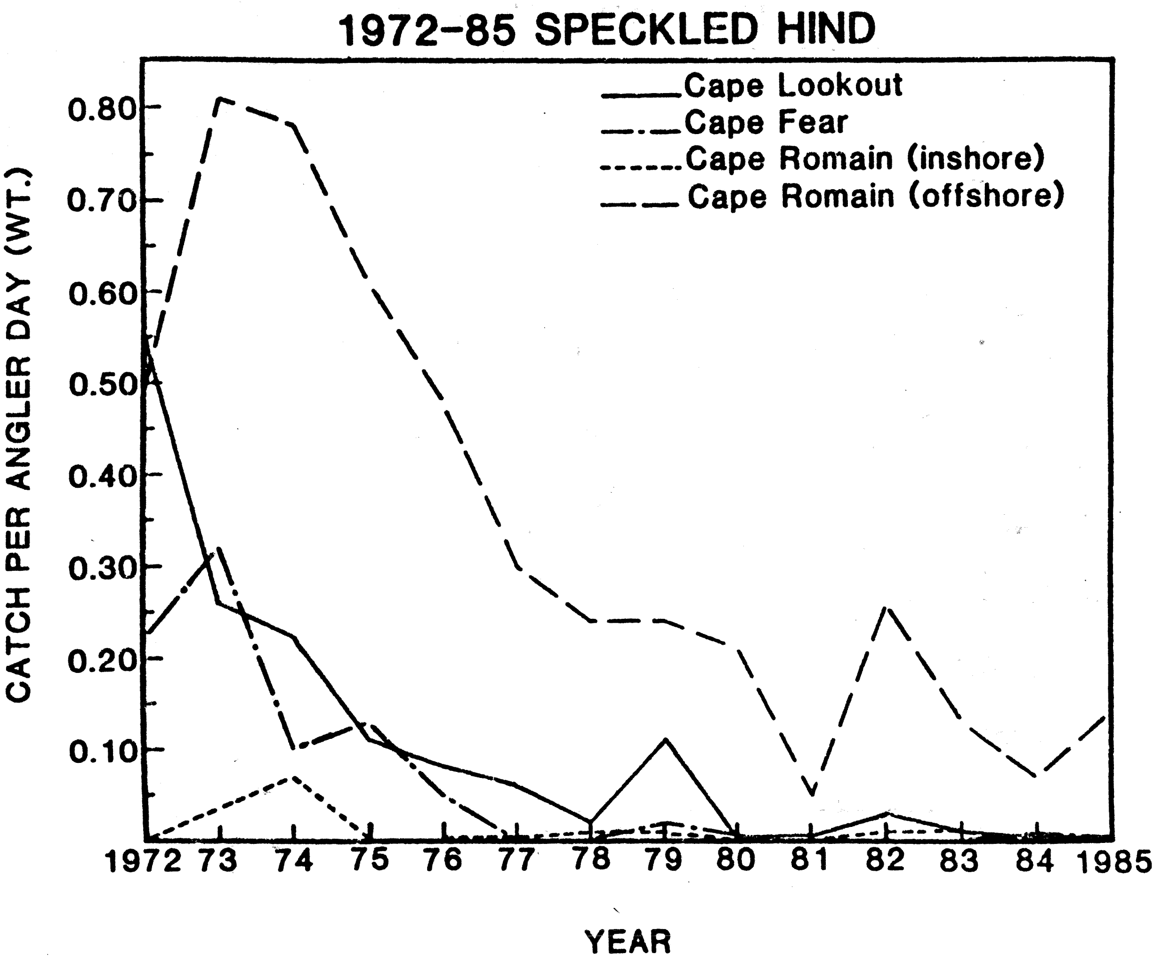

Figure 28. Speckled hind catch per angler day in weight-1972-85.

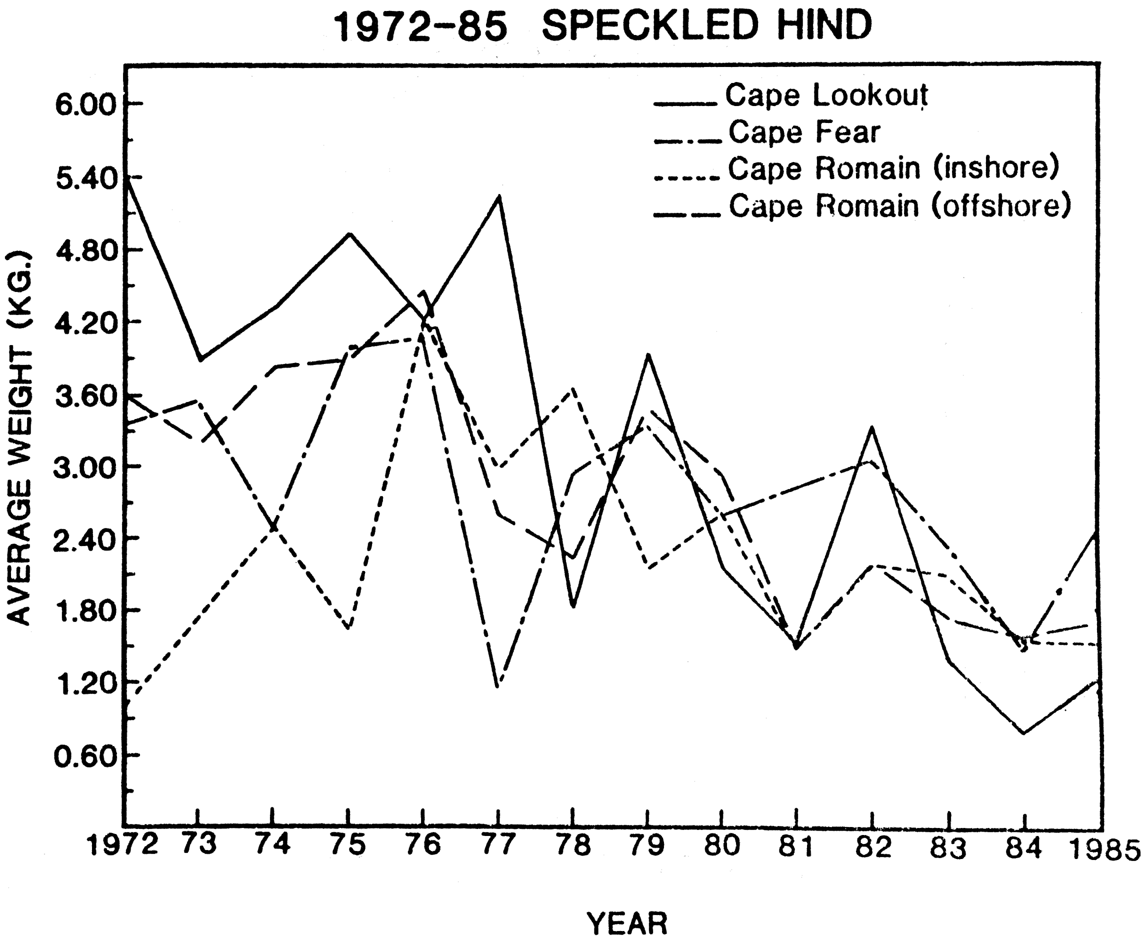

Figure 29. Speckled hind average weight - 1972-85.

Snowy Grouper

Total Catch

Like other groupers, snowy grouper have been scarce numerically but important in providing weight and trophy value to the catch. Only in the Cape Romain offshore district have catches ever exceeded 1000 fish per year and there have fluctuated up to >2000 fish on several occasions (Figure 30). The Cape Lookout catches of 1972-74 quickly fell as the snowy grouper fishing area (approximately 1x5 km) known and available to headboat operators was depleted. Discovery and depletion of other small areas accounted for periodic rises and falls in the catch until the 1980's when operators ceased intense pursuit of snowies. Snowy grouper occupy only deep (>80 m) areas far (≈80 km) offshore that are subject to strong and unpredictable currents. Consequently, fishing for them is expensive, troublesome (much tangling) and chancy because currents that preclude fishing are discoverable only after the 80 km trip to the grounds. Thus, snowy grouper fishing, when possible, must be extremely productive to maintain operator interest.

Catch Per Unit Effort

Catch per unit effort mimics total catch (Figures 31 and 32).

Mean Weight

Mean weight on the headboat grounds of importance has diminished by 50% or more (Cape Lookout 5.0 to 1 kg, Cape Romain offshore 8.0 to 1.5 kg) (Figure 33). In the Cape Lookout area the catch is now predominantly of juveniles.

Summary

Only the offshore areas of Cape Romain and Cape Lookout have been consistent producers of snowy grouper and the peak years for Cape Lookout catches were prior to and during the first year of our survey. Snowy grouper are now so scarce in the Cape Lookout grounds that headboat operators have ceased to pursue them with vigor. Thus the decline in catch overestimates the population decline in recent years. Numbers taken in the Cape Romain district remain approximately constant suggesting no major decline in numbers there. But grounds used by Murrell's Inlet headboat operators such as the Devil's Hole off Georgetown are no longer productive, and the catch has been sustained by increased catches of Charleston vessels occupying new grounds. The decline in mean weight for Cape Lookout and Cape Romain is striking and has two interesting corollaries. First is that the fish on the usual fishing grounds for adults are smaller now than were almost any fish taken on those grounds in the early years of the fishery. This observation suggests a hypothesis

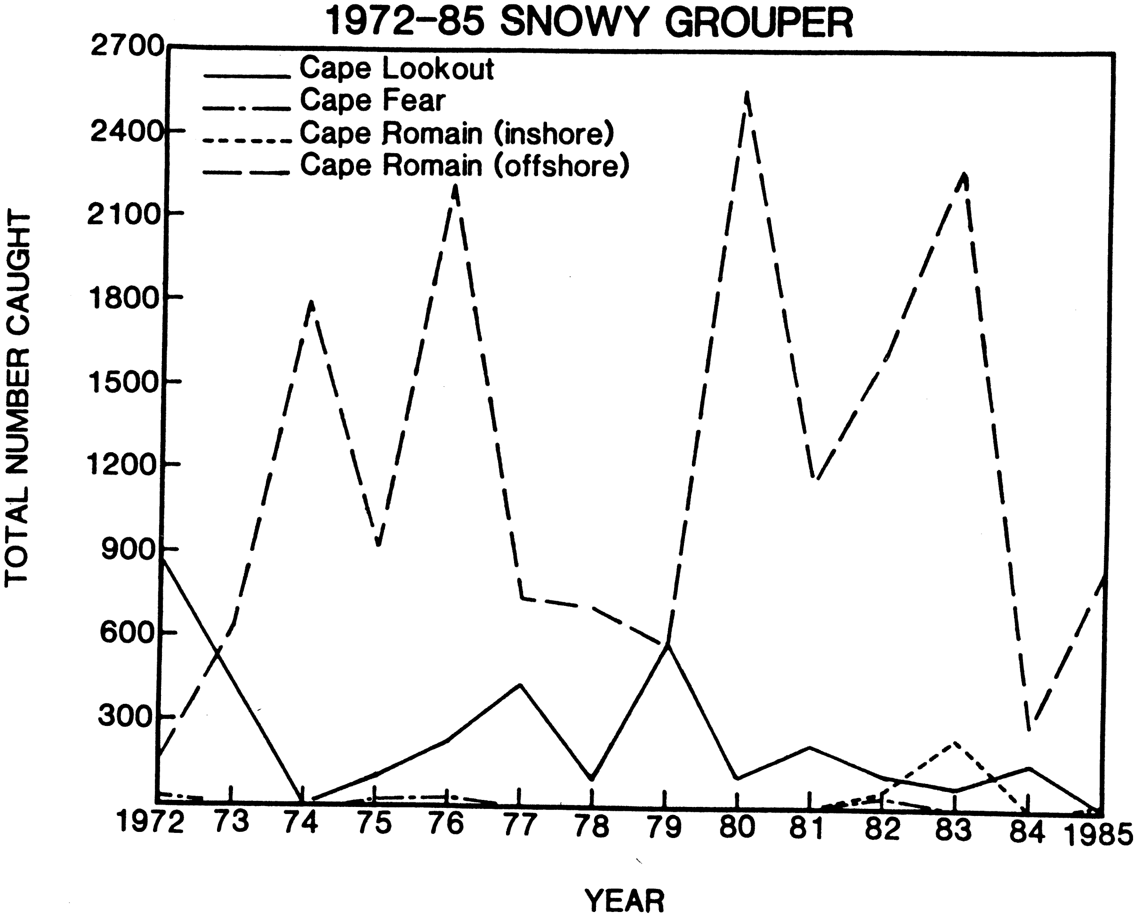

Figure 30. Snowy grouper total number caught - 1972-85.

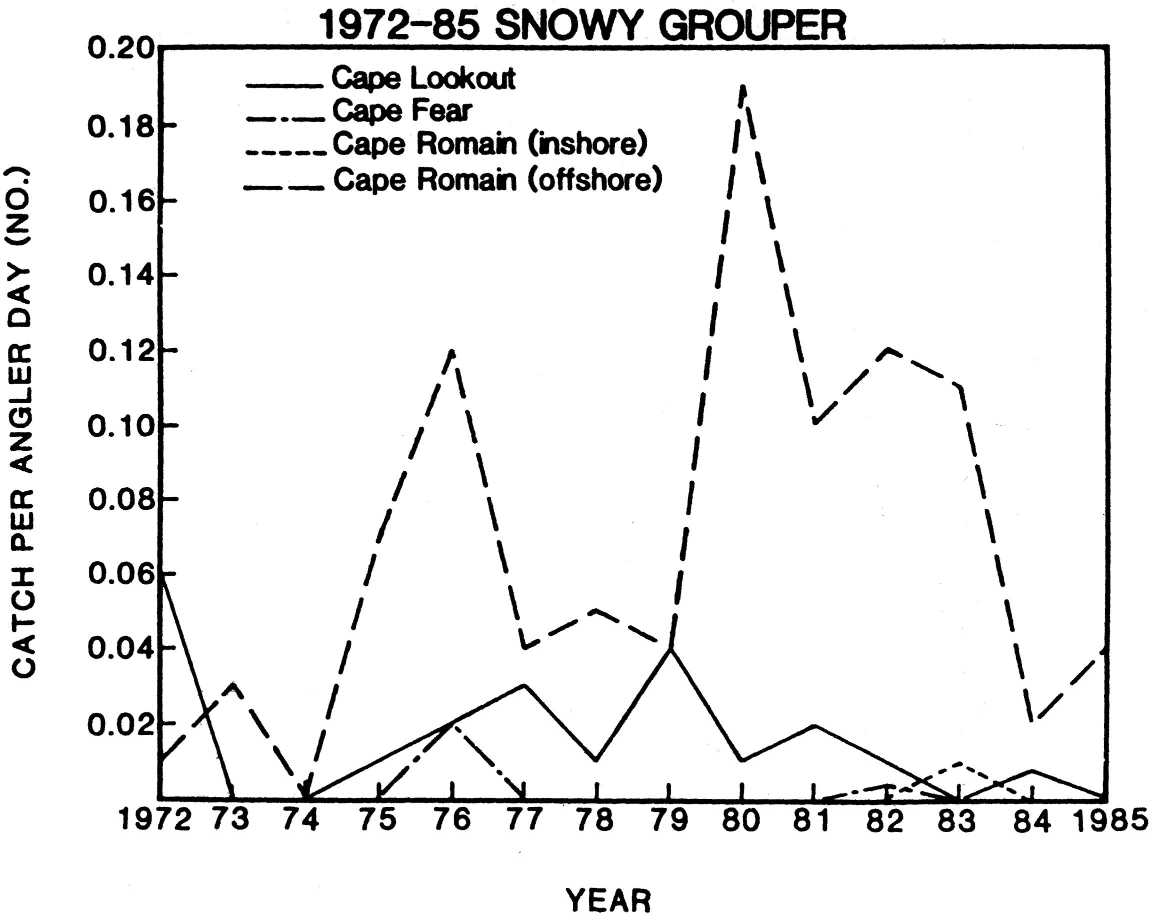

Figure 31. Snowy grouper catch per angler day in number- 1972-85.

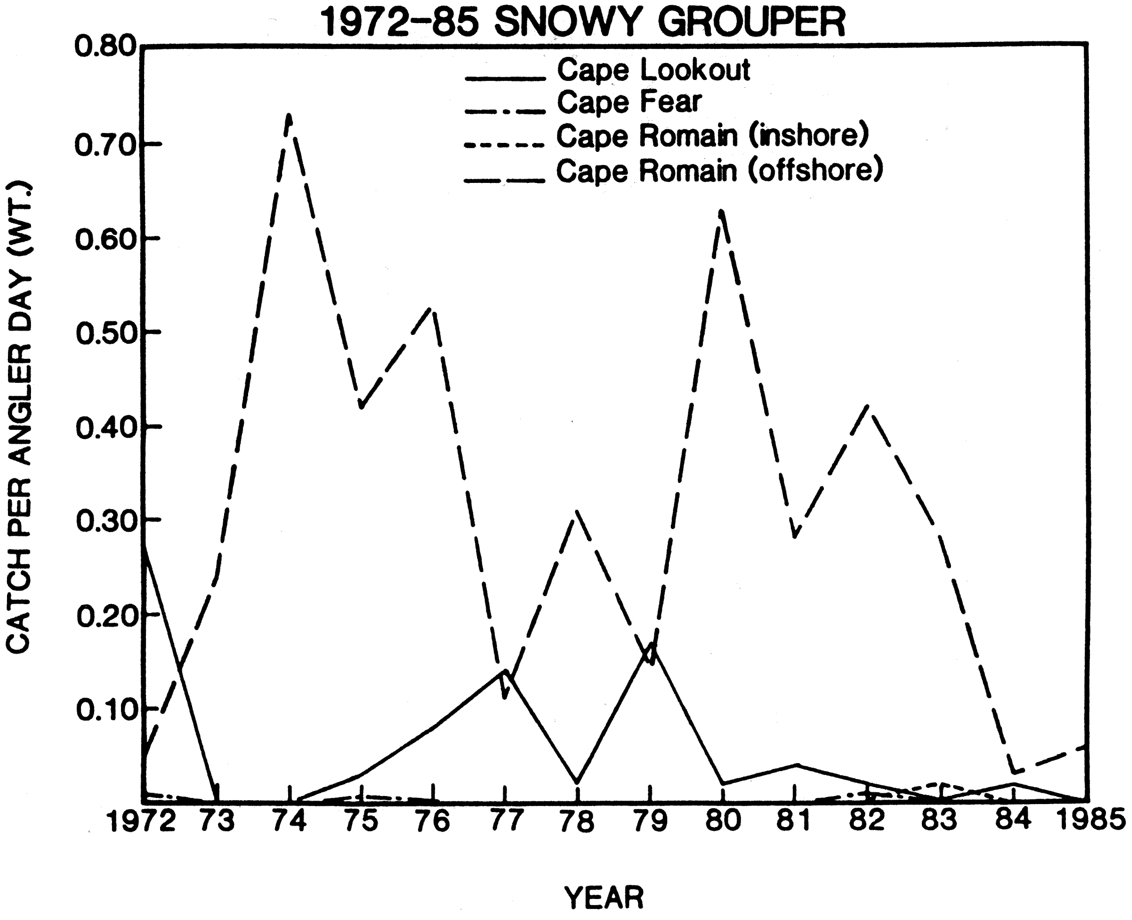

Figure 32. Snowy grouper catch per angler day in weight-1972-85.

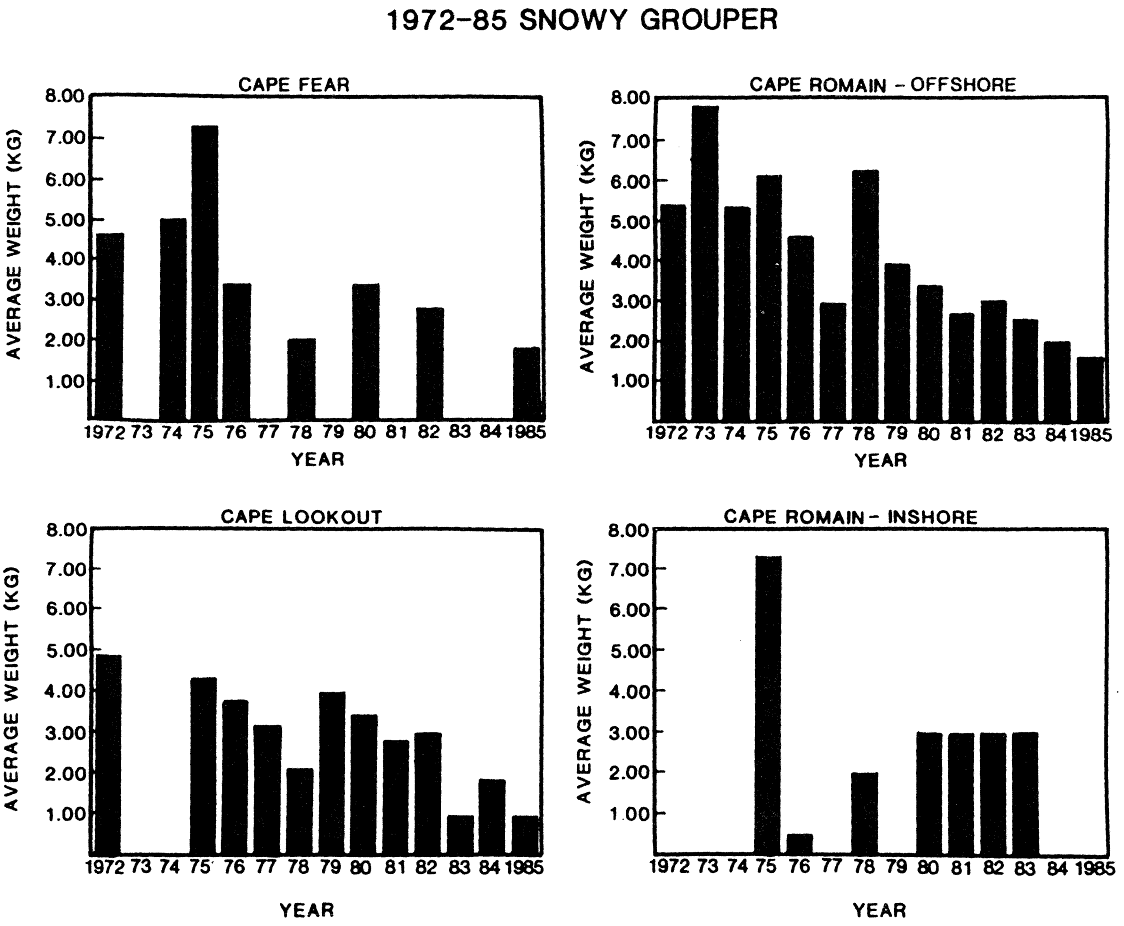

Figure 33. Snowy grouper average weight - 1972-85.

that populations of old large snowy grouper somehow prevent the simultaneous residence of small fish. The second corollary is that small (< 1 kg) juvenile snowy grouper now appear moderately frequently in catches from mid depths, but did not in the 1970's. It appears that a new pattern of recruitment exists. Present mean weights of 1.7 and 1.0 kg approximate the sizes of fish 3 and 4 years old, both of which are substantially below the age of first entry to the fishery required to maximize yield per recruit. Thus it appears that snowy grouper on the headboat grounds are subject to substantial growth overfishing.

Gray Triggerfish

Total Catch

Prior to the early 1970's fishermen and headboat operators, out of ignorance, avoided and discarded gray triggerfish. Widespread appreciation of gray triggerfish and catches (Figure 34) began in 1973 and have decreased steadily in the Cape Fear and Cape Romain inshore districts to the point of insignificance (< 500 fish). Cape Lookout catches interestingly fluctuated from 3000 to 8000 fish from 1973 to 1983 and then jumped to almost 10,000 fish by 1985.

Catch Per Unit Effort

Catch per unit effort mimics catch (Figures 35 and 36).

Mean Weight

There have been no important changes in mean weight (Figure 37).

Summary

Catch data for gray triggerfish are anomalous. The usual pattern for reef fish has been a major decrease in mean weight, often in conjunction with a drop in catch and catch per unit effort. For triggerfish numbers caught decreased but not mean weight. This situation might have arisen from an increase in the abundance for a co-occurring species, such as vermilion snapper for which catches have increased in the Cape Romain offshore district. By competing for the time and (because the vermilion is a preferred species) attention of headboat operators, vermilion snappers could have created a situation in which catch, but not mean weight of another species, has declined.

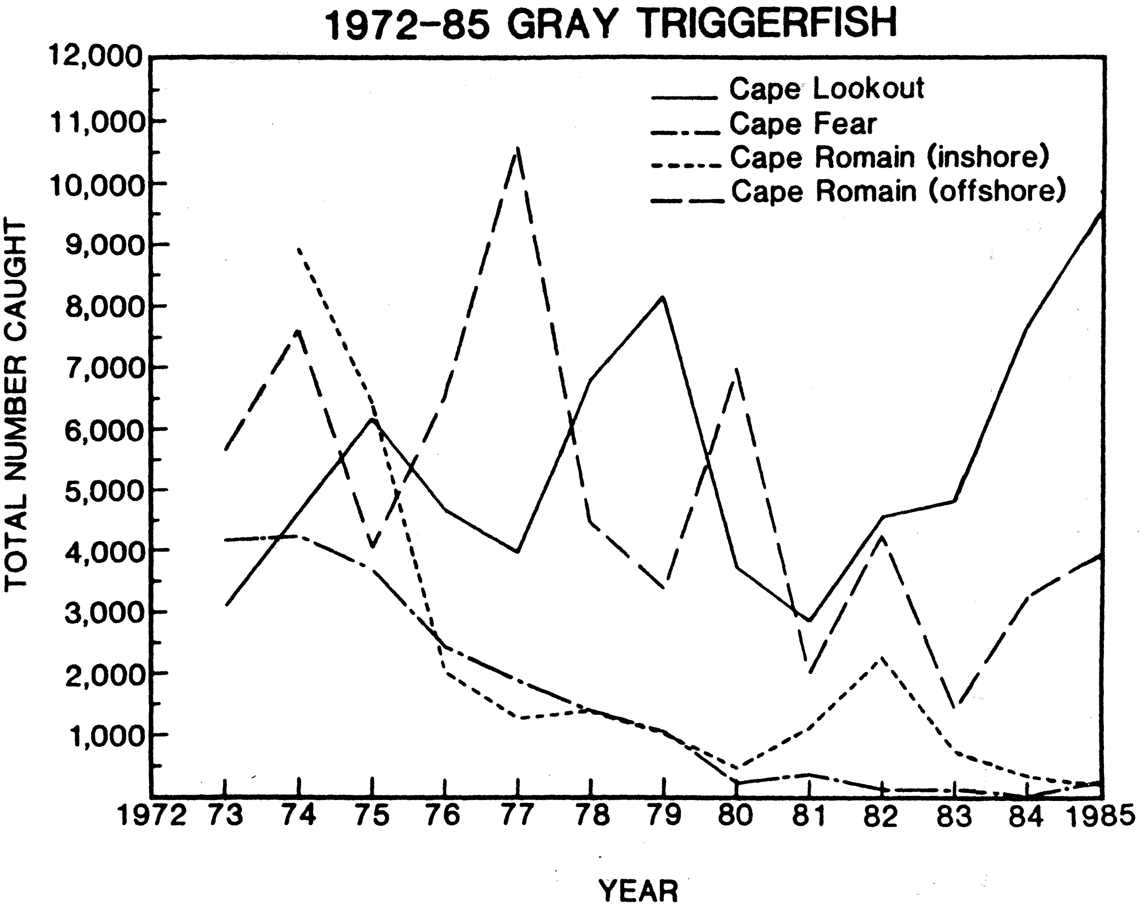

Figure 34. Gray triggerfish total number caught - 1972-85.

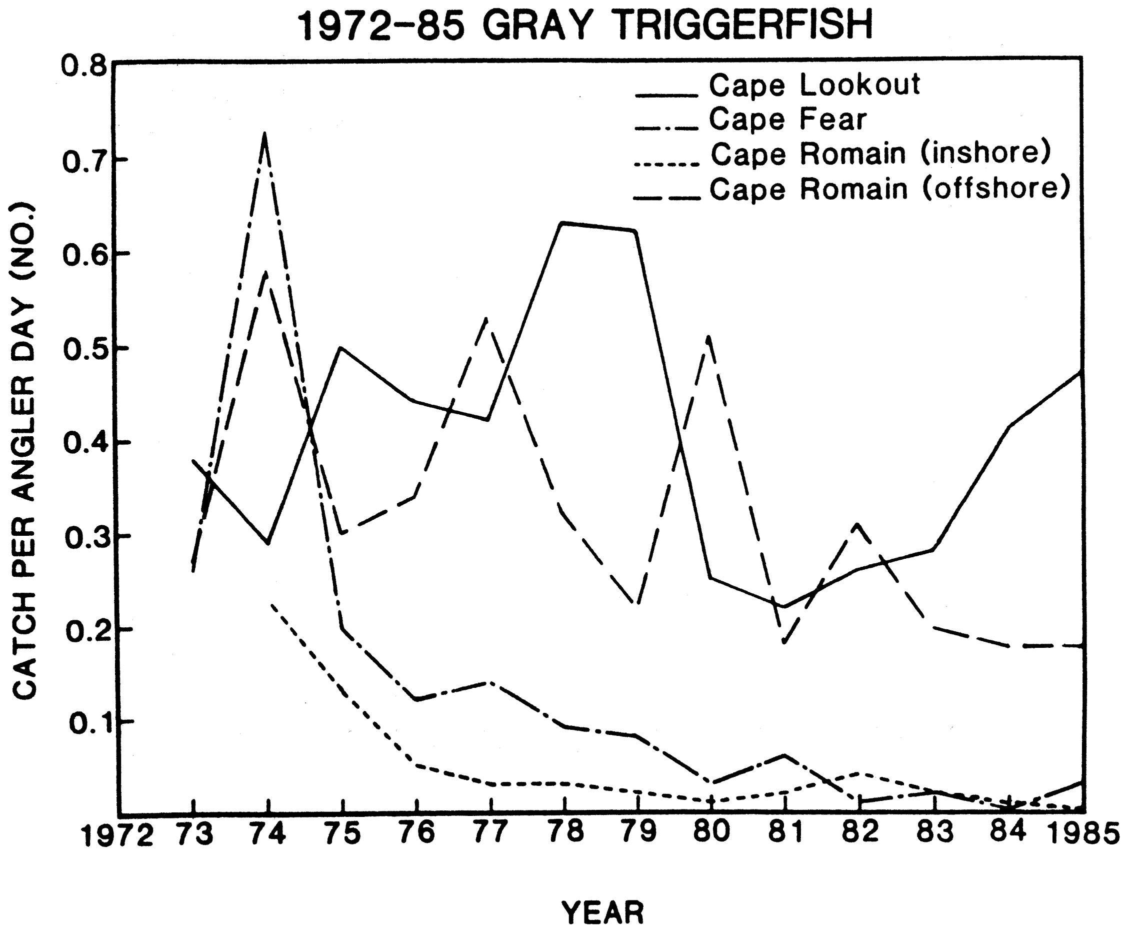

Figure 35. Gray triggerfish catch per angler day in number- 1972-85.

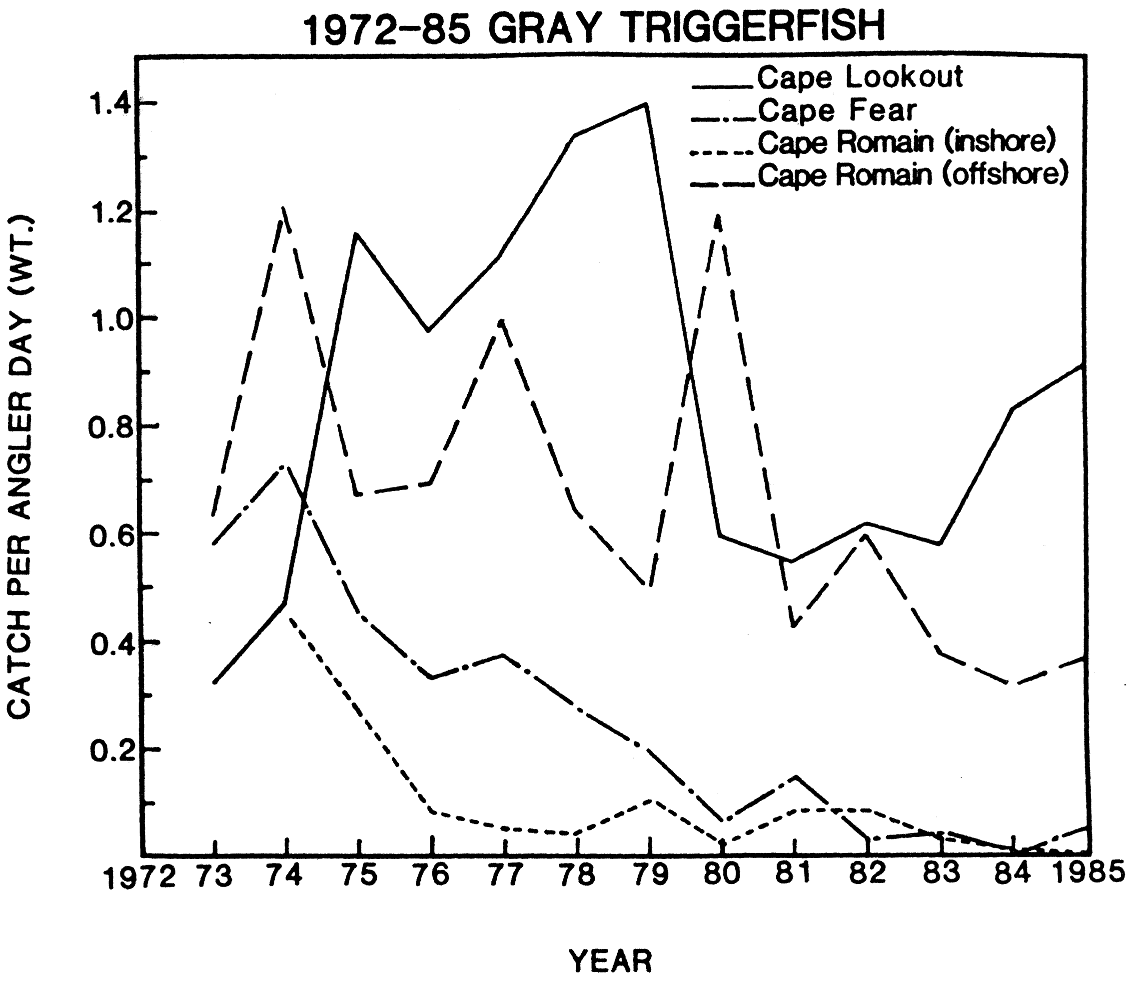

Figure 36. Gray triggerfish catch per angler day in weight-1972-85.

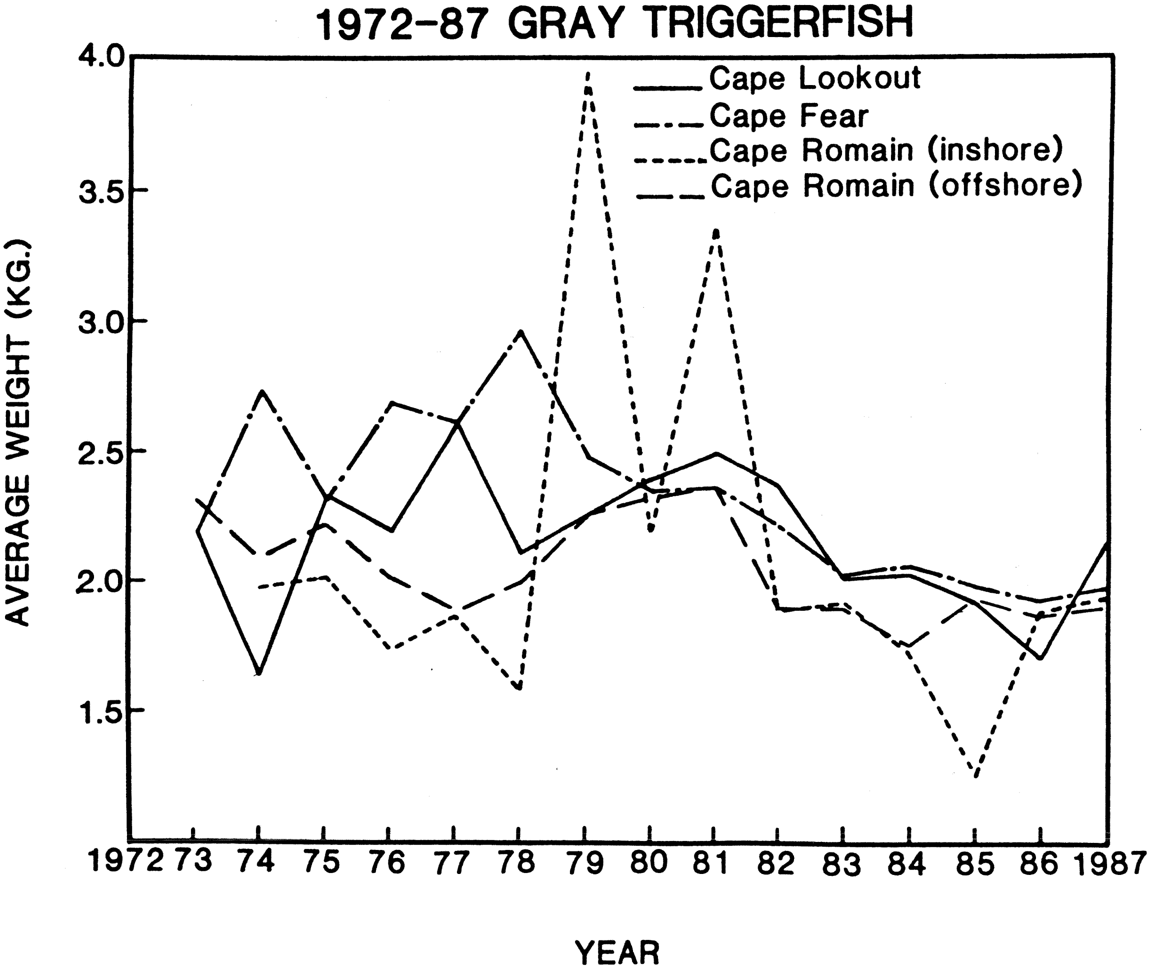

Figure 37. Gray triggerfish average weight - 1972-85.

Black Sea Bass

Total Catch

No appreciable trend in catch in numbers occurs in any district except Cape Romain offshore (Figure 38). There a general increase (especially from 1979 on) probably results from greater use of near shore grounds by the offshore fleet as a response to fuel cost. Early (1975-76) decreases in the Cape Fear catches are not readily explained. The changes in Cape Lookout catches can be attributed largely to reduction of effort (Table 1) for black sea bass.

The Cape Romain inshore catch (number) is almost an order of magnitude greater than that for any other area. A large number of vessels which concentrate almost exclusively on small black sea bass on nearshore grounds operate in the Myrtle Beach, S.C. area.

Catch Per Unit of Effort

CPUE patterns (number) (Figure 39) mimic those of catch (number) but differences in catch by district are reduced to a factor of three to four, except for those catches between Cape Romain inshore and offshore which remained at ten. Catches per unit effort by weight are far more similar among districts and vary by a maximum factor (in 1985) of four. The differences in patterns of CPUE by number and by weight results from large, and compensating differences in mean weight. No substantial trends in CPUE (weight) occur (Figure 40). There appear to be slight decreases for the Cape Lookout, Cape Fear and Cape Romain Inshore districts. Removing the effect of effort moderates apparent trends in the catch, especially for Cape Lookout and Cape Fear.

Mean Weight

Mean weights of black sea bass (Figure 41) for the Cape Lookout and Cape Romain offshore districts have fluctuated greatly, but appear to have decreased little or none. But there appear to be substantial changes in mean weight for Cape Fear and Cape Romain Inshore districts. Averaging about 0.4 kg or greater from 1974 to 1978, black sea bass now weigh an average 0.2 kg in the Cape Romain Inshore district and about 0.25 kg in the Cape Fear District.

Summary

There is little evidence that the numbers of sea bass are reduced in any district and recruitment apparently remains adequate, but harvest is sufficiently intense to reduce mean weights for Cape Romain Inshore and Cape Fear to approximately half the values observed in the early 70's. Catch per unit

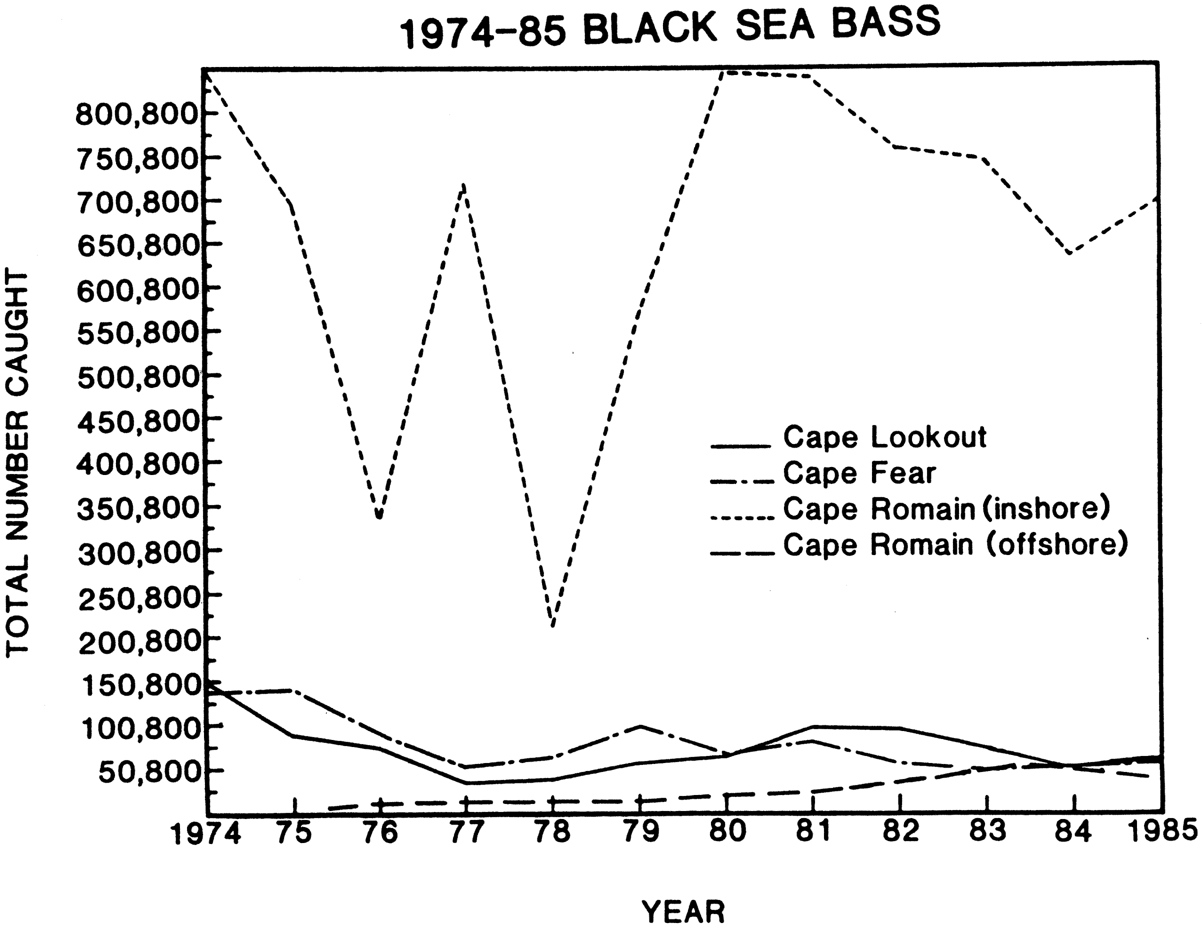

Figure 38. Black sea bass total number caught - 1974-85.

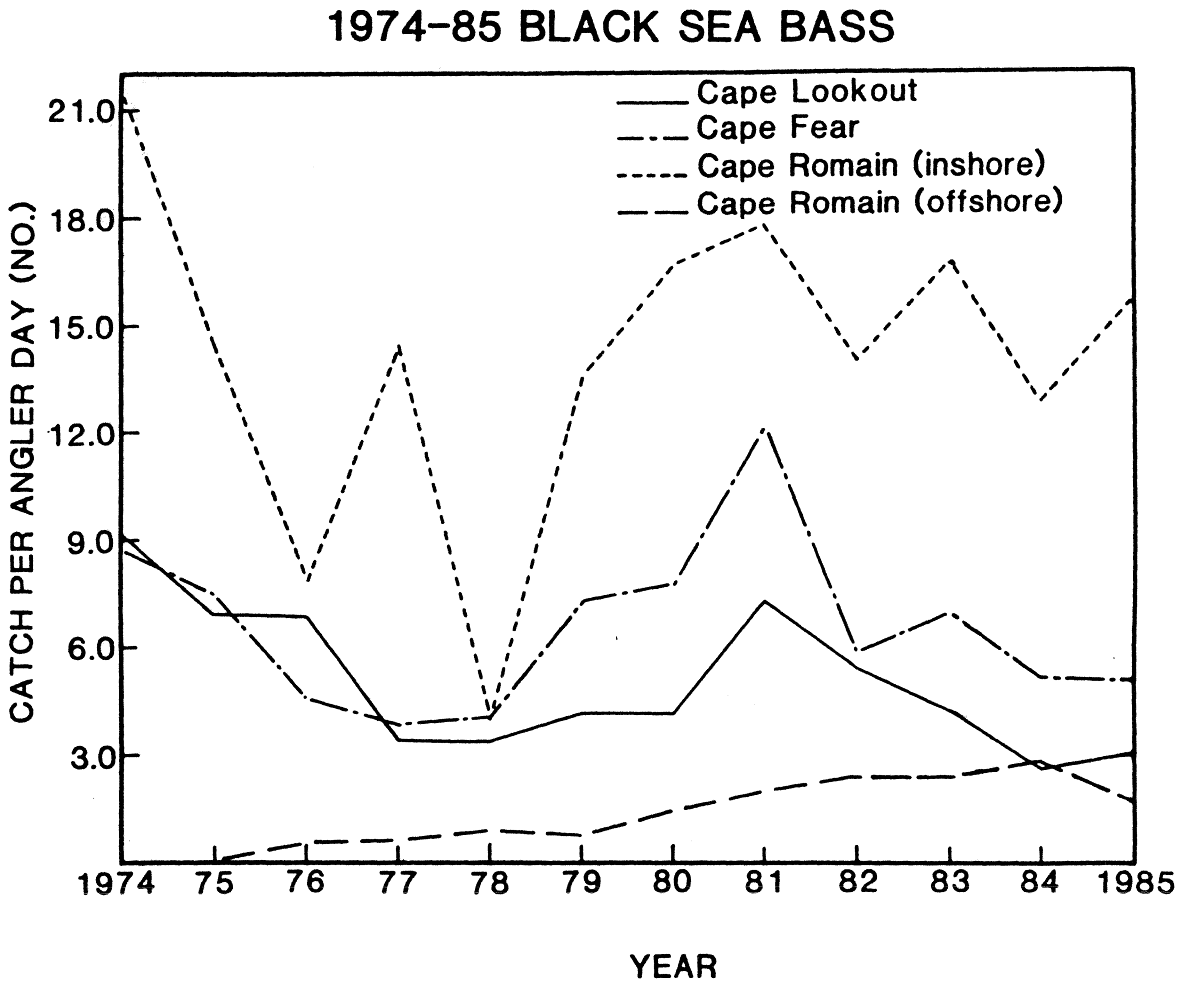

Figure 39. Black sea bass catch per angler day in numbers-1974-85.

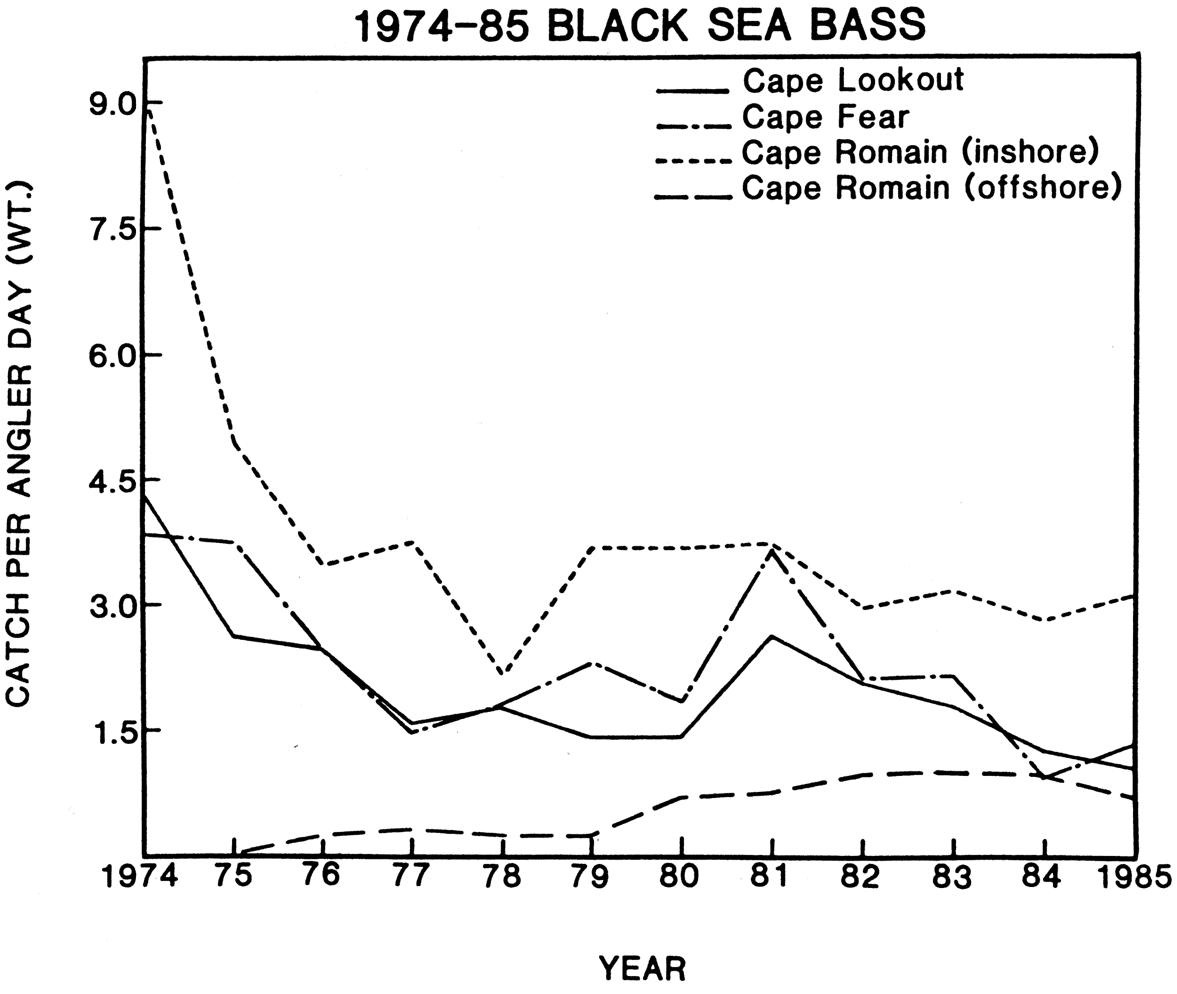

Figure 40. Black sea bass catch per angler day in weight-1974-85.

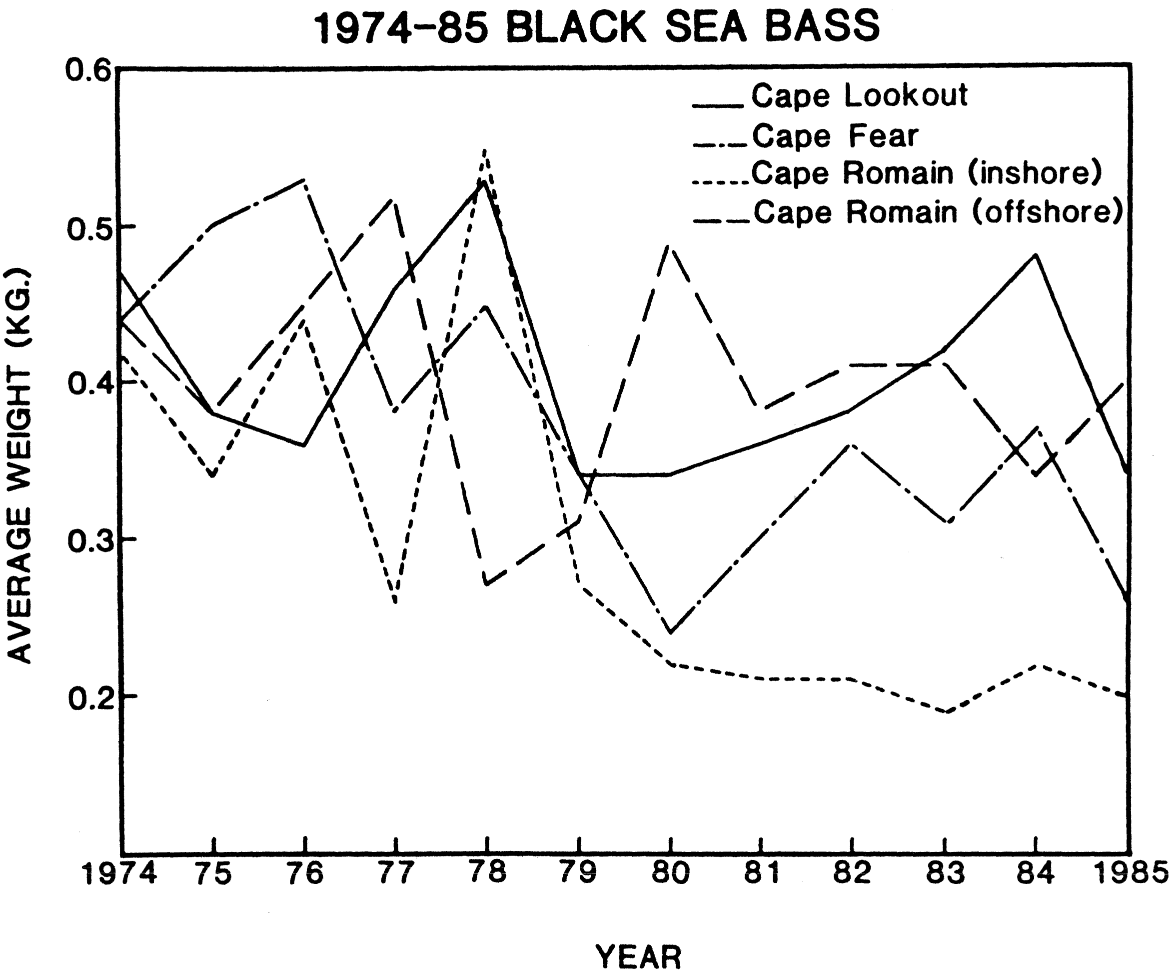

Figure 41. Black sea bass average weight - 1974-85.

effort (weight) has changed in proportion to changes in mean weight. Mean size is now only slightly greater than the size at first entry required to produce adequate yield per recruit (225 mm) (Huntsman and Manooch, 1979). A minimum size limit (imposed by the South Atlantic Fishery Management Council in 1983) theoretically prevents taking of any black sea bass less than 200 mm total length in federally controlled waters. Thus yield per recruit should be partially protected.

SUMMARY AND CONCLUSIONS

Major changes in headboat catches occurred during our observations. While the changes might reflect occurrences that some would say are benefits, from the point of view of the individual headboat angler, these changes are almost certainly detrimental. Mean weight per individual fish has decreased in virtually all areas for eight of the ten species studied: black sea bass, red porgy, vermilion snapper, gag, scamp, speckled hind, snowy grouper and red snapper. Reductions are often 50% or more. Thus a principal ingredient in the quality of the angling experience, fish size, has been reduced. Huntsman et al. (1983) argued elsewhere that large fish might be important in stimulating use of headboats. Since small marine fish are reasonably abundant near shore, the perceived availability of large fish offshore on the headboat grounds must be one of the incentives driving anglers toward the extra expense and rigors of headboat fishing.

Size reduction has consequences to efficient use of the reef fish resource. If fish of any species are harvested at too young an age, potential yield is lost because insufficient growth has occurred. Because of the growth characteristics and apparent low natural mortality rate of most reef species, the smallest size at which they should be harvested is relatively large (Huntsman and Manooch, 1979; Huntsman et al., 1983). Four of the ten species studied are clearly being taken at sizes which are too small (red porgy, gag, speckled hind, snowy grouper). For these species the average size now taken is equivalent to the smallest sizes which should be retained. Given any variability about the mean it is clear that a substantial fraction of the catch (on the order of 50%) is undersized. The mean size for several other of the ten species is sufficiently close to an acceptable minimum size to cause suspicion that too many small fish of those species are being taken.

Harvest appears to be excessive to the annual biomass increase resulting from growth, and for several species, may be impairing reproduction. In at least one area catch per unit effort in numbers has decreased for five of the ten species (red porgy, white grunt, scamp, speckled hind, snowy grouper). Some decreases may be responses to changes in fishing technique or area. Others may represent reduction in the population of large old adults, usual targets of the headboat fleet, but fish smaller than the recruited size may still be abundant. But for some species, (e.g., red porgy off South Carolina, speckled hind overall) reproduction appears reduced and recruits are not forthcoming.

Some species are sustaining their numbers. CPUE (numbers) of black sea bass, gray triggerfish, and red snapper have not decreased. Mean size of gray triggerfish size is undiminished and CPUE of vermilion snapper has increased. Interestingly, in one of the other areas of intense reef fishing, off the Florida panhandle, vermilion snapper make up a large fraction (25 percent by weight) of the catch, and seem to be sustaining their numbers while other species are diminishing. Perhaps vermilion snapper have recruitment mechanisms that enable them to withstand fishing mortality better than other common reef species.

It should be noted that while some factors might cause decreases in CPUE to overestimate decreases in population (e.g. shifting to secondary target species at low populations of the primary target), there have been substantial technological improvements in fishing equipment that would cause CPUE to underestimate decreases. Headboats in the region have become larger more seaworthy, and faster so as to more efficiently search for fish (in a concomitantly larger fishing area), and marine electronics are much improved. LORAN C which replaced LORAN A in the late 1970's made relocation of fishing sites certain and easy. Depth (fish) finders have been improved. Many vessels carry color enhanced sonar systems that simplify detecting fish. Micro-electronic components and computer technology have made operation of instruments automatic and virtually foolproof. Overall the effectiveness of most vessels for finding fish was substantially greater in 1985 than in 1972. Thus decreases in CPUE may conservatively estimate population decreases.

The apparent existence of both growth and recruitment overfishing at the headboat grounds suggests a need for more intense management of the reef fishery. At present only one significant rule applies to reef fishing in Federal waters off North Carolina, the 8 inch (200 mm) minimum length requirement for black sea bass (the size limit for red snapper rarely comes into use). In the face of high demand for reef fish more regulation is required. The following description of potential management measures is offered to stimulate thinking and discussion. The ideas expressed are not policy of either the National Marine Fisheries Service or of the South Atlantic Fishery Management Council.

The exact regulations depend on the goal of the managers. If the only goal is to maximize protein yield from the harvest, establishing more size limits will be at least partly useful.

Size limits protect yield per recruit and if set large enough can protect recruitment as well. Size limits are simple, easily instituted and understood by the public, and are democratic, applying equally to all sectors of the fishery. Unfortunately because some species, because of their physiology (e.g. white grunt) or their usual depth of capture (e.g. snowy grouper), die when released, size limits are not universally useful. For these species a reduction in fishing mortality (F) is required; species like white grunt occur mixed with other species so that a reduction in F can only occur if F is reduced for the species mix as a whole. Seasons and quotas can reduce F, but seasons often are ineffective because effort is concentrated during the season so that annual F is as large as that occurring without a season. Quotas are effective if: (1) they are enforced; (2) an effective and timely catch recording system is in place; and (3) there is sufficient information about the population dynamics of the species to allow specification of the correct quota. In the U.S. South Atlantic these are severe demands that cannot currently be met. With adequate funding they could be.

Another goal managers might consider is reestablishment of the headboat fishery with the catch and size levels of the early 1970's. Those levels depended on large standing stocks of old growth fish and can be established only as a result of low F. Fortunately low F (about 0.3) will take virtually all of the yield available from reef fish if minimum size of capture is kept relatively large (Huntsman et al., 1983). Maintenance of a large minimum size is possible without release mortality if operators avoid small fish. And because many reef species aggregate by size such avoidance is possible and even relatively easy.

However, operators need incentive to practice avoidance. An incentive might be to grant operators exclusive use of sectors of the ocean. Reef fishes are largely sedentary and lend themselves to this scheme. This form of limited entry would provide incentive to prosecute the fishery in such a way as to maintain quality fishing which would allow success in the competition for paying passengers.

An appropriate way to allocate sectors might be to auction them, as we do oil leases. Thus, those able to use the fishery in the most productive way could pay most for the areas. Such a scheme would eliminate part of the need for managers to decide whether a commercial or recreational fishery offers the "best" use of a resource although some management guidance would still be required. Leases would have to be sufficiently long to encourage conservation rather than quick boom and bust, pulse fishing. Choice of a lease period by managers would, in itself, constitute a decision about what kinds of fishing to allow. Managers would still need to maintain an overview of fish size and reproduction so as to ensure that proper results were being achieved. Probably some allocation of area to the general public would be required. Of course the main advantage of the scheme is that operators would be converted from roving hunter-gatherers to husbandmen and Hardin's (1968) tragedy of the commons would be avoided. Peripheral advantages are that operators will become, to an extent, their own police force, guarding against intrusions, protecting their rights, and relieving the general public of much of the cost of enforcement. And the system should encourage record keeping (catches) by operators, relieving the public of another costly responsibility.

Reestablishment of the conditions of the early recreational fishery is a goal perhaps unique to, and politically unrealistic under conditions other than those of, the reef fishery of the Carolinas. For in this fishery there was not, as usual, a long established commercial fishery (other than for black sea bass) which was forced to forego an increasing share of its resource to a growing recreational fishery. Instead the recreational fishery preceded by decades the commercial fishery. Not until 1976, did commercial fishing arrive, fully-grown, in Charleston from Florida and within four years mean weight of several important species (red porgy, gag, scamp, speckled hind, snowy grouper) demonstrated an accelerated decline. The historical precedent, if of any value, suggests that the headboat fishery has prior claim to the resource.

A final suggested goal for management is that speckled hind, and warsaw grouper Epinephelus nigritus, a species not previously discussed, be given special protection. Representing the ultimate predators on the shelfbreak, (warsaw) and outer shelf (speckled hind) reef systems, these species are the aquatic equivalents of grizzly bears, and are no less rare, vulnerable, beautiful, or ecologically intriguing. Attaining weights of >150 kg and ages >40 years, warsaw grouper (Manooch in press) appear only a few dozen times annually in Carolina headboat catches and are the rarest of the large, regularly occurring, members of the reef community. Their rarity precluded an analysis of their catches as performed for other species. Observed by divers to be fearless, even "friendly" they are readily vulnerable to hook and line or spear gun, and only the immensity of adults protects them from even-more rapid eradication. Similar comments adjusted for fish size are true of speckled hind. Because these groupers are among the species that usually cannot be successfully released, the only means of protection is to keep F low, or nonexistent. Restrictions on the upper limits of hook size or line strength would reduce F by allowing escapes at depth of large fish. Under the area-leasing strategy F might remain small enough to allow the growth of these beautiful, little-understood animals. A scheme certain to protect these groupers would be to establish preserves wherein fishing was prohibited. Although a marine sanctuary (Monitor site) exists off the Carolinas and another (Big Rock-Ten Fathom Ledge) has been considered, no site exists where rare vulnerable fish are even theoretically safe from exploitation. Several such sites should be established. Their utility is unquestioned and demonstrated throughout the world (Randall, 1981) and on the successful (= adequate enforcement) sanctuaries, one of the obvious attributes is the presence of large groupers absent from unprotected reefs of the region.

Many reasons exist to establish such sanctuaries. Often in shallower areas they encourage sport diving and are an economic asset, especially to cash-poor third world tropical countries. But sanctuaries for speckled hind and warsaw grouper will be too deep for most sport diving. Certainly the value of unexploited sites to research is easily justified. But perhaps the most important reason is Leopold's (1949) "land ethic" which states basically that we bear obligation to respect fellow inhabitants of this world, that the existences of man and of 150 kg warsaw grouper need not be mutually exclusive. Establishment of marine sanctuaries would be token acknowledgment of the land ethic.

One incentive to proceed with establishment of sanctuaries might be to invoke the Endangered Species Act to protect warsaw grouper. A strong case is easily made. Even the intense commercial fishing of 1983-1985 off North Carolina produced a total of only about 180 fish (Mercer et al., 1986) averaging less than 20 kg apiece. Considering that endangered status was considered (or threatened) for the apparently far more abundant Atlantic bluefin tuna, classification for warsaw ought to be assured. It is perhaps an indictment of reef fishery biologists, that we have not been more diligent in alerting society to the status of these species.

Even cursory analysis of 13 years of data on ten species becomes far more complex than we intended. We mused often during examination of these data that only God and the fish (maybe) knew what had really happened and neither were talking. Nonetheless, it is clear that fifteen years of fishing on Carolina reefs has impaired the productivity of several species, and certainly reduced the quality of fishing in terms of number and size of fish caught. We should have known. The first headboat captain interviewed in 1972 (and every captain thereafter) told us "ya know, fishing ain't what it once was."

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REPRODUCTIVE STRATEGIES IN ELASMOBRANCHS OF THE NORTH CAROLINA SHELF

William C. Hamlett
Department of Anatomy, Medical College of Ohio
Toledo, Ohio 43699

ABSTRACT

The elasmobranch fauna of the North Carolina shelf is rich and diverse. Virtually all the reproductive processes that have evolved in this group of fishes are represented by extant species. Representatives exhibit reproductive strategies that range from simple oviparity to the development of a yolk sac placenta. Reproduction in elasmobranchs is either oviparous (the producing of eggs from which the young are hatched outside the body of the maternal organism) or viviparous (the bringing forth of living young). Of the elasmobranchs frequenting North Carolina waters, 16 are oviparous and 58 viviparous. Viviparity may range from simple uterine retention of yolk dependent embryos up to the bearing of living young which derive nutrition directly and continuously from the maternal organism. The ways in which nutrition is supplied to viviparous embryos vary as the following categories: 1) internal incubators with or without uterine villi; 2) internal incubators with trophonemata; 3) internal incubators with oophagy and intrauterine cannibalism and 4) internal incubators with yolk sac placenta. Oviparous elasmobranchs include the Scyliorhinidae and Rajidae. Category 1 for viviparous species includes representatives of the Hexanchidae, Orectolobidae, Rhincodontidae, Squalidae, Squantinidae, Pristidae and Rhinobatidae. The embryos may be nourished by nutrient histotroph secreted by uterine villi. Category 2 has species in which the maternal uterus displays hypertrophied uterine villi termed trophonemata. These structures produce a copious histotroph during the latter stages of embryonic development to nourish the embryos after their yolk stores have been consumed. Included in this category are members of the Torpedinidae, Dasyatidae, Myliobatidae, and Mobulidae. Category 3 includes the Odontaspididae, Alopiidae and Lamnidae. Embryos in this group have very small yolk stores that are depleted at an early stage. The maternal organism continues to ovulate during gestation and, as the eggs pass through the nidamental gland, fertilization occurs. The embryos exhibit precocious development of functional dentition and begin to sup on uterine eggs (oophagy) and to practice intrauterine cannibalism by feeding on their siblings. Usually only one embryo per uterus survives and it achieves gigantic proportions, hence, the newborn is a huge, practiced predator. Category 4 is restricted to the Carcharhinidae and Sphyrnidae. Embryos are initially dependent on their yolk reserves. As these stores are depleted, the yolk sac becomes modified as a yolk sac placenta. The placenta forms an apposition with the uterine wall to produce a functional placental unit that carries out nutrient

and respiratory functions.

INTRODUCTION

The elasmobranch fauna of the North Carolina shelf is rich and diverse. Virtually all of the reproductive processes that have evolved in this group of fishes are represented by extant species. Representatives exhibit reproductive modes that range from simple oviparity up to the development of a yolk sac placenta.

Reproduction in elasmobranchs is usually either oviparous or viviparous. Although viviparity is characteristic of mammals, the process has evolved independently and repeatedly among divergent taxa of both invertebrates (Hoffmann, 1954; Amoroso, 1955; Engelmann, 1970; Odhiambo, 1971; Roberts, 1972; Saunders and Dodd, 1972; Denlinger and Ma, 1974; and Hogarth, 1976) and vertebrates. All three orders of Amphibia, viz. Apoda (Wake, 1977), Urodela (Amoroso et al., 1979) and Anura (Amoroso, 1952) contain viviparous representatives. In the reptiles, many snakes and lizards are viviparous (Weekes, 1935; Amoroso, 1952; Veith, 1974; Callard and Lance, 1977; Packard et al., 1977; Tinkle and Gibbons, 1977; Yaron, 1977).

Traditionally, organisms have been termed oviparous if they deposit eggs externally to complete development. The embryos are enclosed within an eggcase and utilize yolk stores for growth and development. Animals are said to be ovoviviparous if they retain young that are not physiologically dependent on their mother for nutrition. This simply represents intrauterine incubation or internal incubation. Viviparous animals are those in which embryos are retained in the female reproductive system and receive maternal nutrients continuously during development. Budker (1958), Hoar (1969), and Dodd (1983) have indicated that the distinction between ovoviviparity and viviparity is an artificial one. The term ovoviviparity will therefore not be used in this paper. I have designated the reproductive strategies of sharks as two categories, viz. oviparous and viviparous (Table 1). Oviparous species deposit fertilized eggs in eggcases to the exterior where the embryo completes development with no nutrient contribution from the maternal organism. Viviparous species retain their young for variable periods of time prior to parturition. Viviparous species can be categorized as, 1) internal incubators with or without uterine villi, 2) internal incubators with trophonemata, 3) internal incubators with oophagy and intrauterine cannibalism, and 4) internal incubators with yolk sac placenta. Of the total 74 elasmobranch species of the North Carolina shelf, 16 are oviparous and 58 viviparous (Table 1).

Oviparous and viviparous elasmobranchs have achieved different solutions to the common physiological problem of maintaining adequate urea concentration in the fetal environment. Smith (1937) and Price and Daiber (1967) suggested that the eggcase was impermeable osmotically and provided an isolated environment for the embryo until it was able to retain urea and osmoregulate.

Table 1. Elasmobranch Species of the North Carolina Shelf by Reproductive Mode

I. Oviparous	16
II. Viviparous	
A. Internal incubators with or without uterine villi	13
B. Internal incubators with trophonemata	17
C. Internal incubators with oophagy and intrauterine cannibalisim	8
D. Internal incubators with yolk sac placenta	20
	74

Oviparous species employ a thick eggcase that is impermeable to urea (Hogarth, 1976; Evans and Oikari, 1980, and Mellinger et al., 1986). Reed (1968 a,b) showed that during early stages of development encapsulated *Raja binoculata* embryos are capable of maintaining near-adult levels of urea. Needham and Needham (1930), Hornsey (1978), Foulley and Mellinger (1980) and Mellinger et al., (1986) have shown that the eggcases of *Scyliorhinus canicula* are impermeable to urea. Thus, the retention of urea is secondary to a urea-impermeable membrane (Evans, 1981). However, although embryos can maintain high urea levels, it seems that the full complement of osmoregulatory mechanisms is not present in early encapsulated stages. Libby (1959) showed that if *R. eglanteria* is removed from the eggcase before day 20 of its 64 day development it cannot survive. At day 20, a mucous plug in the eggcase is dissolved allowing sea water to enter. Some viviparous species retain their young for several months within the lower portion of the oviducts, each of which function as a uterus, during gestation. During early development, when the embryonic kidneys are non-functional, the mother maintains the urea content of the embryo at the same level as her blood. Later when the embryo can regulate urea itself, the uterus is periodically flushed with sea water (Burger and Loo, 1959; Burger, 1967; Evans and Oikari, 1980).

Advantages of a given reproductive strategy will depend on the habitat of that species. In that the young of viviparous species are fewer in number, larger, and more developmentally advanced at parturition, a selective advantage in the form of survival bias is conferred on them. The high fecundity and gamete wastage correlated with teleostean oviparity is not evident in viviparous elasmobranchs. Both groups are reproductively successful. They simply have evolved different strategies (Pianka, 1970; Stearns, 1976). Viviparity seems to have evolved in species which already produced a small number of eggs, each with sufficient yolk nutrients for its full development. Thus, simple uterine retention would require only a slight physiological adaption and, thereby, produce an offspring of advanced size and developmental stage better able to survive in the vagaries of the aqueous environment.

As a group, elasmobranchs show a low fecundity relative to body size. Skates usually produce 2-7 eggs per clutch (Ballinger, 1978). Stingrays usually produce 5 or fewer young per clutch. In _Rhinoptera bonasus_ only the left uterus consistently matures and a single embryo develops (Hamlett et al. 1985d). Among the sawfishes, _Pristis perotteti_ shows a fecundity of 7.3 (Thorson, 1976). Litter sizes for most sharks are below 20, with averages generally below 10 (Ballinger, 1978). In the tiger shark, _Galeocerdo cuvier_, litter sizes are from 10 to 82 (Compagno, 1984). Low fecundity and increased size of the offspring among large sharks may reflect the large size necessary for survival in their habitat (Table 2).

Table 2. Litter Size in Placental Sharks (From Compagno, 1984)

SHARK	LITTER SIZE
Carcharhinus acronotus	3-6
C. altimus	3-15
C. brevipinna	3-15
C. falciformis	2-4
C. isodon	1-6
C. leucas	1-13
C. limbatus	1-10
C. longimanus	1-15
C. obscurus	3-14
C. plumbeus	1-14
C. signatus	4-12
Galeocerdo cuvieri	10-82
Mustelus canis	4-20
Negaprion brevirostris	4-17
Prionae glauca	4-135
Rhizoprionodon terranovae	1-7
Sphyrna lewini	15-31
S. mokarran	13-42
S. tiburo	4-16
S. zygaena	29-37

There is a much higher relative reproductive investment in the fewer offspring of viviparous species. In oviparous forms, nutrition is by extracellular digestion of yolk sac contents and subsequent absorption of the by-products by the vitelline blood vessels (TeWinkel, 1943). Recently the process of yolk utilization within the yolk sac of a preimplantation placental shark, Rhizoprionodon terraenovae, (Hamlett et al., 1987) has been elucidated using transmission electron microscopy. This study revealed that yolk utilization is virtually identical in oviparous and early term placental species. In placental species, once the yolk stores are depleted, the yolk sac becomes modified as a yolk sac placenta, (Hamlett et al., 1985a-c). A parallel route of yolk utilization during the early phases of development is the ciliated ductus vitello-intestinalis. This structure transports yolk directly to the fetal gut where digestion occurs.

Gaseous exchange initially occurs over the entire body surface, then is extended to the vitelline capillaries and finally is confined to the gills. Elaboration of elongated external branchial filaments aids this process early in development (Ranzi, 1934). The presence of external gill filaments indicates a low oxygen concentration in the uterus or a great demand for oxygen. In some species, the fetal hemoglobin has a greater affinity than the maternal hemoglobin for oxygen (Manwell, 1963; Hill, 1976). This facilitates oxygen transfer from mother to fetus. A similar adaptation is found in mammals (Guyton, 1981). To cope with increased trophic and respiratory demands, the yolk sac has become ontogenetically modified into a highly vascular yolk sac placenta. During embryonic development, the mother may be regarded as a physical and physiological buffer against an often harsh environment with which an unsheltered embryo might not be able to cope.

Elasmobranchs of North Carolina waters have received considerable attention by workers in the field of natural history, especially Coles (1910, 1915, 1919, 1926) Brimley (1935a,b) and Gudger (1910, 1912, 1913a, 1913b, 1948a, 1948b, 1951). Other works detailing the biology of elasmobranchs include Bell and Nicols, 1921; Hildebrand, 1941; Jenkins 1887; Jordan, 1886; Jordan and Evermann, 1898; Jordan and Gilbert, 1879, 1882; Nichols, 1921; Radcliffe, 1913, 1914; Wilson and Beckett, 1970 and Yarrow, 1877. Smith (1907) published a description of North Carolina fishes. The most comprehensive review of the elasmobranch fauna of these waters remains that of Bigelow and Schroeder (1948, 1953) and Schwartz (1984) has published a valuable field guide to the North Carolina elasmobranchs (Table 3).

Table 3. Reproductive Strategies in Elasmobranchs of the North Carolina Shelf

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OVIPAROUS

- Scyliorhinidae
  - Apristurus laurisonni - flathead catshark
  - Scyliorhinus meadi
  - S. retifer - chain dogfish
- Rajidae
  - Bathyraja richardsoni
  - Breviraja atripinna
  - B. plutopinna
  - B. spinosa
  - Dactylobatus armatus
  - Raja eglanteria - clearnose skate
  - R. erinacea - little skate
  - R. floridana
  - R. garmani - rosette skate
  - R. laevis - barndoor skate
  - R. ocellata - winter skate
  - R. radiata - thorny skate
  - R. senta - smooth skate

VIVIPAROUS

INTERNAL INCUBATORS WITH OR WITHOUT UTERINE VILLI

- Hexanchidae
  - Hexanchus griseus - sixgill shark
- Orectolobidae
  - Ginglyomostoma cirratum - nurse shark
- Rhincodontidae
  - Rhincodon typus - whale shark
- Squalidae
  - Dalatius licha - kitefin shark
  - Deania profundorum
  - Etmopterus bullisi
  - E. gracilispinis
  - E. hillianus - blackbelly shark
  - Somniosus microcephalus - greenland shark
  - Squalus acanthias - spiny dogfish
- Squatinidae
  - Squatina dumerili - Atlantic angel shark
- Pristidae
  - Pristis pectinata - sawfish
- Rhinobatidae
  - Rhinobatos lentiginosus - Atlantic guitarfish

INTERNAL INCUBATORS WITH TROPHONEMATA

- Torpedinidae
  - Benthobatis marcidae
  - Narcine brasiliensis - lesser electric ray
  - Torpedo nobiliana - Atlantic torpedo
- Dasyatidae
  - Dasyatis americana - southern stingray
  - D. centroura - roughtail stingray

Table 3 (con't)

D. sabina - Atlantic stingray
D. sayi - bluntnose stingray
Gymnura altavela - spiny butterfly ray
G. micrura - smooth butterfly ray
Urolophus jamaicensis - yellow stingray
Myliobatidae
Aetobatus narinari - spotted eagle ray
Myliobatis freminvillei - bullnose ray
M. goodei - southern eagle ray
Rhinoptera bonasus - cownose ray
Mobulidae
Manta birostris - Atlantic manta
Mobula hypostoma - devil ray
M. mobular - devil ray

INTERNAL INCUBATORS WITH OOPHAGY AND INTRAUTERINE CANNIBALISM

Odontaspidae
Odontaspis taurus - sand tiger
Alopiidae
Alopias superciliosus - bigeye thresher
A. vulpinus - thrasher shark
Lamnidae
Charcarodon carcharias - white shark
Cetorhinus maximus - basking shark
Isurus oxyrinchus - shortfin mako
I. paucus - longfin mako
Lamna nasus - porbeagle

INTERNAL INCUBATORS WITH YOLK SAC PLACENTA

Carcharhinidae
Carcharhinus acronotus - blacknose shark
C. altimus - bignose shark
C. brevipinna - spinner shark
C. falciformis - silky shark
C. isodon - finetooth shark
C. leucas - bull shark
C. limbatus - blacktip shark
C. longimanus - oceanic whitetip shark
C. obscurus - dusky shark
C. plumbeus - sandbar shark
C. signatus - night shark
** Galeocerdo cuvieri - tiger shark
Mustelus canis - smooth dogfish
Negaproon brevirostris - lemon shark
Prionace glauca - blue shark
* Rhizoprionodon terraenovae - Atlantic sharpnose shark
Sphyrnidae
Sphyrna lewini - scalloped hammerhead
S. mokarran - great hammerhead
* S. tiburo - bonnethead
S. zygaena - smooth hammerhead

* With appendiculae
** This is the only carcharhinid internal incubator that does not develop a yolk sac placenta.

Oviparous Species

Elasmobranchs of North Carolina waters that display oviparity are restricted to the families Scyliorhinidae and Rajidae. Within the Scyliorhinidae, development is usually oviparous but some species give birth to living young. In most species only a single fertilized egg per oviduct is encapsulated by a tough, resilient eggcase. This egg subsequently is laid by the mother and most of the embryonic development occurs outside the mother. This process is termed simple oviparity (e.g. *Apristurus kampae*) (Compagno, 1984) and development may take up to one year. *Apristurus laurisonni* occurs in North Carolina waters and is presumed oviparous. All other species of *Apristurus* display single oviparity or are suspected to do so. Multiple oviparity occurs when several eggs are retained in the maternal oviduct for a prolonged period of time. The embryos consequently develop to an advanced stage prior to the eggcases being deposited to the exterior. These eggs may spend only a month outside the mother. In *Galeus melastomus* up to thirteen eggs are present in a single female (Compagno, 1984). Other species have abandoned oviparity and the fertilized eggs are retained by the mother until parturition.

In *Cephalurus cephalus* the eggcases are very thin and the young are retained within the oviduct until the young hatch. In *Halaelurus boesemani* up to four eggcases may occupy a single oviduct but it remains uncertain if these hatch inside the female or are laid. *Halaelurus buergeri* of the Western Pacific may be intermediate between simple oviparity and being an internal incubator since several eggcases are retained by the mother until the embryos are well advanced and ready to be laid (Nakaya, 1975). *Halaelurus lutarius* has very thin walled eggcases, unlike the stout eggcases typical of strictly oviparous species, and is presumably in the process of becoming an internal incubator.

Two scyliorhinids occur in North Carolina waters viz. *Scyliorhinus retifer* and *S. meadi*. Almost nothing is known of the reproductive biology of *S. meadi*, but *S. retifer* is oviparous. The occurrence of numerous freshly hatched offspring off Cape Hatteras suggests there is a limited nursery area there (Compagno, 1984).

The Rajidae (skates) constitute a strictly oviparous group of elasmobranchs. Fertilization is internal, as with all elasmobranchs, and the eggcase is formed shortly thereafter. Skate eggcases superficially resemble those of the Scyliorhinidae (Figure 1). The cases are rectangular with straight, horny tendrils at each corner. They are laid in muddy or sandy areas and adhere to small pieces of rock, shell or seaweed. The eggcases are laid when the developing embryos are at a very early stage of development. The egg yolk is the sole source of organic material for development. Embryogenesis ensues

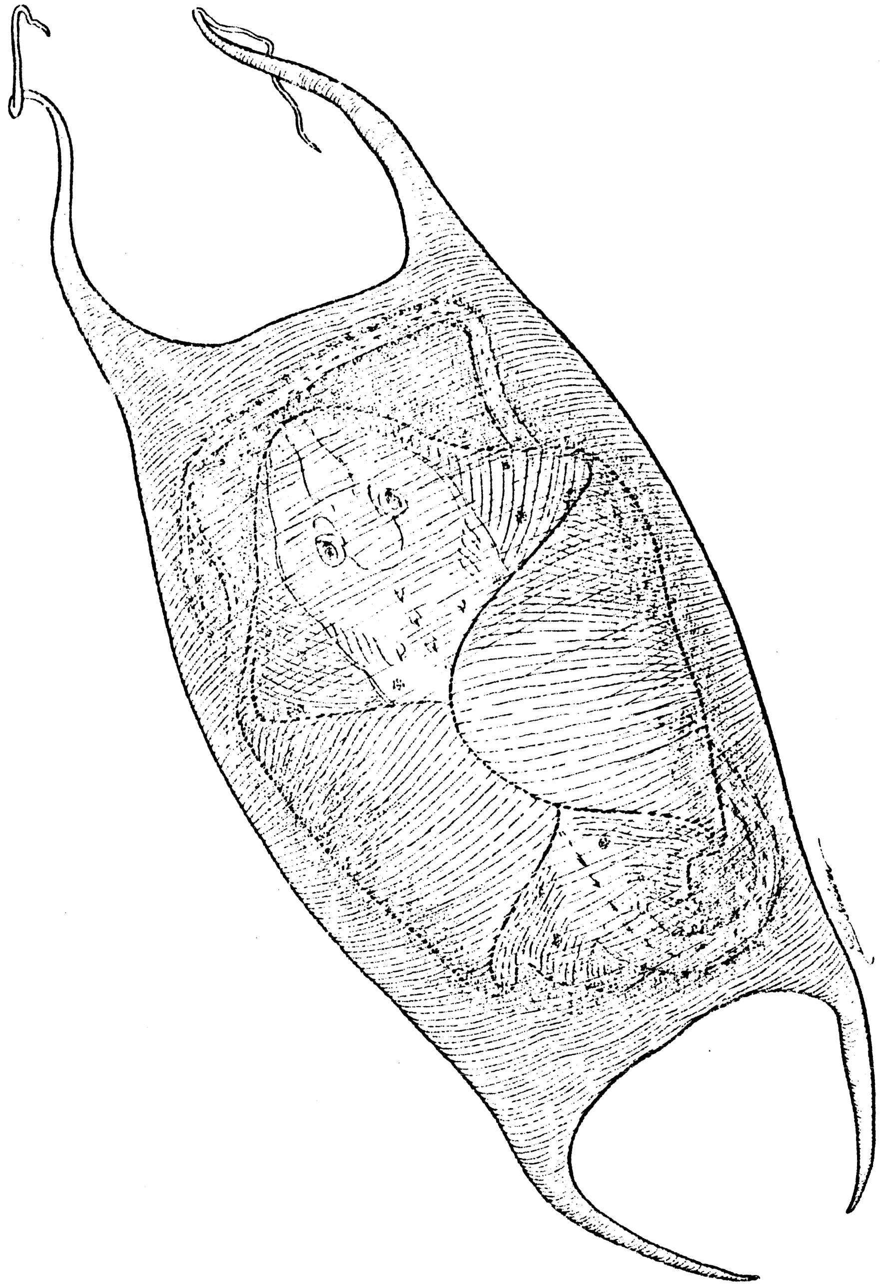

Figure 1. An idealized diagram of a skate embryo inside its eggcase. The yolk dependent embryo resides in the eggcase with its wings rolled on its back. The tendrils at the corners of the eggcase anchor the case.

and at hatching, the embryo emerges through a transverse slit at one end of the eggcase. Empty cases are frequently found washed ashore and are called mermaids' or sailors' purses. Embryonic development may take from 3-8 months depending on the species and the habitat.

In Florida Raja eglanteria from February through June (Libby and Gilbert, 1960), eggs are laid in pairs about 4 days apart with a single female laying as many as 66 eggs. Development takes 9 weeks. After 20 days of development, slits appear in the four tendrils in the impermeable eggcase thereby allowing sea water to enter. The eggcase of a skate is initially pale amber but darkens to almost black just before hatching. Raja erinacea and most other skates are reproductively active throughout the year but tend to show one or two annual peaks of activity (Richards et al., 1963). Thirteen skate species occur in North Carolina waters. Of these, one is in the genus Dactylobatus, one Bathyraja, three Breviraja and eight Raja.

Internal Incubators With or Without Uterine Villi

In the transition from purely oviparous development to viviparity there is a shift in the function of the maternal uterus to one of a nutrient producing organ. This is coincident with the internal uterine retention and incubation of the developing embryos. The uterine epithelium in some species may display a smooth contour or show varying degrees of uterine villi. The uterus produces histotroph or "uterine milk", the quantity and chemical composition of which varies from species to species. The major components are lipid and protein. Histotroph production may be minimal to extensive. Ranzi (1934) made correlations between the degree of presence or absence of uterine villi and the quantity of histotroph. In its simplest form, the uterine epithelium is smooth, as in Squalus acanthias, or may form rows of short villi, as in other squaloids. Squatina also shows the same simple uterine organization. If the dry weight of the egg and embryo are compared, these simple internal incubators show a 15-55% weight loss (Ranzi, 1932). Gilbert and Bevelander (1959) found that no nutrient transfer from mother to fetus was effected in S. acanthias. Jollie and Jollie (1967a,b) have described the changes in the ultrastructure of the yolk sac and uterus of S. acanthias during gestation. The uterus is thought to function in respiration and osmoregulation. Gestation in S. acanthias is from 18-22 months in Massachusetts (Hisaw and Albert 1947).

Among other squaloids the number of young varies as follows: Dalatius licha, 10-16; D. profundorum 5-7; Etmopterus hillianus, 4-5; and S. acanthias 1-20 (Compagno, 1984). In Rhinobatos (guitarfish) the uterus forms villi of moderate length that produce histotroph containing 1.2-2.8% organic material (Ranzi, 1934; Needham, 1942; Amoroso, 1960). The stages of embryonic development for R. halavi were reported by Melouk

(1949).

The sawfish, *Pristis*, is an internal incubator with uterine villi. The sawfish of Lake Nicaragua (Thorson, 1976) bears 1-13 young with gestation taking five months. Prior to parturition the saw is soft, leathery and is covered by a firm membranous sheath (Gudger, 1951). This protects both the embryo and mother. The sixgill shark, *Hexanchus griseus*, is an internal incubator that can contain from 47-108 embryos.

Development in the whale shark, *Rhincodon typus*, is still a matter of debate. Based on a large eggcase, 30 cm long, 14 cm wide and 9 cm thick, containing a near full term embryo 36 cm in length, found in the Gulf of Mexico, it was initially supposed that the mode of reproduction was oviparity, (Baughman, 1955). Wolfson (1983), however, has suggested that the Gulf of Mexico eggcase may have been aborted before term. The relative rarity of whale shark eggs, the thinness and lack of tendrils on the only known case, and the considerable yolk store suggests that the whale shark may be an internal incubator.

The nurse shark, *Ginglymostoma cirratum*, is an internal incubator with intrauterine development primarily supported by the large yolk deposits (Compagno, 1984). The number of young is 21-28 per litter.

Internal Incubators With Trophonemata

Stingrays display aplacental viviparity. There is no direct physical connection with the mother. Amongst the rays, the right ovary and oviduct show a considerable degree of reduction or loss. In the round stingray, *Urolophus halleri*, the left ovary is functional while the right is not. Both oviducts, however, are functional. In *Dasyatis bleekeri* both the right ovary and oviduct are absent (Babel, 1967).

Stingrays possess elaborately hypertrophied uterine villi termed trophonemata. These structures are also present in the sawfish, *Pristis* (Ranzi, 1932, 1934). Wood-Mason and Alcock (1891) introduced the term trophonemata to distinguish them from intestinal villi. Trophonemata are tufts of villous projections of the maternal uterine wall. During the initial period of embryonic development the embryos are lecithotrophic, deriving nutrients from their yolk reserves. During development, and as the yolk is depleted, the uterine mucosa hypertrophies into secretory trophonemata which produces histotroph or "uterine milk" (Needham, 1942). The embryo absorbs and ingests this material to complete its development. In the ray, *Dasayatis violacea*, the histotroph has an organic content of 13.0% of which 8.0% is fat (Ranzi, 1934). In some species the trophonemata may enter the spiracles of the embryo and secrete directly into the gut (Wood-Mason and Alcock, 1891). It has been demonstrated that the gut absorbs particulate matter, viz., India ink, and that the digestive glands of the stomach are functional at an early age (Ranzi, 1934; Needham, 1942). The efficiency of trophonematal nutrient transfer exceeds that of the shark yolk sac placenta. An increase in organic material during development of 1,700-5,000% is appreciated for the rays, Dasyatis violacea, Gymnura micrura, Myliobatis bovina, and Rhinoptera bonasus, as compared with 840% and 1,050% increase in two placental shark species, Prionace glauca and Mustelus laevis (Ranzi, 1934; Needham, 1942).

In Rhinoptera bonasus only the left ovary and oviduct are functional in mature specimens (Smith, 1980). The right ovary shows no evidence of follicular development. The right oviduct is present but not mature. Small trophonemata, 0.5 cm in length, are encountered but no eggs or embryos are present (Smith, 1980). The young are born alive and are miniature reproductions of the adult. Only one young per gravid left oviduct is observed. Its position within the maternal uterus is in the same relative position as the female. The wings of the embryo are rolled around the body dorsally. Embryonic nutrition is biphasic (Hamlett et al., 1985d). Initially, the embryo utilizes yolk reserves that are laid down during oogenesis. The eggs are 3-4 cm in diameter (Smith, 1980). Rays undergo a considerable increase in weight during gestation whereas lecithotrophic species show a net loss. By the time the embryo is 215 mm disc width, its yolk reserves are depleted, (Hamlett, et al. 1985d).

Growth to term is effected by absorption and ingestion of histotroph. The structure of the trophonemata change with gestational age. Glandular crypts are formed on the surface of the trophonemata and secretory cells in the crypts and produce the "uterine milk" (Hamlett et al., 1985d) (Figure 2). Wood-Mason and Alcock (1891) first suggested a nutritive role for histotroph. Gudger (1912) proposed that early myliobatoid embryos absorbed histotroph through their external branchial filaments. He suggested that in the later phases of gestation, when these filaments disappeared, the spiracles conveyed histotroph directly to the gut. Using ink injections Ranzi (1934) showed that early stage embryos of Dasayatis violacea absorbed histotroph through the yolk sac and external branchial filaments. Similarly, he also demonstrated that later stage embryos ingested histotrophe via the mouth and spiracles. In R. bonasas, external branchial filaments are absent in embryos greater than 90.0mm disc width (Smith, 1980). Hamlett et al., (1985d) has recently confirmed that the embryonic gill filaments of elasmobranchs can in fact absorb exogenous material. During all phases of pregnancy the uterus closely invests the fetus and the young are thus brought into close approximation with the uterine lining. Smith (1980) also noted that the consistency and volume of histotroph increased with gestational age.

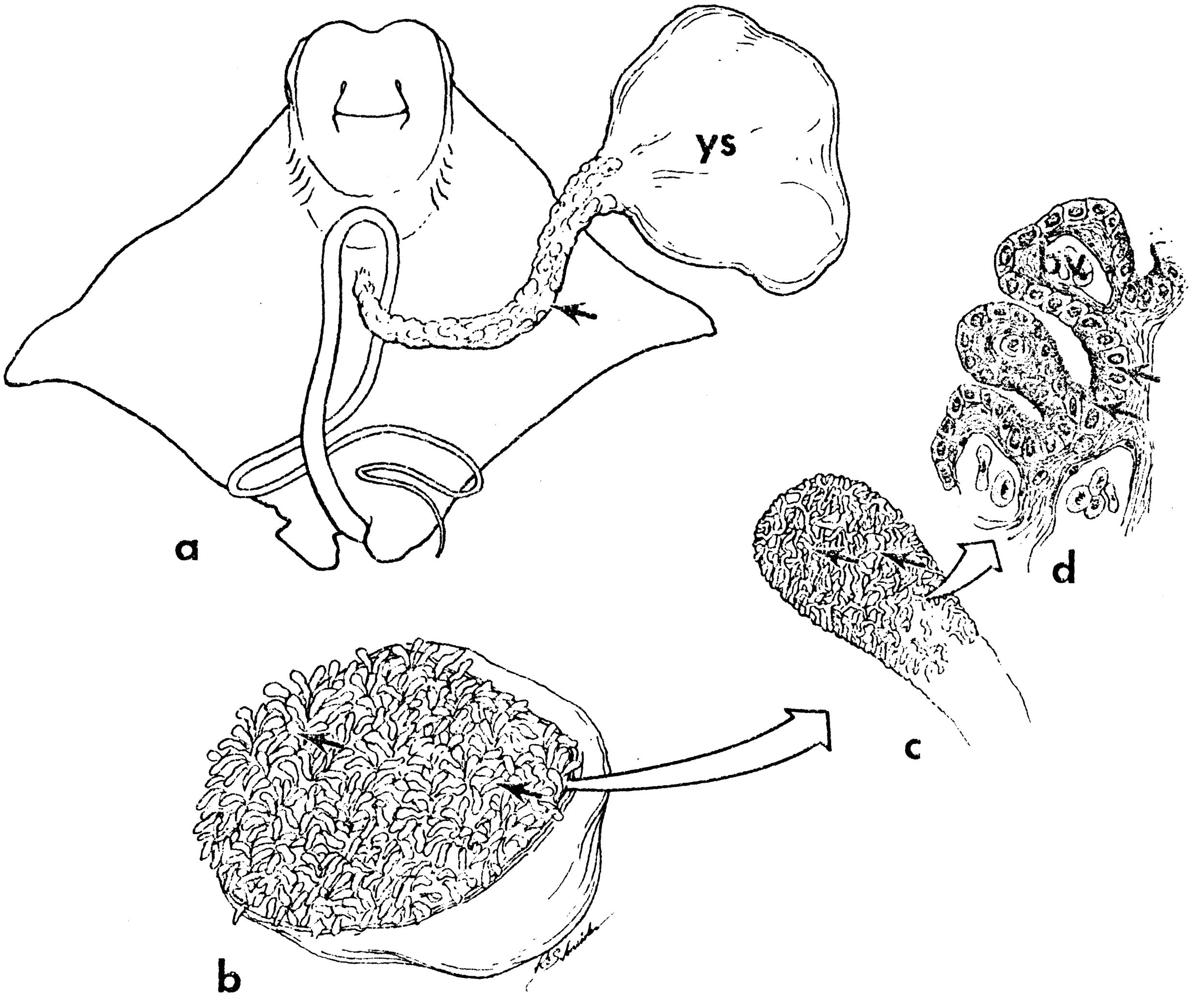

Figure 2. The fetal cownose ray, <u>Rhinoptera</u> <u>bonasus</u> (a) A midterm embryo superficially resembles an adult. The yolk sac (YS) is attached to the embryo by the yolk stalk (arrow). During the early period of development the embryo is dependent on yolk stores for nourishment; (b) A uterus containing a near term fetus has been everted to show the secretory trophonemata (arrows); (c) The trophonemata are tongue shaped and flattened. Ridges form a surface cable pattern (arrows); (d) Glandular crypts contain secretory cells (arrows) that produce "uterine milk" that will nourish the embryo during the latter phases of gestation. The trophonemata are rich in blood vessels (bv).

Development of trophonemata is correlated with hormonal events in the pregnant female. Smith (1980) employed several criteria to determine the state of sexual maturity of female R. bonasus. An immature female possessed thin, flaccid ovaries and a thin uterus with a rugous lining. A maturing female was characterized by an ovary with eggs less than 1.0 cm in diameter and a dilated uterus with trophonemata less than 0.5 cm. A female was considered mature if the ovarian eggs were greater than l.Ocm in diameter and the well developed uterus showed profuse trophonemata greater than 1.0 cm in length. At term, the trophonemata are 2-3 cm in length. Hisaw and Albert (1947) have shown that the pituitary plays no role in maintaining pregnancy in M. canis during the first three months of pregnancy. Corpora lutea have been reported in several elasmobranchs, viz. Rhinobatus granulatus (Samuel, 1943), Squalus acanthias (Hisaw and Albert, 1947), and Cetorhinus maximus. Hisaw and Abramowitz have shown that removal of the ovary from a pregnant M. canis has no influence on the development of embryos in the uterus.

The conclusion is that the pituitary is essential for ovulation and its removal prevents ovulation. No endocrinological work has been conducted with female rays. It seems likely that similar mechanisms and hormones may be functional in elasmobranchs as in mammals. The stimulatory effect of the pituitary may signal the development of corpora lutea. One may hypothesize that progesterone, or a similar hormone may be responsible for the hypertrophy and secretory activity of the ray uterus, much as the endometrium of mammals is maintained during pregnancy. It is certain that secretion by trophonemata is cyclical and closely related to the condition of the ovary.

At birth, the cownose ray becomes free-swimming and is fully equipped to feed. Bigelow and Schroeder (1953) reported that tooth replacement in R. bonasus, begins in utero. In R. bonasus, the trophonemata provide a continuous supply of metabolites and account for a 3,000X embryo weight increase (Hamlett et al. 1985d). This far exceeds the efficiency of the shark yolk sac placenta. Smith and Merriner (1986) have recently summarized the reproductive biology of the cownose ray. The increase in embryonic organic material during development for the placental blue shark, Prionace gluca, is 840% and for the dogfish, Mustelus laevis, is 1,050% (Ranzi, 1934; Needham, 1942). The difference may be accounted for in several ways. There is only one functional oviduct and a single enclosed embryo in R. bonasus as opposed to the placental blue shark, P. glauca which may carry up to 52 fetuses (Pratt, 1979). There is, therefore, a larger energetic investment in the single fetus. At term its disc width is 405 mm which is almost half that of the adult (Smith, 1980), however, only a fraction of the mass. Placental sharks are considerably smaller at birth in relation to the adult. The entire surface area of the ray uterus is hypertrophied into secretory trophonemata. This greatly increases the surface area available for production of histotroph. Trophonemata are not restricted to any area of the uterus, as is the placental attachment site in sharks. The entire surface of the uterus is available for secretion. The pattern seen in R. bonasus can be regarded as typical of elasmobranchs that develop trophonemata. The Torpedinidae, Dasyatidae, Myliobatidae and Mobulidae are all either known to display trophonemata or are so presumed.

Internal Incubators with Oophagy and Intrauterine Cannibalism

Among the chondrichthyan fishes, oophagy has been reported most frequently among the species of sharks that comprise the order Lamniformes as considred by Compagno (1977). Oophagy and intrauterine cannibalism have been found to occur in most lamnoid sharks, viz,

1. Lamna cornubica (Lohberger, 1910; Shann, 1923);
2. Eugomphodus taurus (Springer, 1948);
3. Alopias vulpinus (Gubanov, 1972);
4. Alopias pelagicus (Otake and Mizue, 1981);
5. Alopias superciliosus (Gruber and Compagno, 1981);
6. Pseudocarcharias kamohara (Fujita, 1981).

The great white shark, Carcharodon is probably oophagous (Sanzo, 1912). The remaining families in the order Lamniformes are presumed viviparous and oophagous. They are the Mitsukurinidae and the Cetorhinidae. Lund (1980) has recently reported on fossilized fetuses of a holocephalan, Delphyodontos dacriformes. He concluded that the embryos were probably oophagous and uterine cannibals.

Oophagy in sharks was first reported by Lohberger (1910). The phenomenon was not widely recognized since the report appeared in an obscure publication. Subsequently, oophagy was independently recognized by Shann (1923) in embryos of the porbeagle, Lamna spp. These embryos at term exceed a meter in length and weigh in excess of 9 kg (Bigelow and Schroeder, 1948). Lamna embryos had what appeared to be a large yolk sac. Close examination revealed it to be the grossly distended cardiac portion of the stomach filled with ingested eggs. Springer (1948) was the first to report oophagy and present evidence for intrauterine cannibalism in the sand tiger shark, Odontaspis taurus. Each oviduct contained a single very active embryo that exceeded a meter in length. In addition there were 60-70 egg capsules. Stomachs of the embryos contained ova, egg yolk, and fragments of egg cases. The percent dry weight change from egg to embryo for the sand tiger shark shows a remarkable 1.2×10^6 increase (Stribling et al., 1980.)

Amongst the lamniformes of North Carolina, the most well-studied shark is the sand tiger, Odontaspis taurus. Gilmore et al. (1983) has recently presented considerable information on the reproductive biology of this species and Hamlett (1983) has described the precocious development of dentition and discussed the developmental efficiency of oophagy and intrauterine cannibalism (Figure 3). Using scanning electron microscopy Hamlett (1983) reports that by the time sand tiger embryos are 27 mm total length jaws have formed although there is no evidence of tooth buds. The most striking feature of the 30 mm embryo is the extensive development of the lateral line system. Teeth are represented as rudimentary buds. By the time the embryo has grown to 35 mm the lateral line system is less conspicuous and has begun to acquire its typical fetal morphology. The first teeth have also begun to erupt. By 40 mm functional dentition is established, with teeth in the lower jaw being developmentally more advanced than those in the upper jaw. Teeth in the anterior row are conspicuously elongated and recurved and second row of teeth are beginning to erupt. By 45 mm, teeth are prominent in both the upper and lower jaws. A double row of teeth characterize the 55 mm embryo. By 60 mm the dentition of the embryo resembles that of the adult. Unlike non-oophagous species the yolk sac contents are absorbed at an early developmental stage in the sand tiger. The embryos subsequently adopt oophagy and intrauterine cannibalism. Utilizing this strategy the fetuses grow to the enormous size of 1 m at birth.

Alopias superciliosus, bigeye thresher, usually have litters of two, one embryo in each uterus, however, sometimes up to four (Compagno, 1984). The same is true of A. vulpinus, thrasher shark.

Like other lamnoid sharks where reproduction is based on oophagy and intrauterine cannibalism it is believed that the great white shark, Carcharodon carcharias, also displays this mode of reproduction, although pregnant females have yet to be described adequately. Likewise, the basking shark, Cetorhinus maximus, is presumed to be oophagous and perhaps also feeding on smaller siblings. The shortfin mako, Isurus oxyrinchus, is also a uterine cannibal as is the longfin mako, I. paucus. As previously mentioned, the porbeagle, Lamna nasus, also employs this reproductive strategy.

Internal Incubators with Yolk Sac Placenta

The presence of a yolk sac placenta in sharks is restricted to the Carcharhinidae, requiem sharks, and the Sphyrnidae, hammerhead sharks. There are 15 placental carcharhinids and 4 placental sphyrinids in North Carolina.

The tiger shark, Galeocerdo cuvieri, is the only carcharhinid internal incubator that does not develop a yolk sac placenta. The Hemigaleidae, a sister group of the Carcharhinidae shows placental viviparity and it is uncertain whether internal incubation in the tiger shark is primitive or has been brought about by the evolutionary loss of a placenta (Compagno, 1984).

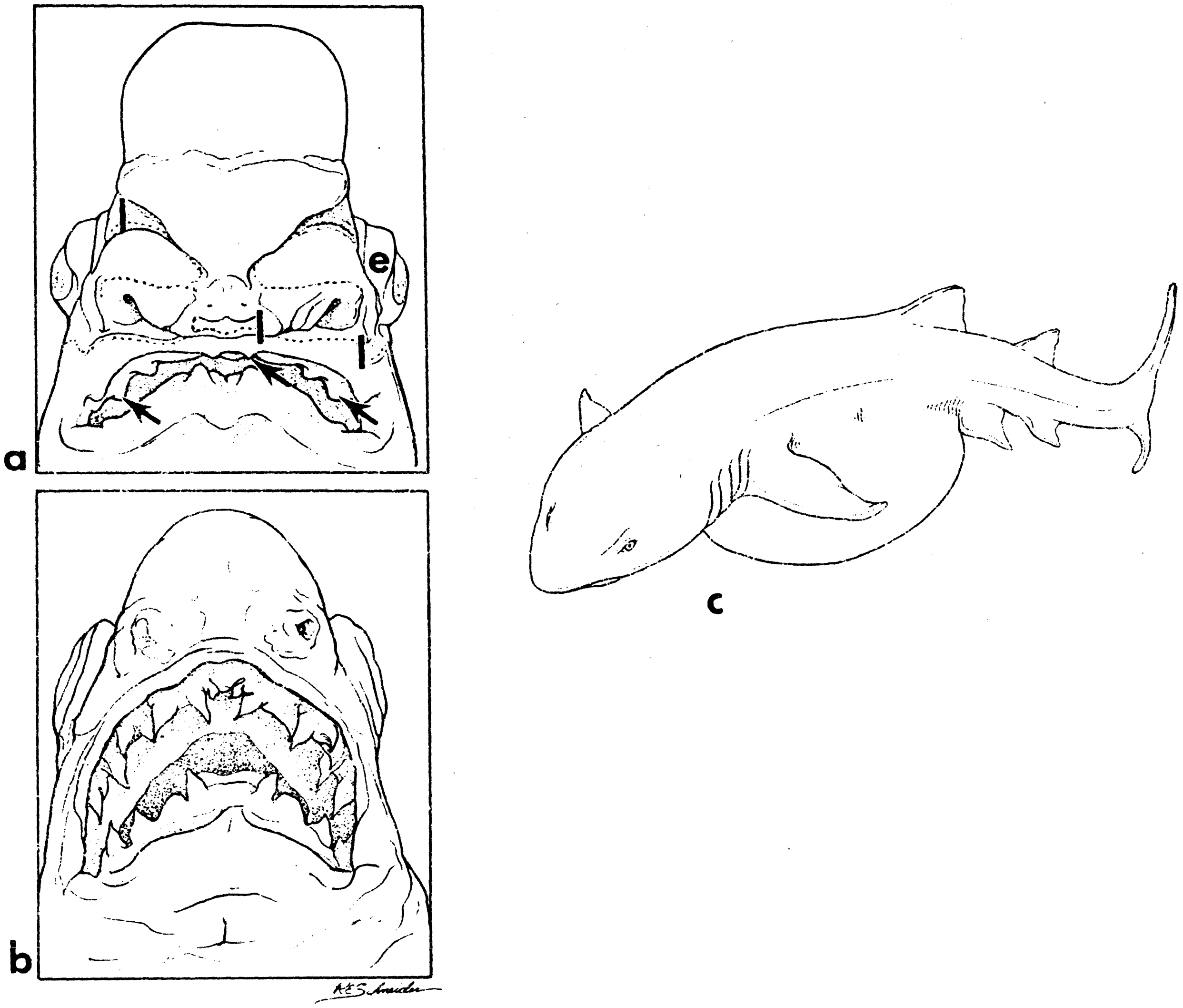

Figure 3. Developmental stages of the sand tiger shark, Odontaspis taurus (a) A 30 mm length embryo shows an extensively developed lateral line system (l), eyes (e) and tooth buds (arrows); (b) A 60 mm embryo shows full dentition resembling that of an adult; (c) A 100 cm. embryo shows its distended stomach containing eggs and siblings.

Litter sizes for the tiger shark are from 10 to 82 with gestation being slightly over twelve months.

Initially all embryos in this category are yolk dependent. Hamlett and Wourms (1984) have described the ultrastructure of the yolk sac and Hamlett et al. (1987) have presented details of the yolk syncytial-endoderm complex in the preimplantation yolk sac of Rhizoprionodon terraenovae. The yolk sac is remarkably similar in fine structure to the yolk sac of the internal incubator S. acanthias (Jollie and Jollie, 1967a). In addition to yolk digestion within the yolk sac, yolk is also transferred to the fetal gut by longitudinal rows of cilia lining the ductus vitellointestinalis. No internal yolk sac exists in placental sharks. It has been reported that external gill filaments of preimplantation sharks may play a role in the uptake of histotroph (Hamlett et al., 1985e).

Near mid-gestation, in carcharhinid sharks when the yolk is almost depleted, the yolk sac differentiates into a functional placenta. An ontogenetic transition occurs in which the yolk sac becomes progressively modified as a placenta for attachment to the maternal uterus and for subsequent trophic transfer.

The shark yolk sac undergoes a dramatic cytological and functional change during development. Prior to implantation the endoderm functions in the absorption of yolk and the transfer of nutrient substances to the vitelline circulation. The ectoderm is initially active in respiration. After implantation the endoderm becomes a quiescent boundary layer and the ectodermal epithelium assumes both nutritional and respiratory functions (Hamlett et al., 1985a,b,c).

Prior to implantation, each embryo resides in a thin amber colored egg envelope produced by the shell gland (Baranes and Wendling, 1981). Uterine flaps grow downward and upward to form uterine compartments which will contain each embryo with its surrounding egg envelope. The egg envelope is of adequate size to accommodate the term shark. An egg envelope reservoir, situated anterior to each uterine compartment, contains the excess envelope. As growth proceeds, the embryo fills the egg envelope and disrupts the septum separating the egg envelope reservoir from the uterine compartment. When the egg envelope is ruptured, at parturition, there is no evidence of the reservoir.

Of the known placental sharks in North Carolina, all possess an egg envelope with the exception of the blue shark, Prionace glauca (Otake and Mizue, 1985). Recently prenatal nutrient absorptive structures in selachians (Hamlett, 1986) and the comparative morphology of the elasmobranch placental barrier (Hamlett, 1987) have been reviewed.

The most thoroughly studied shark placenta is that of the sandbar shark, Carcharhinus plumbeus. Baranes and Wendling

(1981) described early developmental stages as well as uterine compartments and the egg envelope. In a series of papers Hamlett et al. (1985a,b,c) detailed the fine structure of the placenta and the maternal uterus. As described by Hamlett the placental unit consists of: 1) an umbilical stalk, 2) the smooth, proximal portion of the placenta, 3) the distal, rugose portion, 4) the egg envelope and 5) the maternal uterine tissues. Nutrient transfer is effected through the distal portion of the placenta. The smooth, proximal portion appears to be a water transporting structure (Figure 4). The gestation period is thought to be 8 to 12 months (Compagno, 1984). The reproductive biology of the blue shark, Prionace glauca, (Pratt, 1979) and the ultrastructure of the placenta has been described by Otake and Mizue (1985). Gravid females may bear from 4-135 pups per litter. The number of young varies more than any other placental shark and may be correlated to the size of the female (Compagno, 1984).

TeWinkel (1963a,b) described the egg, early embryos, preimplantation yolk sac and the placenta of Mustelus canis. Gilbert and Schlernitzauer (1966) described placentation in the silky shark, Carcharhinus falciformis and the bonnethead, Sphyrna tiburo. Further details of the placenta of S. tiburo can be found in Schlernitzauer and Gilbert (1966). Schwartz (1984) has described the occurrence, abundance and biology of the blacknose shark, Carcharhinus acronotus in North Carolina.

The reproductive biology of the Atlantic sharpnose shark, Rhizoprionodon terraenovae has been described (Parsons, 1983). The number of young per litter is 1 to 7, with 4-6 the most common. During the first 3 months, of a 10-11 month gestation period, the embryos rely on yolk for nourishment. As the yolk is depleted the yolk sac becomes modified into a placenta. It has recently been suggested that it might produce steroid hormones (Hamlett, 1889). The Atlantic sharpnose and some species of Sphyrna display filiform or club-shaped vascular appendages of the umbilical cord termed appendiculae. Hamlett (1986) has reported the epithelial cells to be of two types.viz, microvillar cells and cells engorged with granules. It is thought that these structures and a paraplacental nutrient absorptive organ. The morphogenesis and ultrastructural details of the appendiculae of the Atlantic sharpnose are currently being investigated (Hamlett, unpublished).

CONCLUSION

The reproductive modes of the elasmobranch fishes range from oviparous to viviparous. Extant species show reproductive mechanisms that span the continuum from yolk reliant to placental. All elasmobranchs are reproductively successful regardless of the mode of reproduction employed. These fishes represent an extant group that exhibits an evolutionary progression from egg layers to internal incubators with reliance on the mother for nutrition. Reproductive and evolutionary

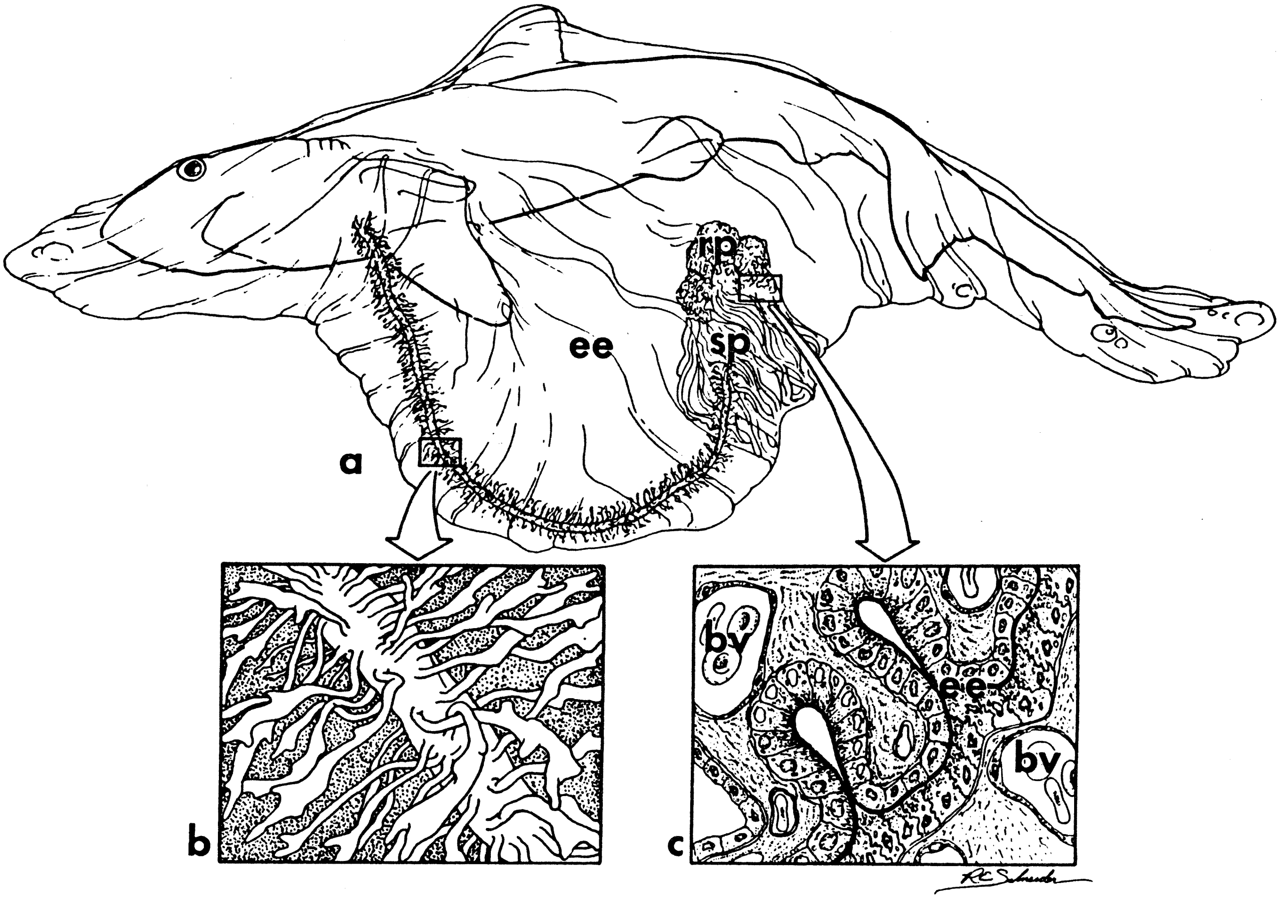

Figure 4. A near term Atlantic sharpnose shark, <u>Rhizoprionodon</u> <u>terranovae</u> (a) The fetus is enveloped by its egg envelope (ee). The placenta is divided into a smooth, proximal part (SP) and a distal, rugose portion (RP). The umbilical cord (UC) connects the embryo to the placenta; (b) Appendiculae adorn the umbilical cord; (c) The egg envelope (ee) separates the tissues of the fetal placenta (upper left) from the maternal tissues (lower right). Both tissues are rich in blood vessels (BV).

biologists can both profit by the study of this group of animals.

ACKNOWLEDGMENTS

I am indebted to Dr. Frank J. Schwartz, Institute of Marine Sciences, University of North Carolina for furnishing many of the specimens utilized in these studies and for access to the Institute's fish collection. Many specimens were obtained during cruises of the R/V Machapunga and R/V Capricorn. Otis Lewis, Joe Purifoy and Glen Safrit were helpful in the field. I wish to thank Roy Shneider for executing the line drawings. This work was supported by BRS grants 2-507-RR05700-14 and 2-507-RR05700-16 awarded by the Biomedical Research Support Grant Program, National Institutes of Health.

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DEEP SEA BENTHIC FISHES AND ISOPOD CRUSTACEANS IN RELATION TO DEPTH OFF THE CAROLINAS

Robert Y. George
Department of Biological Sciences
University of North Carolina at Wilmington
Wilmington, North Carolina 28403

ABSTRACT

The deep sea fish fauna off the coast of North Carolina was investigated on the basis of otter trawl samples from Permanent Study Sites on the Florida-Hatteras Slope (200-400m), Blake Plateau (600-800m) and over the Continental Slope (1800-2200m). The deep sea isopod fauna off North Carolina coast was studied on the basis of small biological trawl samples from the same study sites. The results of this study suggest that: (a) Several fish species off North Carolina in the Florida-Hatteras slope are also found in the straits of Florida. Their northern transport is facilitated by the Gulf Stream, (b) Fish fauna over the Blake Plateau and the continental slope contain typical deep sea elements, (c) Infaunal isopod genera exhibit well defined bathymetric zonation with asellote genera dominating the deep sea.

INTRODUCTION

Agassiz (1888) pointed out that the "fauna found at great depths in the ocean is peculiar and appears to contain many species of extensive geographic range." This broad generalization is based on the results of his extensive sampling of the deep sea fauna off the east coast of the United States during three cruises of the BLAKE. This conclusion is only supported by the pattern of distribution of large epifaunal animals such as the echinoderms and demersal fishes. On the contrary infaunal animals such as the polychaetes and isopods exhibit zonation in relation to isobaths and also exhibit extreme endemism in the abyssal faunal province off North Carolina (George and Menzies, 1972).

Recent studies on the infauna on the slope and rise off the Carolinas, on the basis of 130 box cores, revealed that infauna is not only rich but very diverse (Blake, 1988). This study clearly indicated that the deep sea environment off Carolinas is highly heterogeneous and attributed the cause for the high heterogeneity to the impact of currents, sedimentary regimes and topographic patterns off the Carolinas.

The deep sea environment off the Carolinas is one of the well explored abyssal regions of the World Oceans (Menzies, George and Rowe, 1973; Rowe and Menzies, 1968, 1969; Rona, Schneider and Heezen, 1967; Stefansson, Atkinson and Bumpus, 1971). In this paper, the deep sea fish fauna and the small infaunal isopod genera from the Florida-Hatteras slope, Northern Blake Plateau and the Continental Slope off North Carolina are identified on the basis of samples taken from the IMBR-Permanent Deep Sea Study Sites, along Transect Alpha and Beta, located southeast of Cape Fear, North Carolina. The results include: (1) data on vertical distribution of deep sea fish species and (2) vertical distribution of the infaunal isopods, both groups of animals examined from the same study sites.

Sampling Procedure and Research Vessels

The isopod crustacea in these two transects were collected during the following cruises: R/V EASTWARD cruise in August 1967; three cruises of R/V ADVANCE II in 1974-'76 summers, two cruises of R/V GILLISS in 1977-'78 summers and three cruises of R/V CAPE HATTERAS in 1984-'86 summers. The isopod samples were taken with a small biological trawl (SBT), outfitted with a 0.5 mm mesh net.

The deep sea fish and large epifaunal animals were collected by otter trawl from depths between 200 and 600 meters along seven transects off the southeast coast of the United States during the bench mark studies of the Bureau of Land Management (BLM), Department of Interior investigations that were conducted to obtain baseline data before any oil drilling activities in the Continental Shelf (George and Staiger, 1979).

In addition to the BLM samples, otter trawl samples of fishes and invertebrates were also taken during the cruises of R/V GILLISS and R/V CAPE HATTERAS in the IMBR Permanent Deep Sea Study Sites along Transect Alpha and Beta (Figure 1). The distance from the North Carolina coast and precise location of these study sites along different depth contours are shown in Figure 2.

Vertical Distribution of Deep Sea Fishes off Carolinas

The occurrence of various kinds of fish species from the estuarine waters to the marine waters down to a depth of 600 meters on the slope off North Carolina was the focus of discussion by Schwartz (1989). The fish distribution is undoubtedly influenced by seasonal changes in the shallow environment but in the deep ocean conditions there is a lack of any seasonal change in fish community as pointed out by George and Staiger (1979) in the benthic Ichthyofauna of the slope off southeastern United States. In the outer shelf, the spring fish fauna was dominated by the bothid flat fishes *Bothus ocellatus* and *Syacium papillosum*. These fishes were entirely absent in the Florida-Hatteras slope (200-400 m) which contained a different fish fauna as shown in Table 1. The fish fauna included, however, some shelf fish species such as *Urophycis regius*, mostly represented by adults. The juvenile *Urophycis regius* was dominant in the winter samples of the outer shelf off

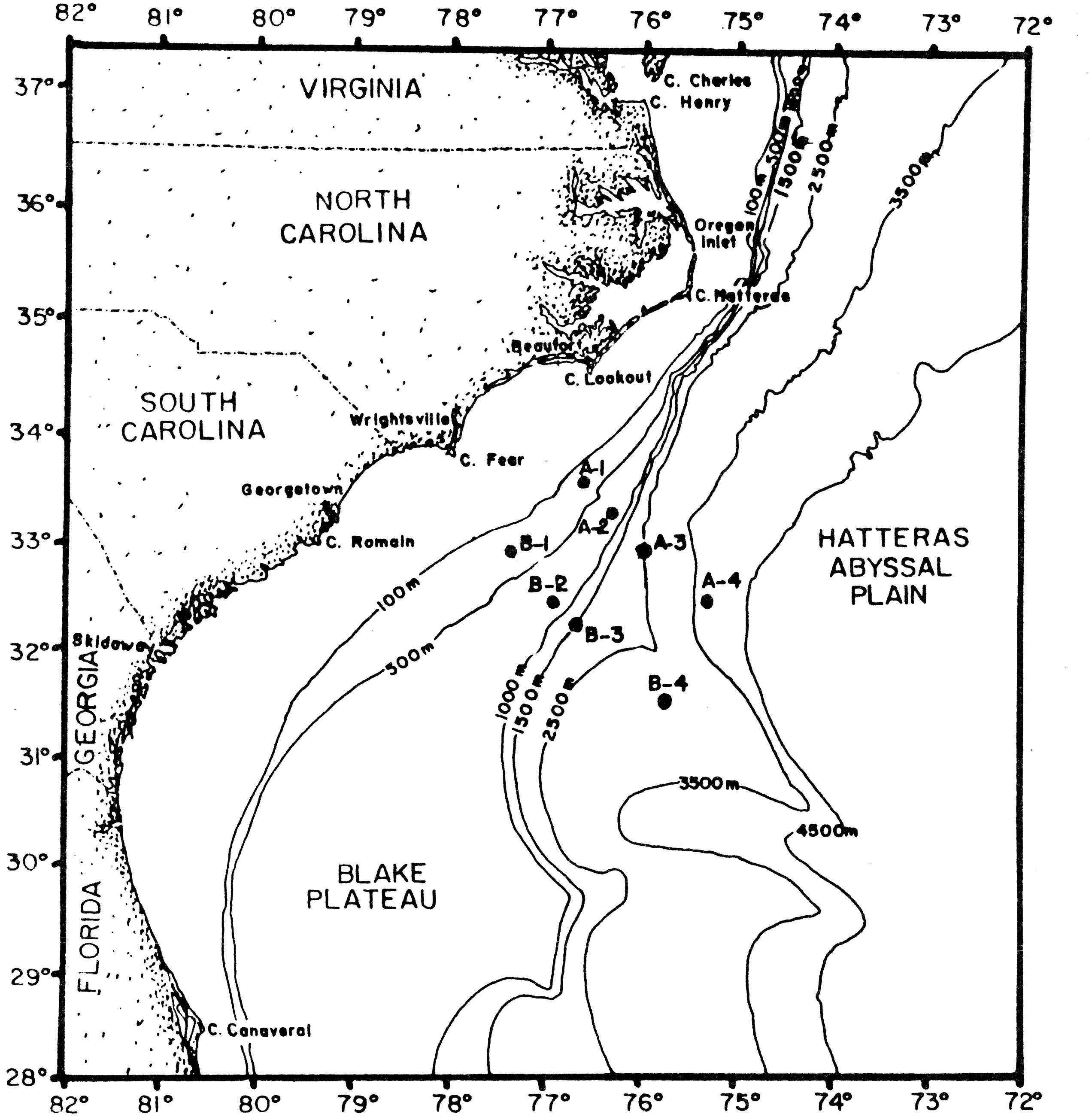

Figure 1. The location of Permanent Study Sites A-1 to A-4 and B-1 to B-4 off the Carolinas.

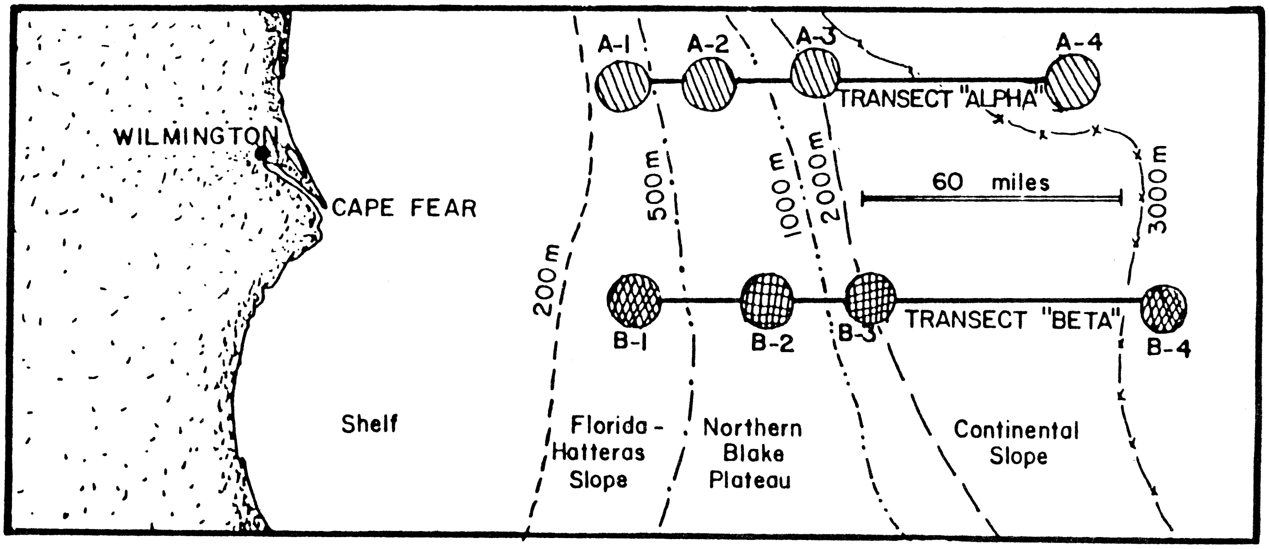

Figure 2. Transect Alpha and Beta, shown to reveal distance from shore, southeast of Cape Fear, North Carolina. Note the depth contours and topographic features.

Table 1. Deep Sea Fishes from Florida-Hatteras Slope (Site A-1 & B-1)

1.	Breviraja plutonia	8.	Urophyscis tenuis
2.	Urophycis regius	9.	Merluccius albidus
3.	Chlorophthalmus agassizi	10.	Perilus triacanthus
4.	Bregmaceros atlanticus	11.	Nezumia bairdi
5.	Laemonema barbatulum	12.	Lepophidium cervinum
6.	Citharichthys arctifrons	13.	Paralichthys oblongus
7.	Phycis chesteri	14.	Enchelyopus cimbrius

North Carolina. The Florida-Hatteras slope site off North Carolina was inhabited by some deep sea fishes such as the macrurid Nezumia bairdi. The fish species were typically archibenthal and therefore, the Florida-Hatteras slope represents a transitional faunal zone that is located between the outer shelf and the abyssal faunal province, as defined by Menzies, George and Rowe (1973).

It is of interest to point out that several fish species in Site A-1 and B-1 off the Carolinas, namely Laemonema barbatulum, Citharichthys arctifrons, Breviraja plutonia and Merluccius albidus are also dominant components of the demersal fish fauna of the straits of Florida (Staiger, 1970). The present study revealed that the fish assemblage in the Florida-Hatteras slope off North Carolina is a typical mixture of shelf penetrants, invaders from the deep sea and also migratory fishes from the Florida strait in the south, probably transported toward the north into the offshore sites of North Carolina by the Gulf Stream.

During the R/V CAPE HATTERAS cruise in November, 1985, two otter trawl samples were taken at a depth of 30 meters in a location between Cape Fear and the IMBR Permanent Study Site ALPHA-1 (Lat. 33° 54.9'N, Long. 77° 17.97'W). The following twelve fish species were encountered in the samples:

1. Sphoeoides dorsalis (Marbled Puffer)
2. Monacanthus hispidus (Planehead File Fish)
3. Lactophrys guadricornis (Cowfish)
4. Bothus ocellatus (Eyed Flounder)
5. Bothus sp. (Spottail Flounder)
6. Prionotus carolinus (Northern Sea Robin)
7. Paralichthys lethostigma (Southern Flounder)
8. Calamus leucosteus (Whitebone Porgy)
9. Haemulon plumieri (White Grunts)
10. Stenotomus caprinus (Long Spinned Porgy)
11. Calamus nodosus (Knobbed Porgy)
12. Rhomboplites aurorubens (Vermillion Snapper)

These are typically mid-shelf fish species and these species are absent in the Florida-Hatteras slope.

The fish fauna of the northern Blake Plateau off North Carolina includes 25 species as shown in Table 2. The data suggest that the fishes represent a distinct deep sea assemblage except for a few exceptions. Dibranchus atlantius is typically a shallow water fish which penetrates down to 1000 m. This species is very common over the Blake Plateau. Similarly, another shallow water fish from the north, namely the hag fish Myxine glutinosa occurs in great number over the northern Blake Plateau off North Carolina. This species is almost littoral in distribution, in the high latitudes near Norway and Sweden but submerges to deeper depths and commonly found between 600 and 800 meters over the Blake Plateau off North Carolina. This pattern of distribution is essentially an illustration of typical submergence of northern species. There are several fish species that occur over the Blake Plateau, which are also found in the continental slope at depths exceeding 1000 m. Such invaders from the deep sea in the Blake Plateau are the abyssal eel Synaphobranchus kampi, the rat tail fish Nezumia bairdii and Coryphenoides rupestris.

Table 2. Deep Sea Fishes from the Blake Plateau (600-1000m) off North Carolina (Site A-2 & B-2)

1. *Myxine glutinosa*
2. *Dibranchus atlanticus*
* 3. *Nezumia bairdii*
* 4. *Synaphobranchus kaupi*
5. *Holosaurus guentheri*
6. *Dicrolene intronigra*
* 7. *Coryphaenoides rupestris*
* 8. *Lycodes brunneus*
9. *Lycenchelys verrilli*
10. *Cottonculus thomsoni*
11. *Macrozoarces americanus*
*12. *Nezumia aequalis*
*13. *Etmopterus bullisi*
*14. *Breviraja plutonia*
*15. *Pseudophichthys splendens*
*16. *Aldrovandia phalacra*
*17. *Chlorophthalmus agassizi*
*18. *Laemonema barbatulum*
*19. *Urophycis regius*
*20. *Merluccius albidus*
*21. *Bathygadus melanobranchus*
*22. *Coryphaenoides armatus*
*23. *Trachonurus villosus*
*24. *Citharichthys arctifrons*
*25. *Glyptocephalus cynoglossus*

*Species collected from B-2 during GILLISS cruise and identified by Dr. Jon Staiger of the University of Miami

The fish species of the continental slope at sites A-3 and B-3 for 1500 m to 2500 m are listed in Table 3 and also shown in Figure 3. These abyssal fishes are not at all encountered in the shelf depths but these species are widely distributed along the slope depth off the east coast of the United States. Most of these deep sea fish species off North Carolina were also captured by otter trawls off the coast of New Jersey at similar depths in the Deep Water Dumpsite Site 106 and adjacent areas (Musick, Wenner and Sedberry, 1975).

There are three congeneric species of the macrurid genus *Coryphaenoides* off North Carolina coast. It appears as though the *C. rupestris* is the archibenthal species living over the Blake Plateau and less dominant in the slope beyond 1000 m. *C. carapinus* becomes a dominant fish species around 1200 m and extends as deep as 2500 m. However, *C. armatus* is the most common inhabitant at depths greater than 2000 m and remains as the most abundant fish in site A-3 at 2500 m.

Coryphaenoides rupestris is also one of the few commercially important fish species off North Carolina. In the northern waters, this deep sea fish species has been exploited by the Soviet Fisheries and its potential for commercial exploitation off North Carolina is still not seriously considered. Musick et. al. (1975) reported catch rates of *C. rupestris* in the Norfolk Canyon as high as 1.6 metric tons per hour with the 45 foot trawl.

Table 3. Deep Sea Fishes from the Continental Slope off North Carolina (Sites A-3 & B-3) (*also found over the Blake Plateau)

1. *Hydrolagus affinis*
2. *Raja bathyptilia*
*3. *Synaphobranchus kaupi*
4. *Holosauropsis macrochir*
5. *Notacanthus chemnitzi*
6. *Alepocephalus agassizii*
7. *Bathysaurus ferox*
8. *Benthosaurus grallator*
9. *Coryphaenoides armatus*
10. *Coryphaenoides carapinus*
*11. *Glyptocephatus cynoglossus*
12. *Antimora rostrata*
13. *Bathypterois grallator*
14. *Ipnops murrayi*

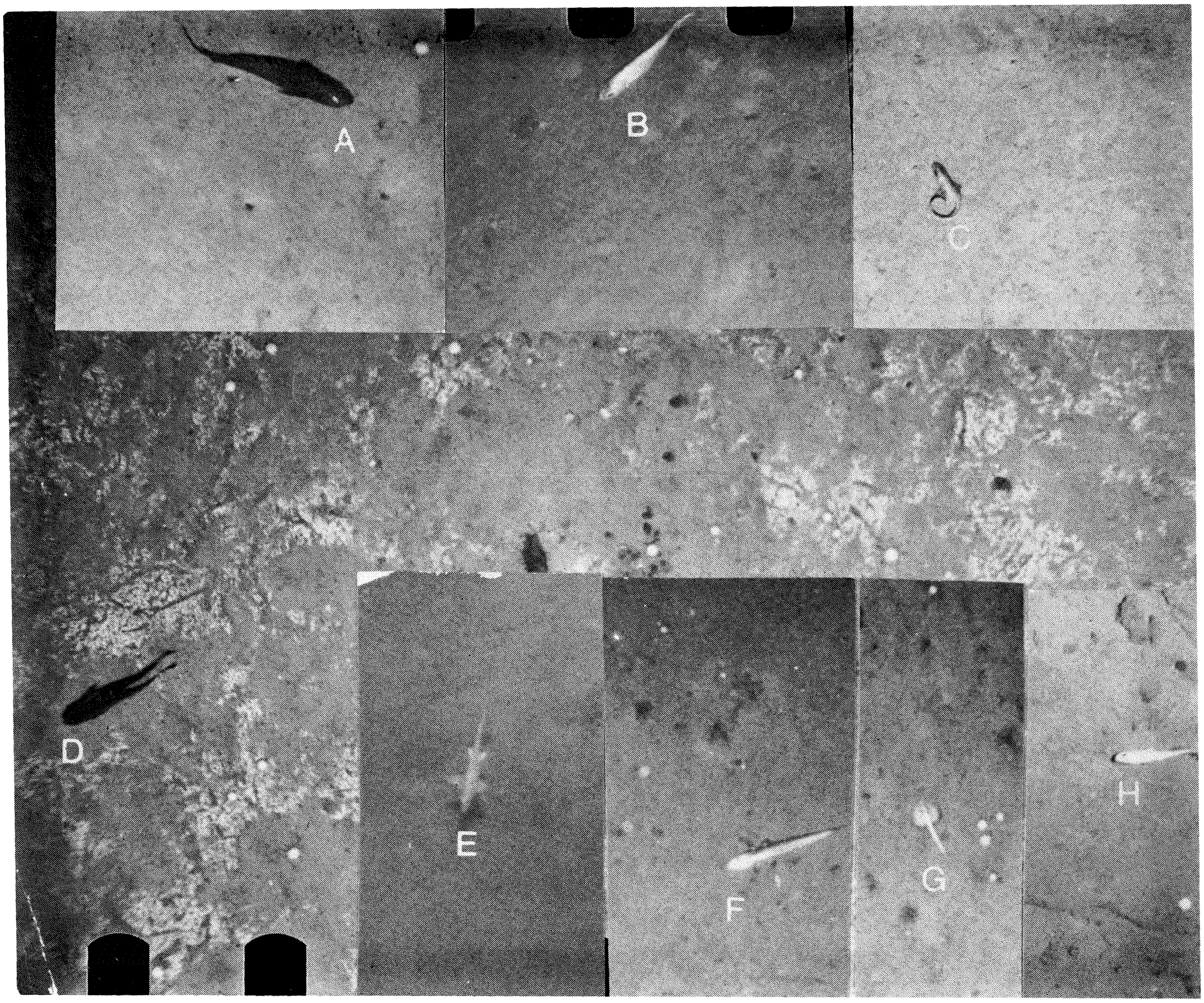

Figure 3. An assemblage of solitary deep sea fishes in Site A-3 over the Continental Slope off North Carolina.

Vertical Distribution of Isopod Crustacea off Carolinas

The vertical distribution of isopod genera and species off North Carolina coast suggested the presence of discrete bathymetric zones in the deep sea (George and Menzies, 1972). On the basis of the small biological trawl (SBT) samples taken in the IMBR Permanent Deep Sea Study Sites (A-1, A-2, A-3 and B-1, B-2, B-3), the isopod crustacea revealed a pattern of distribution that indicated three apparent trends, namely (a) Invasion of shallow shelf genera in the deep sea, (b) *In situ* sympatric speciation of typically abyssal isopod genera and (c) Colonization of the deep sea off North Carolina by isopod genera from distant geographic zones.

In the continental shelf off North Carolina the isopod fauna is largely represented by primitive groups such as Flabellifera (represented by the genera *Cirolana*, *Ancinus* and *Serolis*) and Anthuroidea (represented by the genera *Ptilanthura*, *Horoloanthura*, *Panathura*, *Accolathura*, *Apanthura* and *Xenanthura*). It is evident from the data that Anthurid isopods are the most dominant in the continental shelf of North Carolina (George and Menzies, 1972). In the deeper depths (100-400 m) over the Florida-Hatteras slope, the anthurids are still dominant with species belonging to four genera (Table 4).

The isopod fauna of the northern Blake Plateau off North Carolina (600-1000 m) suggested that the anthurid isopods are completely absent and the most dominant group is Asellota which is represented by six genera, namely *Eugerda*, *Desmosoma*, *Munnopsis*, *Dendromunna*, *Notoxenoides* and *Paramunna* (Table 4). The assellote isopods are evidently more specialized and possibly evolved *in situ* in the deep sea environment. The Blake Plateau isopods belong to two categories; one exhibiting closer affinity to isopods of shallow water origin. Examples for this pattern include species of the blind genus *Paramunna* and *Dendromunna* that are closely related to eye-bearing genera of the family Munnidae. The second category includes genera such as Munnopsis and Desmosoma, having closer affinity to isopods of deep sea origin. The Blake Plateau isopod fauna is, therefore, archibenthal in nature with a combination of isopod genera of both shallow and deep sea origin.

The majority of the isopod fauna of the upper (1200-2500 and lower 3000 m) continental slope belongs to the group Asellota. The upper slope off North Carolina contained species belonging to 10 asellote genera and the lower slope contained species belonging to 13 asellote genera (Table 4). The abyssal isopod genera off North Carolina are Shown in Figure 4. The non-asellote isopods in the deep sea environment off North Carolina belong to two genera, one valviferan isopod *Astacilla* from the continental rise and another Flebelliferan Isopod *Serolis* from 3840 meters over the continental rise. George (1986) described this blind species of *Serolis* as *S. agassizi*,

Table 4. Deep Sea Genera of Isopod Crustacea off North Carolina Coast in Transect Alpha and Beta (see Figures 1 & 2 for location of IMBR Study Sites)

IMBR Study Sites	Depth (meters)	Isopod Genera	Isopod Group
I. Florida-Hatteras Slope off North Carolina			
Alpha 1 & Beta 1	200-500	1. *Ptilanthura*	Anthuroidea
		2. *Accalathura*	Anthuroidea
		3. *Apanthura*	Anthuroidea
		4. *Calathura*	Anthuroidea
		5. *Serolis*	Flabellifera
		6. *Cirolana*	Flabellifera
II. Blake-Plateau off North Carolina			
Alpha 2 & Beta 2	500-800	1. *Cirolana*	Flabellifera
		2. *Gnathia*	Gnathoidea
		3. *Eugerda*	Asellota
		4. *Desmosoma*	Asellota
		5. *Munnopsis*	Asellota
		6. *Dendromunna*	Asellota
		7. *Notoxenoides*	Asellota
		8. *Paramunna*	Asellota
III. Continental Slope off North Carolina (Upper Slope)			
Alpha 3 & Beta 3	1500-2200	1. *Dendrotion*	Asellota
		2. *Desmosoma*	Asellota
		3. *Ilyarachna*	Asellota
		4. *Macrostylis*	Asellota
		5. *Eurycope*	Asellota
		6. *Acanthocope*	Asellota
		7. *Haploniscus*	Asellota
		8. *Ianirella*	Asellota
		9. *Haplomesus*	Asellota
		10. *Heteromesus*	Asellota
IV. Continental Slope off North Carolina (Lower Slope)			
Alpha 4 & Beta 4	3200-3600	1. *Dendrotion*	Asellota
		2. *Desmosoma*	Asellota
		3. *Ilyarachna*	Asellota
		4. *Macrostylis*	Asellota
		5. *Eurycope*	Asellota
		6. *Acanthocope*	Asellota
		7. *Haploniscus*	Asellota
		8. *Ianirella*	Asellota
		9. *Haplomesus*	Asellota
		10. *Heteromesus*	Asellota
		11. *Rhacrura*	Asellota
		12. *Antennuloniscus*	Asellota
		13. *Hydroniscus*	Asellota

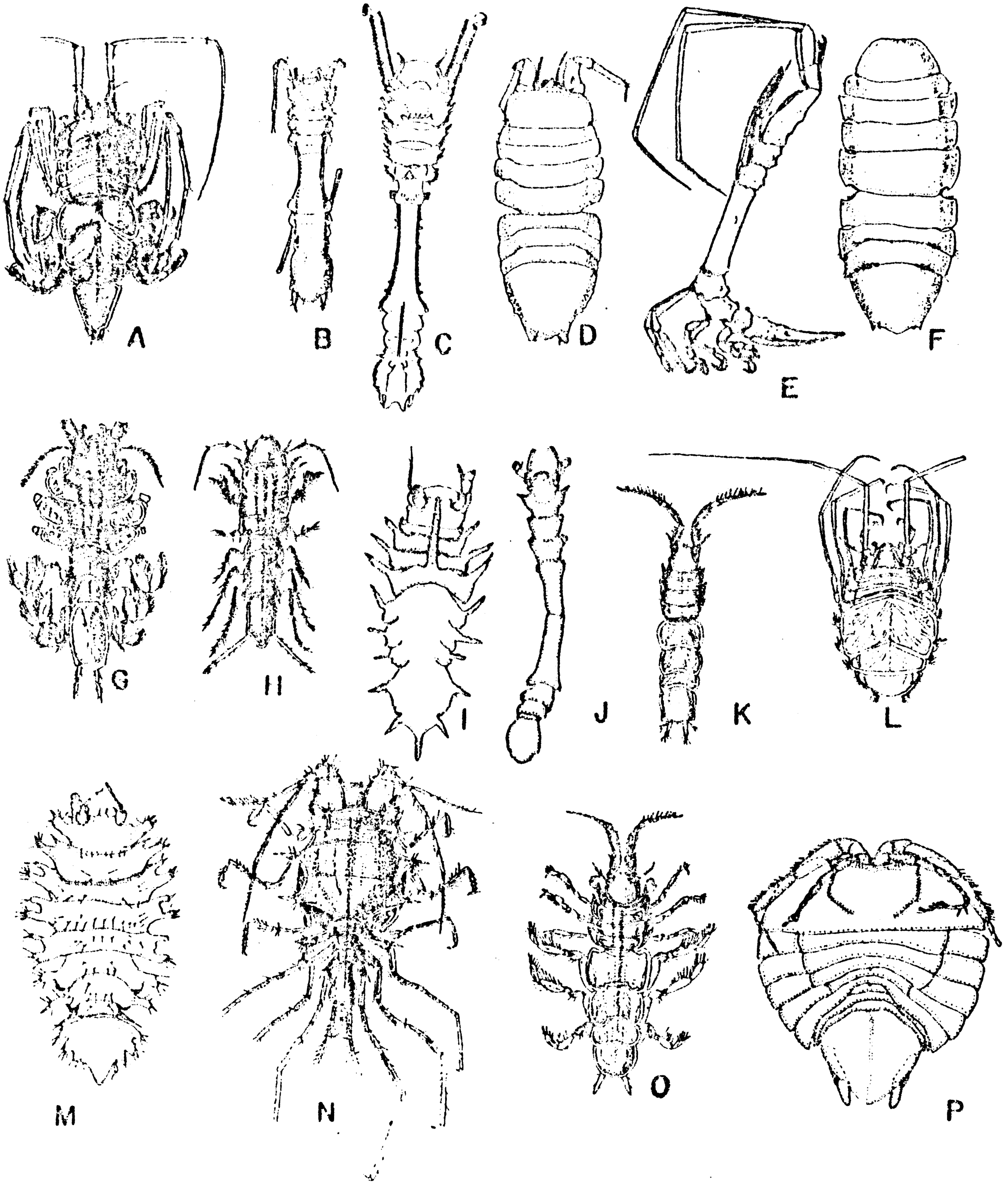

Figure 4. Isopod Genera from the Continental Slope and Rise off North Carolina Coast. A. Ilyarachna; B. Ischnomesus; C. Haplomesus; D. Antennuloniscus; E. Astacilla; F. Haploniscus; G. Munnopsis; H. Macrostylis; I. Acanthocope; J. Heteromesus; K. Desmosoma; L. Eurycope; M. Ianirella; N. Dendrotion; O. Eugerda; P. Serolis.

which is one of the few members of this polytypic genus *Serolis* occurring north of the equator. This deep sea species is markedly different from the shelf congeneric species *S. mgrayi* from a depth of 20 meters off the Carolinas and Georgia. However, *S. agassizi* from the continental rise is closely related to another blind abyssal congeneric species *S. vemae*, known from the Hatteras Abyssal Plain in the North Atlantic Ocean and also from the abyssal depths of the South Atlantic Ocean. *S. vemae* lives in the abyssal plain where the Antarctic Bottom Water (ABW) flows from the southern hemisphere. This bottom current, at depths greater than 5,000 meters, is possibly responsible for bringing *S. vemae* from the south into the Abyssal Plain off North Carolina. Perhaps, in the course of evolution in the deep sea, *S. agassizi* originated from *S. vemae*. It will be of interest to examine the chromosome numbers and configurations of the congeneric species of *Serolis* in the deep sea and in shallow depths off North Carolina.

Vertical Zonation of Infauna (Isopods) versus Epifauna (Fishes)

The distribution of infauna in the deep sea off North Carolina is known to be largely influenced by the sedimentary regimes. Tietjen (1971) reported on the ecology and distribution of deep sea meiofauna off North Carolina. The shelf and Florida-Hatteras slope meiofauna consisted of mainly nematodes (dominant taxon) and large numbers of harpactacoid copepods, ostracods, foraminifera, gastrotrichs and polychaetes. At depths greater than 500 m only nematodes and foraminifera were present in large numbers. The major change in meiofauna seems to occur around 500 to 700 m over the Blake Plateau when the sedimentary regime changes from a sand to silty sand. The same pattern is also seen in the macroinfauna as revealed in the vertical distribution of isopod crustacea. Over the Blake Plateau, the isopod fauna changes from a Flabellifera-Anthurid dominated composition to an Asellota dominated composition at about 500-700 m. These Asellote isopods are suited to live in the silty-sand sediment with their elongated and slender locomotor appendages.

The vertical distribution of epifauna in the deep sea off North Carolina is known to be influenced by large physiographic features and the Western Boundary Undercurrent which impinges on the bottom (Rowe and Menzies, 1968). This current over the lower slope is split into sections, and populations of large epifaunal animals off North Carolina show restricted distributions, which are narrow ribbons parallel to depth contours. The Blake Plateau and the upper continental slope are more under the influence of the Gulf Stream, which shows marked seasonal variations in the boundaries. The demersal fish distribution in the outer shelf and over the Blake Plateau is evidently subjected to the influence of the northward-flowing Gulf Stream.

CONCLUSION

The deep sea fish fauna off North Carolina is influenced by the undercurrents prevailing in this region. There is some evidence that the northward flowing Gulf Stream brings the southern deep water species along the Florida-Hatteras slope. The Blake Plateau fish fauna is a mixture of shelf penetrants, deep sea invaders as well as some northern species. The infaunal isopod fauna over the Blake Plateau is also a mixture of genera of shallow water origin and genera of abyssal origin. A true picture will emerge only after the species of these genera are identified. The slope isopod fauna off North Carolina is composed of exclusively cosmopolitan deep sea isopod genera.

ACKNOWLEDGEMENTS

I wish to thank the Duke-UNC Oceanography Consortium for sponsoring the R/V CAPE HATTERAS cruises. I am also grateful to the U.S. National Science Foundation-Division of Ocean Science for sponsoring the R/V GILLISS cruises and the Office of Naval Research for supporting R/V ADVANCE cruises off North Carolina.

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PART III. NORTH CAROLINA MARINE POLICIES AND PROGRAMS

Chapter 7. Marine Science Policies

Chairperson - Dr. Robert Y. George

WELCOMING REMARKS

Dr. William H. Wagoner, Chancellor
University of North Carolina at Wilmington

Congressman Rose, Secretary Rhodes and other distinguished guests, it is my pleasure to welcome you to this campus.

If I can recall, back in 1968 when I came to this campus, then it was composed of 82 faculty members and 1100 students. I determined in that first week that this campus must make its mark in a very important enterprise and that enterprise would be the study of the rivers, streams and estuaries and oceans, lakes and sounds that are the very essence of North Carolina.

Just a little over four hundred years ago, this state had its beginnings over on Roanoke Island, from the sea. Up and down the coast settlements were made, then the Piedmont was settled and then the mountains. But, we must never forget this state had its roots from the sea and on the sea and in the water.

One thing I was impressed with in 1969 and throughout my tenure here is that with the great surge forward and exploration of outer space, it continually amazes me that today scientists know probably more definitively about the surface of the moon than they know about what is out here now seven miles, five miles, three miles down. I have this strange feeling that the salvation of the human race on this planet is, somehow or other, inextricably linked to the ocean and the aquatic nature of this planet. I am sure, this symposium on Coastal Oceanography of North Carolina will make contributions to a better understanding of the waters of North Carolina.

CONGRESSIONAL PERSPECTIVES ON MARINE POLICIES

The Honorable U. S. Congressman Charles Rose

Thank you, Dr. Wagoner. Secretary Rhodes, Dr. Costlow, Dr. George, distinguished participants in this Oceanography Symposium, it's a pleasure to be here and to say a few words of welcome and to express to you my support for this conference and the subject matter of your discussions here for several days.

The bottom line for me in the subject matter is whether or not we are properly <u>using</u> or whether or not we are <u>abusing</u> our oceans' resources. That is a difficult political problem; that is where politics and science need to learn how to cooperate better.

In Washington, yesterday afternoon, we passed a piece of legislation, called HR1171; it's called the National Oceans Policy Commission Act. That legislation was widely lobbied for by the Coastal States Organization. You're familiar with that organization and its concern about the exclusive economic zone, the 200-mile limit that surrounds the United States, and its territories. Those of us in Congress who have coastal districts, have a very unusual responsibility to make our other colleagues from inland districts aware of what is happening at the coast. So, with my welcome today, I will challenge you to find new and creative ways that attract our colleagues from land-locked districts to come to Beaufort and Wilmington, to talk firsthand with scientists about what is happening with our ocean resources and what, if anything, we should be expecting for the future. The tough political problem, of course, is, are we doing things now that will jeopardize the future and, if so, can we pinpoint those things with certainty and do we have the political will and the courage to take steps to stop them if what we are doing is harmful? I would say that I challenge you as participants in this Oceanography Symposium to challenge us where you think the future is in jeopardy; let us know. Where you think the regulatory process is working, tell us that, too. Give us your input. This is not a flower garden for the sake of just growing flowers; this is an opportunity for you to give critical input to policy makers.

I certainly hope that as the final report of this Symposium is written that it will be communicated with us the kinds of things that you would recommend. We are very fortunate to have here today the man in North Carolina who has the hands-on responsibility for policy as it relates to our ocean and coastal resources. I am sure Secretary Rhodes is sensitive to what you have to say and to what your science discovers and deals with.

It is my privilege as a federal representative of this area, to deal rather consistently or continuously with the Corps of Engineers. I have observed for many years the conflict that they have had with conservation groups over such issues as the use of wetlands, all of which ultimately has its effect on our ocean policy and marine resources.

I have had a very interesting summer and fall working with an inventor from Wilmington, on a device that he and I believe will stop beach erosion. I wish I could tell you all the details right now, but I can not until the device is patented. New Hanover County is blessed with fertile fields as well as fertile minds and this one has come up with a design for a movable sea wall that I hope and believe will challenge the imagination of regulators and policy makers at some point in the future. We've got to do something constructive and creative about beach erosion. As you know, the discussions range from pouring more federal money into beach renourishment, to doing nothing. If something else could come along that would be useful, it would be very good, in my opinion.

I am going to have to leave you in a few minutes and go back to Washington, but I did want to come here and say that this is an important area of life and an important area of concern. I commend those of you who have given your career to oceanography, marine resources, and the marine sciences. We, in Washington, need more input. We need to know more about your craft and your art. When I first went on the Agriculture Committee, I went to North Carolina State University with some of my colleagues from the House of Agriculture Committee and we said to the people in Raleigh in the School of Agriculture, "tell us what you think we need to know about the future of agriculture." We spent two exciting days being given many lectures by professors. I would say to Duke and to UNC Wilmington, put something like that together for the North Carolina Congressional Delegation. Let us bring them to Wilmington and you tell us what is happening in ocean research, what is taking place in our rivers and in our streams. I get letters from people who say we will never have enough shrimp in this part of the world as long as we allow shrimpers to shrimp our rivers and our backwater areas, such as our sounds. Is that correct? I would like to sit down with some of you and discuss that sometime. It would be a nice little political problem if you all decided that we are going to have no more shrimping in the Cape Fear River, the inland waterway or the Pamlico Sound; but is that best, would that be best for the future of the shrimp industry? We ought to sit down and try to discuss tough questions like that sometime, as soon as possible. I will be happy to organize it from the North Carolina Congressional Delegation's point of view. Have a good Symposium and let us hear from you. Thank you very much.

POLICY STATEMENT ON NORTH CAROLINA MARINE RESOURCES

The Honorable Thomas Rhodes
Secretary, North Carolina Department of Natural Resources

Thank you, Dr. George. Any of you who have been to sea should realize the significance of going out and doing work in the offshore waters. Sometimes it is not all the glamour that it is made up to be, between the rocking and the rolling. Because oceanographers like Dr. George and others are willing to go out and endure that sometimes harsh environment, we are able to learn what we need to know in order to ensure the future of that very valuable resource. Dr. Costlow, it is good to see you today. He is involved in this project as well, in trying to ensure the protection and future of the state's fishery resources. We appreciate that, as well.

We are all located here today in the state in an area that was once, and I think very aptly, described as the "goodliest land under the cope of heaven." I think when Governor White first landed on this land back in the year 1585, I doubt if he was spending much time at that point speculating on how he could overwhelm the natural resources of the area. In fact, he was probably scared to death, because the natural resources were in great danger of overwhelming him. But, for the next century after that, the trees grew faster than they could be cut, the rivers flowed faster than they could be polluted, and things went along pretty well. I suppose the second century after that, we began catching up doing our share to try and cut the trees a little faster and pollute the streams a little faster. By the end of the third century it became apparent to everyone who was looking that the ecosystem was being strained, and strained mightily, by the rising populations that were taking place. I think nowhere in the state had demands been made on our natural resources than on the coast; not only because of the state's rise in population, but also because people like to live near water; the coast, the sounds, the oceans, the beaches and, even in some inland areas near the lakes. That brings its own unique set of problems as people begin to migrate to those very sensitive and critical areas.

We have got problems in North Carolina, not only because people are moving down to the coast because of their interest in what a coast has to offer them. Also, for the fact that great rivers that wash down to the coast carry with them the jetsam of all of the industry and growth that is taking place in the piedmont that washes into the rivers, be it through agricultural runoff, urban runoff or just discharges from our lakes and rivers, typically finding its way into the coastal area. So, we not only have to deal with cleaning up our own act in terms of people who live on the coast, we also have to worry about what is happening 100 miles upstream; that makes our job much more difficult. Whatever the cause, whether it be people or pollution or industries upstream or the increasing material standard of living on the coast, I think it is imperative that we all work together to try and come up with solutions to ensure our future. I think that is the value of a symposium such as this, where we can bring together the knowledge that we have today so we can see what has been done and maybe from that learn, in fact, what we need to do in the future, where the proper money needs to go and where the research needs to be aimed in order to get any answers that we seek. We have come a long way from those early days; I think we have gone from punching a road through the wilderness, to try and make sure that something is at the end of the road. We, even today, are thinking more in terms of maximum sustained yield and maximum sustained service instead of maximum rate of extraction. We are also vitally concerned about even protecting some of those areas and leaving them preserved, unchanged for future generations to enjoy. All of that is good, but I think we need to do more.

The Department of Natural Resources and Community Development, which I represent, has the responsibility for helping solve part of this puzzle. This primary agency in North Carolina is responsible for environmental protection and conservation of our natural resources. To do that, we administer a wide range of natural resource programs within our Department. Our divisions of Marine Fisheries, Coastal Management, Environmental Management, Water Resources, Soil and Water Conservation, Forestry and Wildlife Resources all play a vital role in protecting marine resources and ensuring environmentally sound development along our 300 miles of ocean front and over 4000 miles of estuarine shoreline that we have in the state. There are probably few programs, few functions and, in fact, probably few individuals in the state that are not impacted by what we do. Even the Community Development side of our Department is heavily involved in the coastal area; our Division of Community Systems is working on a day-to-day basis with local governments in helping them develop good land-use plans and carrying those out. Our Division of Parks and Recreation is trying to help provide parks and recreational opportunities in the coastal area. With this broad range of activities and responsibilities, the Department has to play a major role in the development and implementation of state policies that effect marine resources. If you wanted to break down the overall goals and objectives of the Department, the NRCD (that is an acronym, you have to learn that in order to get into government - that is Natural Resources and Community Development), into three major goals or three major areas that we are working on, it would be these:

1. To preserve and enhance the existing environmental values through our efforts to protect our estuaries, ocean waters, beaches, natural areas, and fish and wildlife resources and habitats.

2. To promote and protect the health of our traditional coastal industries, especially commercial fishing and tourism.

3. To help ensure that the economic development that is going to take place in the coastal area is done in a manner that is high quality and environmentally sound.

Although these policy objectives on the surface may appear simple and straightforward, the manner of implementation is very complex and is often impeded by an equal number of complex problems and, at times, lacks a very clear definition. To support our policy objectives, the Department must invest considerable time and funds in research and information collection before effective programs for protection and resource enhancement can be designed. Lack of solid information on which to base policy decisions and program design presents a formidable obstacle when attempting to deal with problems as complex as estuarine water quality and the productivity of our marine fisheries.

With this in mind, I believe overall state policy can be best understood by taking a look at some of the initiatives the state now is taking in trying to accomplish our overall task. One is the area of coastal water quality. North Carolina faces a continuing threat of degradation of our coastal water quality from a lot of sources: accelerated urban development on the coast, large-scale agricultural operations near the coast, urban and industrial development upstream, degradation of our estuarine waters by a large number of factors, all of which have an impact on coastal life.

The closure of shellfish waters in the state is sometimes a good key indicator of our overall water quality. We are pleased with the fact that the number of acres in the state closed to shellfishing has actually decreased since 1976. That does not mean we have solved the problem because in a lot of areas, in fact, the number of acres closed has increased. Overall, though, it has decreased and that means at least we are trying to do some of the right things. But, we remain concerned that the largest cause of pollution today is probably the combined impact of urban residential development, agricultural development and discharges from municipal and industrial waste treatment plants. We try to focus our attention on those areas and deal with those particular problems, hoping that if we can do those jobs better we can have a further impact on the coast.

The major thrust of our efforts to protect marine resources and enhance the health of our commercial fishing industry is a comprehensive state initiative to try and protect estuarine water quality. This initiative has both immediate and long-term priorities that we have developed. Our most immediate concern is to restore the health of the commercial fishing industry which recently has been hit by a number of problems that apparently are related, in some way, to deteriorating ocean and estuarine water quality, ulcerative mitosis being one of these is a growing threat to certain commercially valuable species. The recently discovered crab disease taking place primarily in Albemarle and Pamlico, but widespread, is of considerable concern to our shellfishermen and, in all likelihood, appears to be related in some way to estuarine water quality, even though the particular source of the cause of that has of yet been undetermined. Algae on some of our major rivers continue to pose a threat to primary shellfish nursery areas and contribute to the overall degradation of the estuarine system. We need to be working as fast as we can to try to solve these problems. We cannot and must not let them overwhelm us in the final analysis. We have active ongoing programs and departments to provide monies for research and provide technical assistance to try and overcome these problems.

The Department is also involved in several other shorter-term initiatives that are designed to help us protect coastal water quality. One initiative is Coastal Water Classification Studies, which need to be done to ensure that all of our sensitive waters in the state are properly classified to protect our shellfish and other sensitive uses while allowing responsible growth and development where environmental impact is known. This is a formidable task which is not as easy as it might sound. We need an updated mapping system, which we are now working on, of our shellfish beds throughout the state so that we will know where those valuable resources are. This has really never been done in a comprehensive way in the state, and something that we are working on. This, however, will support reclassification of coastal waters - the first step that you need before you can properly classify is to know what a resource is, how valuable it is and what the impact is. It will also allow us to refine, or fine-tune, our regulatory program to provide opportunities for development that we know will take place and have minimal impact on our environmental system.

Regarding continuation of our studies of the impact of marine operations and urban stormwater runoff, I will mention that marinas, incidentally, have kind of a separate impact of their own and we are doing marina impact studies that we hope will result in new standards for marina construction and maintenance and that is an important part of our process. We have coastal stormwater regulations in the state. Governor Martin instituted in North Carolina, for the first time ever, stormwater regulations through the Environmental Management Commission. I think that is a great undertaking. There is one catch to that in that the regulations carry a "sunset" clause and are due to expire on December 31 of this year. This means that the Environmental Management Commission is very busy right now trying to take a look at how to implement stormwater regulations, deciding whether to reauthorize or whether to modify the regulations. There is a lot of discussion going on about that. You will be reading more about that in the coming days; in fact, the Environmental Management Commission in the state has it on their agenda to try and reach a resolution on this matter.

Our long-term objective in dealing with the complexities of maintaining coastal water quality is a thorough and comprehensive understanding of all the factors that contribute to the deterioration of estuarine water quality. A major initiative in this area is the Albemarle/Pamlico Estuarine Study, a major effort in the state including several federal agencies, our Department, other state agencies, local governments, private citizens all trying to work together in what is now a five-year and a $5 million project to help provide the federal and state resource managers and local officials with the best possible information they can have so that the decisions are based on sound information and we can minimize the given impacts on the environment.

Tourism and recreation is another area that plays a very important role in any coastal environment. We have a new state policy that is currently in the planning stages. Governor Martin has asked us to do this planning. It is known locally as a "coastal initiative." The goal is to better plan how we can promote tourism and recreational opportunities in and around our sounds, beaches and coastal area while, at the same time, providing any necessary levels of protection that are needed to environmentally sensitive areas in the coastal region.

While coastal water quality, fisheries research, planning that is going on for marine recreational opportunities are major initiatives underway, we are also involved in a lot of other important programs related to marine resources and oceanography. I can mention just a couple of these. Our Coastal Management Division is responsible for the North Carolina Beach Access Program. We have established more than 150 ocean and 10 estuarine access ways so that the public can enjoy the use of our beaches without having to own property or a home. I think it is very important that all citizens of North Carolina have access to the public beaches.

We are also heavily involved in coastal wetlands protection. Our state Dredge and Fill Permit Program has had a very positive impact in helping curtail losses of salt water and brackish water throughout the state. A key element, incidentally, in wetland protection is their identification and characterization, which is going on right now: we need to know, in fact, what wetlands are and what it is all about so that we can protect it better. Our Division of Soil and Water Conservation is, at this time, conducting a comprehensive wetlands inventory for the entire coastal area so we know where the wetlands are. It is surprising to have come this long in a state where environmental protection has become the norm (in fact, we are recognized nationally for our environmental protection programs in North Carolina), to have come this far to make basic decisions about the coastal area and find out that we really never have done a wetlands map of the state - we do not know where the wetlands are, we do not know really very much about them to not have mapped the shellfish beds comprehensively throughout the state so we know where our natural resources are. We have to back up a little bit and get that done because it is very, very important in our decision-making process.

We now have our own state Estuarine Sanctuary Program which supports areas that have been designated under the federal program. North Carolina's new program allows us to include sites that are of state significance that may not fit into the federal standards. We have just added an area into this and that is Bermuda Island, up in Onslow County. An estuarine sanctuary is a place that is to be preserved in its natural state for research and educational opportunities and just for people to see what a wetlands area and marsh area looks like without having it disturbed. We are also working in this area on getting Masonboro Island completely purchased and into the estuarine sanctuary system.

What I have discussed involves inshore and estuarine systems. We are also pretty heavily involved in offshore studies and opportunities that are taking place and I am glad to see, Dr. George, that this particular symposium is not like a lot of others that just concentrate on the estuaries and sounds, but gets us off into the deep sea and blue water areas of the state, which was really one of the driving efforts in trying to put this symposium together. We really never had a situation where we've looked from the highlands to the deep sea in one meeting, so, this conference is very significant.

We get involved, not only in trying to provide research opportunities, but we're heavily involved with the Department of the Interior and their oil and gas exploration program. We have those activities that are taking place off the coast and we want to make sure that we stay on top of it and that we have the information we need, the research that we need, in order to make sound decisions. I now serve on the National OCS Policy Committee for the Department of the Interior so that North Carolina has a direct input into decisions that are made on a national basis.

We are also working very closely with the Mineral Management Service to determine the potential for non-energy mineral mining out on the outer continental shelf. There are a lot of phosphates underground in North Carolina and that runs out into the ocean in a lot of areas. We have formed a joint federal/state task force to look at the economic feasibility of recovering phosphorate from the ocean surface and subsurface, particularly in Onslow Bay. The economic study will be completed next month and the joint task force, at that time, will recommend to the Secretary of the Interior and to Governor Martin what should be the next step, if any, taken to pursue potential marine mining opportunities in the state.

I see from your agenda that you are going to discuss many of these topics that I have covered, in much greater depth, over the period of the Symposium and it is always professional forums such as this that play an extremely important role in the understanding of scientific information that must form the basis for all the public policy decisions, particularly in marine resources and oceanography. We certainly look forward to listening, learning and gaining the results of all the brainstorming and discussions that are going to take place here. I have several members of the Department who work with me who are going to take part in this over the next three days and they are going to be listening and learning at the same time they are talking and discussing.

Assuring a secure future in our coastal area has got to be a cooperative venture. We all have to work for it together. Dr. George, I am glad to be here and talk with you about what we are doing in the state and look forward to the rest of the Symposium. Thank you.

POLICY STATEMENT OF NORTH CAROLINA FISHERIES COMMISSION

Dr. John Costlow, Director
Duke University Marine Laboratory, Beaufort, N.C.
Chairman, Marine Fisheries Commission+

Chancellor Wagoner, Secretary Rhodes, Dr. George. About one year ago, Bob George approached me and asked if I would present some views on marine fisheries in North Carolina. At the time of the request I was the Chairman of the North Carolina Marine Fisheries Commission. However, in exactly thirteen hours and twenty-seven minutes, I will no longer be in that position. I am not certain that Bob was aware of that at the time since I was not either! Therefore, if I am going to speak in that capacity, and with what is left of the authority, I best speak rather quickly!

What does one say about a way of life that may well have been the original life-style in eastern North Carolina when it was a colony? Marine fisheries has been a basic economic function of life in Eastern North Carolina for at least that long and, in more recent years, has become a tremendous, recreational pastime. I have had two and one-half years as Chairman of the Commission to ponder just what one might learn about the marine fisheries of this State.

When I first began to develop this presentation for Bob, I thought. "Well, I can give a very, erudite presentation of fisheries statistics and identify the decline in several of our traditional species". Then I thought, "No, I will leave that up to Dr. Bill Hogarth. After all, he is the Director of the Division of Marine Fisheries and it would be more appropriate to leave this depressing series of topics to him".

Then I considered discussing some of the more recent regulations relating to marine fisheries passed by the General Assembly. On second thought, however, in light of some of them, perhaps I best not touch on such sensitive issues!

The next idea was to develop a presentation on problems, progress, and policy but I knew that Secretary Tommy Rhodes would be present, and I did not wish to completely duplicate his talk. An excellent summary of this, at least a portion of it, is contained in a document which many of you have either never known about or conveniently forgotten: "The Future of North Carolina; Goals and Recommendations for the Year 2000". Published in about 1981, it represents a census taken of all 100 North Carolina counties in an effort to determine the way in which the citizens of each of these counties wished to see their county develop by the year 2000 AD. There are a number of objectives, lots of goals, and even some recommendations, some of which Secretary Rhodes has touched on. I would urge you to review it from time to time as it relates to your area, if only to find out to what degree we are achieving the goals which were identified.

The other, more recent volume which I urge you to read, summarizes the contributions of North Carolina to a number of areas of its economy and environment in 1987. Are you aware, for example, that the contribution of the coastal area to the economy of North Carolina in that year, from a variety of individual sources, amounted to two billion dollars? This represents a considerable "return" on the investment, much of which is natural and annually recurring.

But, I decided not to speak on either of these volumes since, if you are sufficiently interested, you can read them at your leisure, as you can about another area in which I am involved, the Albemarle/Pamlico Estuarine Study, a cooperative venture involving North Carolina, the Environmental Protection Agency, and the National Oceanic and Atmospheric Agency. Somehow, as I prepare to step down from the position of Chairman of the Marine Fisheries Commission, it would seem more appropriate for me to speak on things which are not, and will not, be written down. One of my series of experiences involves the "Public Hearings" which the Commission has conducted over the last several years. We have had public hearings from Southport to Morgan's Corner; from Hatteras to Winston-Salem in the interest of including the recreational fisheries interests. At this point I must mention, with considerable pride, the diligence of not only the staff of the Division but also a goodly majority of the Commissioners with whom I have been privileged to serve! That bunch, whether they were from Winston-Salem or Wilmington or wherever, were religious in showing up at these public hearings, frequently several in a row (the meetings, not the commissioners!). Most of you in the audience today will never have the opportunity to participate and hear the types of things which we have heard over the past two and one-half years as we sat in Southport, Morgan's Corner, Hatteras, Elizabeth City and so forth, frequently with threat to life and limb! You have all heard the old tune "Go tell it on the mountain"? Well, we went and "Heard it on the beach" and some of the things we heard were most interesting!

At the risk of getting Dr. B.J. Copeland all excited, it seem best to present these items as an acronym as they would in some of the important meetings which he attends in places like Washington, D.C. The acronym is "THEMUSMENOWBUT" and I will not pretend that it is derived from an ancient Gaelic root! Actually, it incorporates four of the topics which we continually heard in these numerous public hearings, and not always from just the commercial fishermen!

The first can best be identified as the ancient concept of "Them versus Us". There is this long-standing conception of the function of the Secretary of NRCD, and especially of the Marine Fisheries Commission, that their only goal in life is "nothing more than a vast communist plot to prevent US from catching fish, when we want to, where we want to, and how we want to!" Frequently this argument is reinforced by a demonstration of one of the older fisheries regulations books in comparison with the most recent one. The newer volume is considerably thicker, does contain more regulations, as well as verbiage, and it should be obvious to any observer that its primary function is to make life more difficult for the marine fishermen! This demonstration is usually followed by the contention that the Commission has no interest in "natural resources" and, when it comes to fishing, many assume the Commissioners would not know a gill net from a haul seine! In the opinion of many, all the Commission wants to do is complicate the regulations to prevent the fishermen from catching fish. Now, how does one develop a program, basically in "communication" to convince the average fisherman, commercial or recreational, that the Commission does not wish to prevent them from fishing? We do wish to manage the fishery in an intelligent way in the hope that there will be some fish and shellfish left for their grandchildren?

The second component of the acronym is <u>ME</u>. It is the component which is always very discouraging. In it's entirety, it is usually "Why are you picking on me? Why don't you pick on agriculture, or perhaps industry, or even tourism? Why are you always picking on me? They are polluting more than I am and you should start with them!" Time after time this conversation goes "round and round" with the general idea that the Commission, in combination with the Coastal Resources Commission and the Environmental Management Commission, should be focusing our efforts somewhere else and, when we have "cleaned up" that general category, then, perhaps, we can come back to them.

The <u>NOW</u> part is equally discouraging! In essence, it is "I want mine NOW! I have got an expensive rig, a hydraulic dredge, I am paying a mortgage on it, and I want my clams right NOW. If, in the process I should accidentally tear up some sea-grass, that is not really important. All we ever hear about these days is saving something for that bunch called "Posterity"! The hell with "Posterity", I want mine NOW!". Ask Bill Hogarth about this part of the acronym: some number of times each day, at least each week, he is pressured, by fishermen or legislators, to open up additional areas for fishing! I am certain that he must get very tired of hearing "Why can't you open this up?" or "Why did you close the season so early?" How can we better communicate the fact that with the tremendous increase in demand for the fisheries, the increase in numbers of commercial and recreational fishermen, and the improvement of fishing gear, the existing areas available for harvesting must be carefully managed, or, not only will there be nothing left of "Posterity" but it will run out long before!.

Now, the final component, <u>BUT</u> is equally disturbing, in part because it frequently comes from individuals who should know better, from virtually every walk of life. It is, "I'm really genuinely interested and very concerned about improving the quality of the environment, BUT - - - ". We hear this from just about every conceivable source. Some industries "claim" to be interested in being good neighbors BUT, when their effluents exceed the discharge limits established by the Environmental Protection Agency/Division of Environmental Management, what happens? Frequently, there is much discussion as to the tremendous costs which will result in reducing the levels of the emissions or effluents, in other words, "BUT"! The environment will have to wait! Some developers, when confronted by regulations relating to "non-point runoff", restrictions on how close one may build to estuarine waters, immediately contact their legislators to either delay such deliberations or implement new regulations which will be more in line with the developers' thinking - e.g. increased profits! Many politicians, in casual conversation, assure you that they are all for a cleaner environment but, if an issue arises which requires a "stand" that could jeopardize future campaigns, or their financial support, the necessary legislation never seems to get out of committee. For example, on two occasions "Bottle recycling bills" have been introduced in this State and in both cases, extreme pressure from a variety of opposing sources prevented any real consideration of the issue. Some housewives, assuring you in one breath that they are totally dedicated to improving the environment and the resources dependent upon a cleaner environment, will immediately be offended if it is suggested that this will require them to switch from the detergent which gets their "whites" cleaner to one which has lower levels of phosphates! "I am certainly all for a cleaner environment, but don't you dare raise the price of our detergent!"

Some sportsmen, and on occasion I really wonder just how that term originated in light of some of their modern practices, take highly visible and positive positions on a cleaner environment but, when it comes to taking more fish than the limits provide for, or actually selling their catch in outright competition with the commercial fishermen who do it for a living, it is a totally different story.

The new Commission currently being formulated is going to have plenty to do, if only in dealing with these four, "simple" issues within the acronym! One approach would be to concentrate on what might be identified as the "Four P's". These are: Productivity, Pressure, Pollution, and Politics. We must continue to explore ways to improve our management of the coastal environment to assure the highest productivity! We must constantly examine ways to fairly balance fishing pressures as demands increase and gear improves. We should be obligated to strive to improve the public awareness of and need to reduce pollution. And, through communication and cooperation, individual citizens and organized interest groups must continue to inform their appointed and elected officials of their concerns and willingness to support them in intelligent legislation for proper management of our natural resources and the environment upon which we all depend for our very existence.

At this point, it is possible that some of the audience may be asking, "Why should I care?" There is one, very simple reason which each and every one of us should care: we are the ones who actually own the estuarine environment with which we have been so blessed and which has provided for us so magnificently for several hundreds of years! The Government, in this case Secretary Rhodes and those Commissions appointed by our Governor, has the distinction of being charged by our Constitution to manage this environment and its resources for all of us. You, as well as the other 6.2 million citizens of North Carolina, each own some number of cubic yards of the estuarine systems, some number of blue crabs, some of the scallops, and some number of flounder. If you, as the owners of this resource, do not take an active and informed interest in it, special interests whose primary interest is to make a "quick buck" will take an active and selfish interest. If this is permitted to happen, the real owners will discover within the next few years that the resource is gone. From experience in other areas of the United States, we know that once it is gone, it is much more difficult, as well as more expensive, to attempt to put it back!

I sincerely hope, as Congressman Rose has suggested, that you will tell Secretary Rhodes, as well as your own elected officials at all levels of government, that you are concerned about the coastal area and its resources and that you are prepared to help them manage the environment which they hold in trust for you, the real owners.

\+ Dr. Costlow's appointment as Chairman of the North Carolina Marine Fisheries Commission terminated on October 1, 1987.

Chapter 8. Where are we now? - Scientific Assessment

Chairperson - Dr. Robert Y. George

ACADEMIC PROGRAM IN MARINE SCIENCES IN NORTH CAROLINA - HISTORICAL PERSPECTIVES

Dr. Jasper Memory
Vice President for Research
and
Mr. Charles Wheeler
Associate Vice President for Research
University of North Carolina at Chapel Hill
Chapel Hill, North Carolina 27514

My remarks will neither be scientific nor philosophical but purely historical today. I am going to make a few comments about where we have been and where we are now. It seems appropriate to make a few remarks about the history of marine research in both the United States and in North Carolina. This, in essence, is my introduction to this session this morning.

North Carolina has had a long and distinguished history in marine research and instruction. I think it is appropriate that we expand on this historical background. A few minutes spent on that history will provide us an interesting consideration and impression on what we are doing now and where we are planning to go. This history shows the development of an interdependent network of instruction, research, and public service programs as it continues today in North Carolina. This background is taken largely from apparently an unpublished paper prepared by Dr. R. E. Coker of the University of North Carolina at Chapel Hill, and the paper was written back in 1967. The recent painful experience of Senator Biden has prompted me to be very careful in citing the fact that this was originally by Dr. Coker.

The great Swiss/American Naturalist, Louis Agassiz is credited with establishing the first marine laboratory in the United States. He joined the Harvard faculty in 1848, but at least two years earlier he had emerged as a strong advocate of laboratory and field work in the natural sciences. Prior to that time, instruction had been almost exclusively through text books, lectures, and recitations. Agassiz was also a researcher and may have been the first major "grantsman" in United States higher education. He found the seacoast an ideal site for biological studies and established the first marine field station in Buzzards Bay, Massachusetts, in 1873. This facility is considered a forerunner of the Federal Woodshole Fisheries Laboratory and the Woodshole Marine Biological Laboratory, both established between 1880 and 1885.

William Keith Brooks, who had briefly been a student of Agassiz, became head of the department of biology at Johns Hopkins University. In 1878, he established a roving summer field program, which was conducted in various places along the east coast, most frequently in Beaufort, North Carolina.

Then, in 1981, Dr. H. B. Wilson became head of the department of biology at the University of North Carolina at Chapel Hill. He had worked at Woodshole as Chief Naturalist and almost immediately began to conduct field work at Beaufort. This activity lead to the purchase of Piver's Island, off Beaufort, and the opening in 1902 of the second federal marine fisheries laboratory on the island. Duke University established its marine laboratoy, also on Piver's Island, in 1938. Then, in 1947, the University of North Carolina Institute of Fisheries Research, now the Institute of Marine Sciences, opened in Morehead City.

This background demonstrates that North Carolina has been in the forefront of marine research since the beginning of marine research in this country. I might note that, from the outset, these efforts were directed toward the public service role of improving the productivity of marine industries, as well as instruction and research. The University of North Carolina remains a major participant in marine research. The university is consistently among the top ten institutions in the nation for marine activity. Marine projects have been undertaken on at least seven campuses of the university, with major programs at North Carolina State University, the University of North Carolina at Chapel Hill, East Carolina University, and the University of North Carolina at Wilmington. Currently, about 50 principal investigators have underway 136 projects with external funding in excess of $9 million. We estimate the total number of faculty involved in marine science at about 100. The academic disciplines involved range from anthropology to zoology, from A-Z in a scientific sense. Since virtually all of these grants are obtained on a competitive peer review basis, this record attests to the quality of marine sciences activity in the University of North Carolina.

A major marine sciences activity in which the university is involved is the Sea Grant Program. This program is a state/federal partnership, jointly funded by the National Oceanic and Atmospheric Administration in the Department of Commerce and by the University. Two thirds of the funding comes from the federal agency and the remainder through the North Carolina General Assembly. This program is designed to promote the widest use of the nation's coasts and oceans for research, instruction, and public service.

The University of North Carolina first became involved in the program in 1970 and was recognized by the federal agency as a Sea Grant university in 1976. Since that time, it has grown from a small applied research effort to a major university thrust. The current level of Sea Grant support is $1.8 million a year. Dr.Copeland, who is Director of that program, will give you more detailed information regarding that program in his comments, shortly.

The new UNC-Duke Oceanographic Consortium is another important marine sciences activity in which we are engaged. The Presidents of The University of North Carolina and Duke University, in 1980, entered into a joint venture to operate a research vessel. For the preceding 17 years the Duke marine laboratory had operated the EASTWARD, an oceanographic vessel which served North Carolina institutions and many other universities along the east coast of the United States.

The consortium applied to the National Science Foundation and, in the face of strong competition, secured the charter of one of two new vessels being constructed by the NSF. The new vessel was christened the CAPE HATTERAS and became operational in late 1981. The consortium has at its disposal one of the two most modern, best equipped, and most efficient vessels in the entire academic fleet. During the first five years of operation, the CAPE HATTERAS has been intensively used for research projects of national significance. In fact, the number of days at sea in most years has exceeded somewhat the desired maximums established by the National Science Foundation. With the support of the National Science Foundation, the consortium has engaged in a continuing process of upgrading the gear and scientific equipment on the vessel. The goal is to make the latest and best technology available to principal investigators in the universities. The consortium reflects outstanding cooperation between Duke University and constituent institutions of the University of North Carolina. As a result, the individual institutions of the state and in the nation all benefit.

The final marine science activity in the university that I will mention is the National Undersea Research Program here at the University of North Carolina at Wilmington. This program, established in 1980, used the research vessel SEAHAWK as a movable platform from which to test the usefulness of various diving systems in meeting undersea research needs. This program has undergone extensive review and revision within the past year or so.

The various marine science programs at the University of North Carolina that I have described are coordinated by the Marine Science Coordinating Council of The University. This body is composed of two members from each constituent institution with a marine science program. The Director of the Sea Grant Program is an exofficio member, and I serve as chairman. The Council also advises the president of the university on marine science affairs.

In conclusion, The University's marine science programs had a rich and illustrious past. They are strong and productive today. They serve the state and nation through the training of a new generation of scientists, through the discovery of new knowledge regarding our marine environments, and through the application of that knowledge to improve the quality of life of our people. We appear to be positioned well as we look forward to a leadership role in the advance of marine sciences in the decades ahead.

UNIVERSITY OF NORTH CAROLINA SEA GRANT COLLEGE

Dr. B.J. Copeland, Director
University of North Carolina Sea Grant Program
North Carolina State University
Raleigh, North Carolina 27607

The University of North Carolina Sea Grant College Program is a university-wide activity supported jointly by the federal government and the state of North Carolina. We are involved in promoting marine research, public service and education. I am going to take all these together and try to give you a broad flavor of our activities. We have people involved in the program in the University of North Carolina system and Duke University.

One aspect of our program is dealing with the barrier islands; where the land meets the sea. North Carolina is blessed or plagued (depending on your point of view) with a long strip of barrier islands at the edge of the sea. A lot of people want to go there to live, to recreate and to try to make a living; so there is a lot of pressure on these valuable resources. We are involved in research and extension activities in this area. We encourage the use of resources by the people of North Carolina in balance with the environment and the developmental activities that inevitably occur there.

Barrier island dunes are striking features along the coast. They are natural defenses that these barrier islands have in order to maintain themselves. We are involved in many research projects, for example, modeling the response of dunes to wave surges so that we can advise coastal management on how to deal with factors affecting them.

A hurricane is a very important force in coastal areas. Building in the face of hurricane and storm pressures is a very important problem facing coastal people, so we have been involved in research and extension activities dealing with the building of structures and having those structures maintained in a hazardous zone. We were successful, for example, in helping the Building Code Council of North Carolina change building codes for coastal areas to accommodate storm problems.

Another area that we are involved in has to do with the extensive estuarine coastal waters. North Carolina has about 2.3 million acres of estuaries, sounds and marshes and is third in the country (exceeded only by Alaska and Louisiana). Within those shorelines and inside these barrier islands is a tremendous mixing pot of activity. It ranges all the way from Mother Nature trying to make the systems behave the way that they have always behaved to the kinds of activities that man has developed in order to increase his return. In the peninsula between Albemarle and Pamlico Sounds, for example, there is a large effort to clear land of primeval forest for agricultural activities. In order to farm, one must drain the water-logged soil. When you drain it, the water runs downhill into the estuaries. So, we are conducting a large research program, in coordination with the Albemarle and Pamlico studies and all kinds of management activities of the state government, to try to manage these systems so that the farms can operate there.

Much of coastal North Carolina has small towns next to the water. Most of these places use individual septic tanks for their waste disposal. About 85% of the soil in coastal North Carolina does not support conventional septic tanks. So, you have to dispose of the waste while also worrying about the availability of drinking water, which is primarily ground water. We have a problem of trying to balance these activities.

Around the edges of these estuaries are very important areas of productivity, called primary nurseries. The nurseries are shallow embayments next to the land and are, therefore, vulnerable to activities that occur on the land. Most of the organisms that occupy these zones are spawned in the ocean and migrate there at certain times of the year -- the spring is a highly productive season -- and in a short time return to the ocean. How we manage our fisheries is dependent upon the knowledge we have as to how the ecosystem works. We are actively involved in and are currently trying to solve these kinds of problems.

You occasionally read about blue-green algae blooms in newspapers. Blooms result when nutrients drain from upstream water sheds into the estuaries. We are actively involved in research to try to determine how blooms form, how to control them and what happens when we can not. We have a national reputation of both types: we produce the blue-green algae blooms and have the scientists who can characterize them.

A third area of traditional involvement is fisheries. Our fisheries are declining. We have several problems. One problem is that of how to utilize the fish that we have. I might note that about ten years ago we were marketing about 52 or 53 different species in North Carolina, but today we are marketing 75. The pressure on the fisheries has increased. Ten years ago we had about 1.5 million man-day/year recreational fishing activity; today there are about 4.5 million. The number of fish has not changed much but the number of folks trying to get them has. There are all kinds of innovations which might be useful in terms of increasing or enhancing the productivity of our fisheries. We are involved in both research and extension.

We have a little over 300,000 acres closed to commercial shell fishing because of pathogenic contamination. We are actively involved in a very major research program in this area. Traditionally, since the days of typhoid fever, we have used coliform bacteria. It has become clear that coliform tests are not really indicative and, of course, we do not have typhoid fever any more. As you know, we have outstanding biologists working on new techniques.

Regarding the quality of our fisheries products, over the past two years the yield for blue crab canning activities improved about 10%. That is 10% they were throwing away. Shelf life for canned crab meat was short enough to bring pressure to change the pasteurization process. Another research activity involves development of products from existing seafood. We discard, for example, 30% - 45% of the edible seafood from filleting operations. By using a "deboner," you can crank out superior fish flesh from wasted fish. We have a plant located in Raleigh in the last two years, based on our research, and it is manufacturing surimi products.

Recreational fishing has become extremely demanding. I mentioned the increase in man-days of effort. How we allocate those resources, commercial versus recreational, has become an important subject.

A fourth area of emphasis is aquaculture. We are currently developing the hybrid striped bass as a commercial activity. There are now two farmers in production, with more waiting to see how it goes before entering the business.

ROLE OF AQUATIC AND MARINE BIOTECHNOLOGY IN NORTH CAROLINA

Mark Messura
North Carolina Board of Science and Technology
North Carolina Department of Administration
Raleigh, North Carolina 27603-8003

First of all, I would like to apologize for Norman Cohen, who could not be here this morning. I would like to accomplish two things this morning. First, I would like to familiarize you with the North Carolina Board of Science and Technology and second, bring everyone up to date on what our current efforts are in marine and aquatic biotechnology.

The North Carolina Board of Science and Technology is a 15-member board officially located as a state agency in the Department of Administration. The Board is made up of members from academia, the public sector and industry representatives. Governor Martin serves as Chairman of the Board and Earl Mac Cormack serves as the Executive Director of the Board.

The philosophy of the Board has been and continues to be to pursue economic development through research in science and technology. This has led in the past to projects such as the Microelectronics Center, the North Carolina Biotechnology Center and the North Carolina School of Science and Mathematics.

Currently, the Board runs a small research grants program which, the Board is proud to say, has demonstrated a history of funding support for many projects in marine science and also for a number of the researchers who have been here over the past three days.

Through the efforts of the long-range planning committee of the Board, we have identified marine and aquatic biotechnology as a field with high potential for North Carolina. This naturally lead us to the North Carolina Biotechnology Center, which is <u>the</u> state organization for biotechnology efforts.

The North Carolina Board of Science and Technology and the Biotechnology Center have formed a joint task force. This task force is planning three meetings over the next year with the specific goal of identifying research efforts, at least for the state, in marine and aquatic biotechnology. I am going to just mention a few of the members of this task force: Senator Marc Basnight; Dr. Stuart Bondurant, of UNC Chapel Hill Medical School; Mr. Van Brown, of C. R. Brown Enterprises; Dr. G. R. DeMarco, who is the Vice-President for Research and Development at R. J. Reynolds Tobacco Company; Mr. Tom Hexner, of Crux Incorporated; Mr. Robert Mayo, of Mid-Atlantic Fish Farms in Ayden, North Carolina; Dr. Charles Putman, who is the Vice-Provost for Research and Development at Duke University; and Dr. Donald Wrenn, from the FMC Corporation.

The task force met in early September and began what would turn out to be a full day of deliberation as to what opportunities exist in the state and which direction the state should move into. This resulted in initially a first step of forming a researcher/industry roundtable; this will effectively bring researchers and industry representatives together to talk about short-term research projects and industry problems: what problems are out there and how can these, in the short term, be addressed by some of the current research efforts. This arrangement is a dramatic link - this link between biotechnology and aquaculture and which, in the short run, seems to be the best bet for seeing some immediate application of biotechnological principles in marine science.

In the long term, we are looking at the legislation and regulations affecting aquaculture in North Carolina. We hope to establish a study commission which will investigate this issue and form recommendations as to how best to balance the concern for protection of the environment and the economic needs of the state.

The task force is also considering formally establishing an Aquaculture Development Center and this will be located, at least initially, within the North Carolina Biotechnology Center. The purpose of this Development Center is, again, to emphasize marine and aquatic biotechnology within the state, with an emphasis on applications in aquaculture, at least in the short run. It is possible that this Aquaculture Development Center will establish a funding program for short- and long-term research projects.

In conclusion, I would just like to point out that we are at a fairly early stage in terms of our involvement in forming marine and aquatic biotechnology. We have identified a high potential for marine and aquatic biotechnology within North Carolina and we hope to work with the Biotechnology Center in establishing some short-term linkages between marine biotechnology and some aquaculture projects within the state. We also realize that simultaneously we should undertake some long-term research projects and programs that will move this state toward some of the very high potential economic development projects. We feel our goals are certainly within the reach of North Carolina in the long run. This symposium offers an excellent opportunity for us at the Board of Science and Technology to learn and interact with those in the marine science community and we thank Professor George for giving us the opportunity to participate in this marine science symposium. We look forward to receiving input and working with those of you in the marine science community to develop effective and efficient state programs in marine and aquatic biotechnology.

ENVIRONMENTAL STUDIES AT RESEARCH TRIANGLE INSTITUTE

Donald R. Johnston
Environmental Sciences and Engineering
Research Triangle Institute
Research Triangle Park, North Carolina 27709

I appreciate the opportunity to talk about some of the environmental studies we are doing at the Research Triangle Institute (RTI). I think if you look at our programs--I can not touch on all of them today--we pretty much reflect what is happening nationally, as far as environmental studies go. For example, RTI mineralogists are looking at ways to improve our ability to quantify asbestos in the environment. As long as it's been around, we still can not measure asbestos very well. Our environmental management specialists are developing standards for asbestos in the atmosphere. Also, RTI hydrogeologists are engaged in a national study of pesticides in ground water. The study is designed statistically so that we will have the ability to make some generalizations on a national basis. We are also working on radon in homes and on surface water quality problems.

At the Institute, we do not generally do environmental impact assessments, at least not as a routine sort of thing. However, we have done two studies that may hold some interest for you. The first of these was an Environmental Impact Statement (EIS) prepared for the Prulean Farms project in Dare County, North Carolina. In this project, the owners were proposing to convert 20,000 acres of land, some of it wetlands, to rowcrop agriculture. They intended to grow corn, soybeans, and winter wheat on a rotating basis. Draining the water off the fields would be a necessity; the issues naturally, then, were water related. One issue was the potential intrusion of freshwater into saline water. Since the drainage would be directed to Milltail Creek and the Alligator River, essentially freshwater streams, freshwater intrusion was not found to be a problem. Another issue was a concern regarding nutrient enrichment of the Alligator River and, ultimately, the eastern part of Albemarle Sound. RTI engineers were able to determine that the nutrient issue could be resolved through the use of overland flow. By directing the drainage flow over a minimum of a half-mile of vegetated land, the nutrients would be removed and the receiving streams protected. As it happened, just as we thought the project was about to be approved and receive a permit under Section 404 of the Clean Water Act from the U.S. Army Corps of Engineers, the owners decided to make a donation of land in excess of 100,000 acres to the Federal Government. Apparently, the economics of the project had changed over the time that the EIS was being prepared. That donation is now known as the Alligator River National Wildlife Refuge. Some would argue that was the best possible outcome of that project.

A more recent project, and one that we found extremely challenging, was an environmental assessment performed for First Colony Farms (FCF), a part of McLean Industries. About 3 years ago, FCF embarked on a study of the feasibility of a project that would use peat as a fuel for electricity generation. The peat resource was located on property owned by FCF in Washington, Tyrrell, and Hyde Counties, just south of Phelps Lake. The project would have harvested 15,000 acres of peat for use as a fuel for a 200-megawatt steam-electric generating plant. The electricity produced would have been sold to a utility, presumably Virginia Electric Power Company (VEPCO). And the project would have been economically viable over a 20-year project life. Water management is, of course, an essential part of harvesting peat. About halfway through the preparation of the environmental assessment, the North Carolina Environmental Management Commission adopted a peat mining regulation that required the average annual runoff from a peat mining site to be no greater than that which would run off an undrained site covered with mature, natural vegetation. RTI engineers, working with Dr. R. Wayne Skaggs and his associates at North Carolina State University, were able to determine that compliance with the regulation could be achieved through the use of a permanent 1,500-acre reservoir, adherence to a specified sequence of mining, and the use of temporary reservoirs and flow control devices in the drainage canals. This determination was the result of extensive engineering analysis. It appears that consumptive use of water, i.e., evaporation from either the permanent reservoir or the steam plant cooling tower, would be necessary in order to comply with the regulation. So, I can assure you that the peat mining regulation is very protective of the environment.

As another part of the assessment, we did a 1-year baseline water quality monitoring study. In that study, we established 16 stations at various locations on canals draining the proposed peat-harvesting site, as well as on the Pungo River, the Intracoastal Waterway, Southwest Fork Creek, and Northwest Fork Creek. These last two locations are small streams that drain into the lower Alligator River. In the monitoring study, we looked at several parameters, including temperature, pH, salinity, light penetration, turbidity, suspended solids, dissolved oxygen, nutrients, chlorophyll-a, and selected metals. The most interesting thing that came out of the study was that, in some of these small, completely undeveloped streams, e.g., Southwest Fork Creek, it was not uncommon to see anoxic conditions. That was about the only remarkable finding that showed up in the monitoring study.

Another thing that we looked at in the FCF project was the question of what would happen to the level of Phelps Lake if water were pumped from the nearby peat deposits. Would you, by reducing the head in some of the canals, cause the lake level to drop? Our hydrogeologists were able to provide pretty convincing evidence that there would be no adverse impacts on Phelps Lake from the project.

Well, this project also ended up a little differently than the sponsors intended. If you keep up with these matters, you know that McLean Industries filed for reorganization under Chapter 11 of the bankruptcy laws in late 1986.

We also work with the Federal Government. Currently, we have a major contract with the U.S. Environmental Protection Agency (EPA), Office of Water Regulations and Standards. In this contract, we are doing a lot of work with water quality models. By models, I am referring to computer-based, predictive mathematical models that allow us to make some judgment beforehand of the effect that a waste discharge will have on a receiving water, e.g., the effect of sewage on dissolved oxygen concentrations. One of the exciting things that is happening under this contract is that modeling technology is being made more widely available. Most of the water quality models were written originally for mainframe computers, which are large, costly machines. As a result, modeling technology was not available to many potential users. So, a lot of our effort has been devoted to converting modeling software from mainframes to micros, the relatively inexpensive, personal computers available today. What this means is that some of the less affluent State and local pollution control programs can begin to use water quality models as tools in managing their water resources. We think that is a very important development.

Another area of activity under the EPA contract is the development and manipulation of large data files. The EPA, like most government agencies, amasses enormous amounts of data, such that computerization of the data base is essential if the data are to be used. To illustrate, we have been assisting EPA with the computerization of their fish kill file. This file consists of information on fish kills occurring throughout the country over a number of years.

I also want to note that RTI will be involved in the Albemarle/Pamlico Estuarine Study (APES). We will be evaluating environmental management and resource protection programs in the Albemarle/Pamlico Region. Since management of estuarine resources is the thrust of the APES, we feel that our project will provide a benchmark alongside the biological, chemical, and physical studies of the estuaries.

THE NATIONAL UNDERSEA RESEARCH CENTER AT THE UNIVERSITY OF NORTH CAROLINA AT WILMINGTON

Alan W. Hulbert, Center Director
National Undersea Research Center
Wilmington, N.C.

I appreciate the opportunity to address you today on behalf of the Undersea Research Center. I would like to discuss two topics, a description of the Center and some of its capabilities.

The National Undersea Research Center at the University of North Carolina at Wilmington conducts research on the continental shelf and slope off the southeastern United States and the Gulf of Mexico. Direct funding for the Center comes largely from the National Oceanic and Atmospheric Administration (NOAA) although most programs are heavily co-funded by various other agencies. The Center tries to build research programs which coalesce national and regional research objectives with the active scientific expertise of the region. Center research objectives are dynamic in that they are continuously being revised and updated as a result of changing national needs, local workshops, management issues and scientific activity. The Center attempts to be an integrator drawing scientists together to address important and fundable research programs, often for resource management issues.

The Center conducts many varied activities but at the heart are the "core research programs." These are peer reviewed individual and collective projects which have been scrutinized by peers as being excellent science and evaluated by the Center as directly addressing important issues. Center staff are actively involved in research projects from the initial preproposal stages to publication of the results.

The real strength of the Center in terms of operations is the expertise of the scientific staff in the application of undersea technology to very precise, in-situ, experimental protocols. The Center regularly conducts mixed gas diving, a remotely operated vehicle, and submersible cruises to accomplish research goals.

In summary, the Center conducts research in high priority offshore issues in the southeastern United States and Gulf of Mexico with an expertise in undersea technology. The Center attempts to serve as an integrator and collaborator of research efforts, defining important research issues, drawing in scientific expertise and participating on projects.

MARINE CORROSION TESTING AT WRIGHTSVILLE BEACH

W.W. Kirk and K.L. Money
LaQue Center for Corrosion Technology, Inc.
Wrightsville Beach, North Carolina 28480

We would like to tell you about the LaQue Center for Corrosion Technology, a testing and consulting facility with locations both at Wrightsville Beach and at Kure Beach, North Carolina.

We have heard some earlier discussion about the formation and operation of marine science groups and departments as early as the early 1900's in North Carolina. Our Center was established in 1935 and has been operating "full steam ahead" ever since. Primarily, the laboratory is dedicated to the study of the behavior of materials in the marine environment. In the last several years, we have expanded to include the non-marine environments such as those in the chemical process industry and a variety of other aqueous environments. We also pride ourselves on being a technology transfer center. We operate the laboratory as a profit center; that is, we are a subsidiary company, totally owned by a parent company in Canada. We are independently operated so that we are able to perform and record our work in an unbiased nature; that is, we do not depend on any one person or group for the source of revenues to operate our Center. Therefore, the analysis of work that we do is reported in a formal, unbiased format.

One current area of technology that we are involved in is the localized corrosion behavior of materials in the marine environment. This is a very serious problem for stainless steels and some nickel-based alloys. They do have a tendency to suffer from pitting and, in some cases, it can be quite catastrophic. Our Center has been doing a lot of work for the last 10 to 15 years on the mechanism involved that one calls "localized corrosion" and how we can go about preventing it. We have developed mathematical models so that we can enter data into a computer program that we have developed and hopefully be able to predict the performance of materials as it relates to their localized corrosion behavior.

We also have been doing a lot of work recently in the area of high-strength materials for such applications as submarines, bathyspheres, deep diving research vessels and other components that would be subjected to alternating pressure. We are investigating subjects like the joining and welding of high-strength materials as well as the fabrication and corrosion behavior of composite materials. We are trying to develop fiber reinforced materials and other kinds of composite materials which will increase the strength to weight ratio so that they might be able to accomplish more challenging objectives.

Unfortunately, current technology sometimes combines materials in composites to develop attractive mechanical properties, but which display poor resistance to corrosion. For instance, graphite fibers combined in an aluminum matrix develop a very high strength to weight ratio, but involve two materials near the opposite ends of the galvanic series of metals and alloys. The resultant tendency toward rapid galvanic corrosion of aluminum in an environment such as seawater destroys the composite.

The electronics industry has necessitated corrosion testing of not only contact surfaces but complete components and devices that must operate in aggressive environments. Many computers and electronic controls originally were developed to operate in air conditioned, dehumidified, pristine atmospheres. Today, however, one can find an endless line of computers and electronics throughout an industrial plant, a university laboratory or even in field operations. Unfortunately, the internal electrical contact surfaces, circuit boards, etc. are often subjected to hostile environments that cause corrosion and premature failures. In our ongoing corrosion control program we are investigating means of controlling corrosion, such as better materials selection, effective composite surfaces or better control of humidity. We have developed methods to monitor the environment inside equipment chambers or electronic equipment rooms. This program is designed to give the owner and operator of the equipment some advance notice of corrosive conditions existing in the environment. We can predict with a fair degree of accuracy when the environment becomes corrosive to the equipment so that the operator may be able to change air purification or handling methods and preclude the loss of use of equipment.

In the technology area, we conduct, as was previously mentioned, a symposium called the Sea Horse Institute every two years. This is an informal forum for the exchange of information on materials performance in marine environments. No prepared papers are permitted and no proceedings are published. The total informality of this meeting allows a free and open discussion of topics without fear of being quoted or seeing one's name in print. The dialogue can become quite involved and exciting and often leads to debate that can only be resolved by later discussion outside the conference room. This conference was first held in 1939 and annually until 1980, after which a two-year schedule was adopted. Its longevity speaks well for its success.

We also have available through our Center educational aid materials to help people who are trying to learn, study or teach in the field of corrosion. They range from films and books to indicators and publications of corrosion behavior, data on materials and corrosion theory. Biofouling of materials in the sea has been an ongoing program in the Center for almost 50 years, where we look at the fouling of materials, both micro- and macro-fouling, as it might relate to the performance of materials in the marine environment - ships, condensers, piping, plumbing and valves. We also look at not only the intrinsic, non-fouling materials but we also look at fouling mitigation techniques through a variety of paint systems or other systems likely available.

We operate a continuing industry corrosion program at Kure Beach, North Carolina, where there are some 30,000 specimens or components of working equipment being continually exposed to the aggressive marine atmosphere in that particular site. Our staff is also actively involved on a daily basis in the field of consulting and analysis for those who have corrosion problems in their plants or operating equipment.

THE NORTH CAROLINA MARINE SCIENCE COUNCIL: COASTAL AND OCEAN POLICY INTO THE 1990'S

Michael K. Orbach, Chairman
North Carolina Marine Science Council
East Carolina University
Greenville, North Carolina 27834

At meetings like this, I am usually the "odd bird out" in terms of discipline: I am a cultural anthropologist. People knit their brows and say, "cultural anthropologist in a marine symposium?" My answer is fairly simple, and I only point it out to you because it is fairly similar to the approach that the Marine Science Council is taking these days to ocean policy. When you make a policy about something, you do not often get the chance to alter the behavior of fish or a rock or a coast; what you alter is the behavior of people. Therefore, that is what we have to look at if we're doing policy, including the funding of science - altering the behavior of people and what they do. So, that is how I justify my existence as cultural anthropologist.

I am the Chairman of the North Carolina Marine Science Council, which is a 28 member body appointed by the governor of North Carolina, on which I serve as the Chair at the pleasure of the Governor. Those members are from all different state agencies and areas of expertise in the state, from all different locations. The Council has two principle functions. The first is to serve as principal coordinating body for the marine and coastal and ocean policy in the state of North Carolina. The second is to provide policy oversight to the three North Carolina aquariums. We are set up in the Office of Marine Affairs in the Department of Administration. Donna Moffitt is the Executive Director of the Council.

What I want to do before I give you a little bit of background on what the Council is doing, is to do a "snapshot" history of what I view as the important parts of marine policy in the last 30 or 40 years. In the post-World War II era there was tremendous expansion of activity on every front: people came back from World War II with the experience from submarine technology; military uses had expanded tremendously; television came along to increase our mass communications; there was economic prosperity in the United States - a tremendous expansion in all kinds of environmental and oceans activities. It is interesting to note that before World War II, the majority of the ocean science - oceanography for example - funding did not come from the federal government; it came from other sources. It was in the post-World War II era that this expansion of the federal role came. Now, I claim, as a cultural anthropologist, that there are three things that are important to understand about the interest in the marine environment and they largely stem from one personality and two television programs. That personality is Jacques Cousteau. Even though we might say, "That guy is not really scientific," he is the one who provided popular support in the world and the United States to study the seas. The two TV programs are "Flipper" and "Sea Hunt." If you do not think those were important, wait until we get to the national legislation that passed, like the Marine Mammal Protection Act. Do you know where that came from? "Flipper." That is not an animal; that is a little person in funny skin. We all know that. He is like us and we have to protect him. Those kinds of factors - TV programs and Jacques Cousteau - provided the cultural base of popular and political support for what we do, and we should not forget it.

In the 60s and 70s all this broad base of cultural support, popular support and awareness, and this expansive mentality about what the federal government should do led to a lot of consolidated activity in marine policy. Can you all name the president of the United States under whose administration the vast majority of the significant environmental and marine policy legislation was passed? Richard Nixon. In the period from the late 60s to the middle 70s, beginning with the National Environmental Policy Act and continuing on to the Marine Mammal Protection Act, the Endangered Species Act, the Coastal Zone Management Act and the Fish and Conservation Management Act, there was more significant federal legislation passed on the environment in general, including the marine environment, than had ever been passed before or has been passed since. We essentially have done very little since the mid-70s (if you exclude the OCS Lands Act Amendments in 1978, which was basically part of the same process). So, the 60s and 70s produced a big consolidation and a "coming to fruition" of all this popular support from the post-World War II era. Now, included in that are the law of the sea negotiations, and I will not get into that at all except to note that the United States did not sign the LOS Treaty, although we were a significant participant in those events. That is, to me, the key to understanding what is happening in coastal ocean policy in the 80s. I would not exactly call it benign neglect, but it was in 1982 that we formally declined to sign the LOS Treaty and the federal government has basically taken the position that we really have enough ocean policy and should concentrate on specific issues having to do with economic development and other interests of the constituencies. That is important to do, but there is no new initiative in terms of how we govern ourselves or stimulate scientific activity in the marine environment coming out of the federal government these days. This is where the Marine Science Council of North Carolina comes in.

The responsibility for developing new initiatives and new programs and addressing the needs of the marine environment and its constituencies has fallen largely to the states. In that light, the Marine Science Council, in the last several years, has taken its authority for advice on marine policy seriously and in 1985 published a report called "North Carolina Sea: Ocean Policy Analysis", wherein we identified 16 different ocean policy areas. Our question was, what happens in the ocean that either effects

North Carolina or is effected by peoples' behavior in North Carolina? We listed 16 different areas, from fisheries to coastal erosion, ocean transport and cultural resources. In that report we also made nine recommendations which we are now in the process of implementing.

The key to coastal and ocean policy in the 1990s, which is the title of this talk, is going to be the initiative of the states, where the people who use the ocean actually reside. In light of that, we have taken several initiatives in North Carolina having to do with the possibilities of ocean mining, aquaculture, and many other subjects. We are now initiating a new plan to do a comprehensive coastal, ocean and atmospheric planning exercise. We can not look at the coast apart from the ocean and we can not look at either one apart from what happens in the air. So, we are going forward to try and put the whole planning picture together and to look into the 1990s.

Chapter 9. North Carolina Oceanography: Where Are We Going?

Chairperson - Dr. Robert Y. George

NORTH CAROLINA FISHERIES

Dr. William Hogarth, Director
North Carolina Division of Marine Fisheries
Morehead City, North Carolina 28557

Thank you, Dr. George. In talking about where we are going, I am not sure that we know where we are going because we have got so many challenges before us right now. One of the biggest things we are faced with right now is to try to do some zoning in the coastal area. We are faced with development, we are faced with a lot of leasing property and we are getting involved with agriculture. I personally think that one of our top priorities right now is to try to do some work in the coastal areas of North Carolina to define where our resources are, where there is all that could be leased, where there is all that could be developed and where minimum impact could be.

North Carolina is a very diverse fishery. Ten years ago we issued 2000 commercial licenses; today we are issuing over 21,000. One of our biggest challenges for the future is user conflicts. We have more and more sport fishermen, more and more commercial fishermen. North Carolina is probably one of the most open states as far as commercial fishing is concerned. We are regulated by a fifteen member commission. We have proclamation authority, which now rests with my office. We can manage those things by proclamation; we are one of the few states that has proclamation authority. Some things the Commission puts a sort of bracket on and we regulate within it. We allow inside trawling (and we're one of the few states that allows inside trawling) for shrimp, primarily, and for crabs and fin fish. One of the big issues we are faced with now is, should we limit it? Ten years ago, when we had 2,000 boats, the scrap fish impact was not as bad as now when we have got 20,000. So, what are you doing to your small spot and croaker and other organisms that utilize the inside waters?

We also are the only state, the only area that allows mechanical, hydraulic clamming, that allows hydraulic boats and clam digging boats to go into an area and collect clams. The clam population is not what it used to be. Once you watch this type of operation from the air, you can see it looks like a bare bottom and you try to keep them out of the shallow areas, to keep them out of the grass beds and those areas utilized by clams and also utilized by other organisms such as scallops, shrimp and young fish.

We are faced now with water quality problems. The Division is very involved in fish diseases. This year and last year we had a crab disease which was prevalent in the Pamlico River. We recently had a workshop and in that workshop we probably gained more and know more about ulcerative mitosis and crab disease than any other area, which bothers me somewhat. We can get the crabs infected pretty rapidly in certain areas in the Pamlico area. But, as far as being able to duplicate it to really get at the bottom line, we cannot do it.

We do have a person who reorganized the Division to try to react and respond better. I think sometimes we overreact and we want to get to the point of acting. We have one person, who reports to me now, who does work with the federal agencies on federal management plans to try and take advantage of all the data that is being collected up and down the coast to try to come up with a management plan that we will utilize within the state as well as in the coastal areas. We realize that with the species that we see all up and down the coast, we need to be involved with all plans available. I think what we need is to take advantage of all the data that is being collected in order to manage. We open and close seasons, as I said, by proclamation and we can take advantage of what is going on and try to manage it. We cannot manage the resources; there is no way we will ever manage that. What we have got to do is to try to manage the people. We have a dockside value of $64 million in just commercial fishing in the state. When you take all the processing that goes into this, take in the recreational value of the people coming to the coast for all the sport fishing, it is about a $2-billion-a-year, reoccurring industry of the state.

We do not have a salt water fishing license and, right now, there are no plans to go to one. We keep hearing the federal government propose the use of these and if the federal government proposes use of these, the state will have to go to some form of salt water recreational license. One thing we do have to do is to determine who is "recreational" and who is "commercial"; most people, we do not know. "Recreational" fishermen are allowed to sell $500, except they sell a lot more. We have got a lot of meat fishermen and I think we have got to identify them.

I think a top priority is the five-year-management plan or research plan for the state. What we are trying to have done by the first of the year is to try to identify areas as "need-research" so that everybody will know what we are looking for and trying to find funds to get this work done. Then, we need to get a better licensing structure so we will know who is doing what. Right now you can buy a license for $1.50 per foot; for about $18.50, you can do anything you want to in the state. So, we do not know who is doing what; we do not know how many crab licenses, for example, are in the state, we may have five million crab licenses in the state. So, we have the capability now in that new bill and we also have a task force that has been set up to look at the whole licensing and penalty structure.

In conclusion, let me add a statement on coastal development. There is too much emphasis being put on coastal development and not really on what is happening in the whole water basin. Coastal development influences what is going on in the whole system.

NORTH CAROLINA - MARINE CRESCENT CONCEPT

Dr. John Manock, Director
Research Administration
University of North Carolina at Wilmington
Wilmington, North Carolina

I will talk about the Marine Crescent in the context of where we are going. However, to do this, first I need to talk about where it has been and where we are.

The Crescent was established four or five years ago by community leaders who were trying to look for ways to promote the development of southeastern North Carolina. It has a rather simple mission which is to attract, support and develop marine-related research and industry in southeastern North Carolina. There are five counties involved, from Carteret County to Brunswick County, forming a crescent, which is how the name was derived. The crescent is really in its infancy and has now been funded by Z. Smith Reynolds and the Biotechnology Center for a little over a year. A program manager is in place. The process of developing the database on the regional resources is now beginning. Twenty-four (24) industries in the region have been identified who have either marine-related facilities, equipment, or personnel to support and attract marine-related industry and business. The Crescent is viewed as a catalyst and facilitator to help with this type of development and supports such endeavors as the Venture Symposium conducted in conjunction with Marine Expo '87.

Where is the Crescent going in terms of the next five years? In assessing the Crescent, one must look at organizations that have been successful in supporting regional economic development. I have looked at numerous university/industry corporative, research parks, incubator facilities, or cooperative centers that have been established to accomplish regional economic development. It is my opinion one could make the argument that where the driving force behind these is the government agency or a specific institution that once that driving force loses interest these institutions tend to lose their momentum. One of the hopes is for the Crescent is that the momentum will be continued because of the support it is getting from the community. Currently there are five counties involved, of which four are giving some funding toward the Crescent, plus, we have a lot of strong people from the regional community involved.

In my opinion, for an organization like this to be successful, there are four criteria which the Crescent meets in addition to the broad base support. These make me optimistic about its.

The first criterion is that an organization has to be uniquely fitted to the region. One must capitalize on a region's strengths. One may take something which perhaps works in Tennessee or western North Carolina and transfer it to the coastal region, but not attempt to replicate all features of other organizations. All features may not be transferable. With the representation from the five counties, the Crescent is insured that it will be structured to fit with the needs of the region.

The second criterium is that there must be a clear purpose or mission; this seems to be done. What is seen in many organizations where this is not done is the organization has no focus and momentum is quickly lost. As previously stated, the mission of the Crescent is to attract, support, and develop marine-related business and industry in southeastern North Carolina.

For the third criterion there needs to be an effective partnership involving three components: education, government, and the private sector. If one looks at the composition of the Board, I believe it will be found the Crescent has this.

Finally, the fourth criterion requires it to be regional in scope. Anything less than this, in my opinion, will have limited impact. I feel we have here is a true commitment to that.

Further, as Director for Research Administration, I feel the Crescent can serve as an active advocate for university strengths and resources which I consider to be one of the most underutilized resources in our country. I believe with the Crescent the university strengths can be targeted and a vehicle can be established for technology transfer between our university communities and the private sector.

Thus, in conclusion, I am optimistic about the future for the Crescent. I feel the potential for the Crescent is great, and I see the Crescent as potentially a viable factor in the future development of southeastern North Carolina. Thank you.

OUTER CONTINENTAL SHELF (OCS)

Donna Moffitt
Office of Marine Affairs, Department of Administration
Raleigh, North Carolina 27601

Thank you, Bob. I want to talk about two programs today that are essentially federally funded and mandated but the states have significant participation in both of those activities. One is the Federal Offshore Oil and Gas Leasing Program; the other is the Hard Minerals Mining Program.

The Department of the Interior has recently approved its next five-year leasing schedule, approved in June, and it essentially reflects what is happening in the oil and gas industry right now, in that the oil companies are pulling back because of the drop in oil prices. They are going to the proven areas of the Gulf of Mexico and offshore California. So, for the next five years, the leasing schedule calls for annual sales in less highly proven areas and then sales over three years in what are called "frontier" areas. The frontier areas are off Alaska, off Washington and Oregon, the straits of Florida, and all the Atlantic coast - the north, mid and south Atlantic OCS areas. Those are areas where there has never been a commercially proven area or find of oil and gas or areas where no exploration has taken place. The five-year plan is already under litigation. If you are familiar with this program, you know that there are an awful lot of law suits at all levels of the Program. Florida, Massachusetts, Alaska, California and Oregon have entered into a lawsuit over the five-year plan already and, depending on the outcome of that lawsuit, the five-year schedule may change some or it may not, it depends on how successful the plaintiffs are in that.

North Carolina is divided at Cape Hattaras; we are in the mid-Atlantic region and the south Atlantic region. The last two sales that were scheduled off our coast were cancelled because there was virtually no interest by the industry in the Atlantic. The next sales that are scheduled for North Carolina, the south Atlantic is scheduled to have one in late 1989 and the mid-Atlantic in late 1990.

We presently have six blocks under lease off North Carolina and industry paid considerable amounts of money for those blocks. Unfortunately, most of them are located just beyond the shelf break in very deep water, and also in the Gulf Stream. So, industry is going to have a major problem even doing exploration on those blocks. Forty-three of them are due to expire in '91, six in '92, and the remaining eleven in '93 and we really do not anticipate seeing industry doing anything on those blocks before they expire.

We have a couple of studies going on relating to the Gulf Stream frontal vents. Those were initiated because of a pre-litigation settlement that the state entered into with the Department of the Interior in 1983 and the results of those studies will be coming in within the next year. They are essentially to help us determine trajectory and the speed of oil spills.

The Interior is taking a slightly changed philosophical approach to its Environmental Studies Program. I think we were lucky to get these last two studies done because they are essentially now only going to fund studies that can be used precisely for making decisions on lease/sale activities. No longer are they going to be doing the "nice-to-know" kind of research; it will have to be related specifically to the decision-making of the Secretary of the Interior as to whether or not you go to court with an actual lease/sale.

The second program is the Offshore Hard Minerals Mining Program that is really just getting started by the Interior Department. It is conducted under the OCS Lands Act, which is also the controlling federal legislation of oil and gas. However, there is only one sentence in that whole Act that has anything to do with hard minerals. Though it is quite controversial, Congress is now looking at a bill that would set off a completely new hard-offshore-mining program and it would be housed in Commerce (which is probably going to kill the bill) but there are a lot of very good points to the bill. The Marine Science Council, and I in particular, have been tracking that litigation and we will see just where it goes and maybe some aspects of it can still be useful for the states.

There is a recent report that came out in July of 1987, from the Office of Technology Assessment; I was an advisory panel member on it. The study was called, "Marine Minerals: Exploring our New Ocean Frontier." It essentially looked at what is happening now with offshore minerals and tried to make some projections for the future. I would like to just read a few excerpts from the report because I basically agree with the findings.

It states that, "although only a fraction of the U. S. EEZ (Exclusive Economic Zone) has actually been explored for minerals, several types of mineral deposits are known to occur in various regions. These include sand and gravel; heavy mineral sands that contain titanium, chromium, gold, phosporites, possibly platinum and other minerals; metallic crusts and nodules containing cobalt and manganese; and sulfide deposits of copper, zinc and associated minerals. The mining minerals are the greatest future potential for development of the high-value, low-volume precious metals such as gold and platinum and, if located in high-demand areas, low-value, high-volume sand and gravel. With two possible exceptions, that is, sand and gravel and precious minerals, the commercial prospects for developing marine minerals within the EEZ appear to be remote for the foreseeable future. Marine minerals cannot now compete for price, quality and reliability of supply with other foreign and domestic mineral suppliers. Because of economic uncertainties and financial risk of EEZ mining, it is doubtful that the private sector will undertake substantial exploration in the EEZ until the government.." (federal government, I am assuming, since the state does not have any money)..actually gets out and begins to provide the preliminary information about location and extent of marine minerals. An example of that is our own state/federal phosphate task force that is looking at the feasibility of offshore mining for phosphorites in Onslow Bay.

"The immediate challenge to the United States is to gain a better understanding of the physiography and geology of the sea floor and its environment and to inventory mineral occurrences within the U.S. jurisdiction. The possible strategic importance of several minerals in the sea bed, that is, cobalt, chromium, manganese, and the platinum group minerals, could make future economic considerations secondary to national security controls."

MEDICINE FROM THE SEA

Thomas Long, Director
Maricultra Inc., Wrightsville Beach, North Carolina

From 1960 to 1986, medical costs have gone up from 5% of the Gross National Product to 11% of the Gross National Product and we are only beginning to see the grade of the American population. So, medicine is important. In order to support our population, we are going to have to become more productive. The only way we can do that is to make an investment in the future and this investment has to be, I think, in new industries and a part of these that are going to be very important, I would assert, would be the medical industries and others from the marine biology end of things.

We are involved in this right now, in some ways, as a small, new marine biotechnology venture, one of the few broadly-based marine biotechnology ventures in the nation. The reason that we are interested in the medical area is that a lot of people believe that some of the real breakthroughs are going to come from the marine side of things. The National Cancer Institute, for instance, has a large screening program for anti-cancer, anti-neoplastic agents from marine sources. The reason that they believe that they are going to be successful in this is that those materials showing anti-carcinogenic properties, anti-neoplastic properties, from marine sources, whenever they test them, they get a "hit" rate of about one out of every ten; for terrestrial sources, the "hit" rate is one out of every one hundred; and for synthetic materials developed as anti-neoplastic materials, the "hit" rate is zero. Only three weeks ago, I received a large packet from the National Cancer Institute, for instance, that requested proposals for a multi-million dollar program on anti-AIDS materials derived from marine sources - screening materials for that purpose. Already, one of the first materials (Dr. Colwell may have told you about this the other night, or someone may have; I, unfortunately have not been able to attend much of this Symposium, having been out of town) to be tested in populations as an anti-carcinogenic agent is called Didemnin-B, derived from a colony tunicate. It is an anti-leukemia drug and it went into testing last year. So, we have, I think, some possibilities of real medical advances from the marine side.

My company is working on some shorter-term perspectives on the medical end of things. I do not know if you have heard of fish oils and their effect on cardiovascular disease; it is advertised on television a lot. The active substances in fish oils are omega-3s, omega-3 fatty acids, as they are now generic. About two years ago, we recognized that the fish do not really make the omega-3 fatty acids; that, instead, they only absorb them from their diets and their diets are the microorganisms that actually are the producers of the omega-3 fatty acids. We also recognize that there are severe limitations on quality fishing, catches of marine fish, and that the U.S. population was not going to be able to derive their omega-3s from the source of fish (salmon, tuna and mackerel) that contain the omega-3s; fresh water fish do not contain them. So, we decided we would go to the original source (the microorganism) to produce these materials, cut out the "middle man" (the fish) and we have developed technology that we have applied for a patent on.

The omega-3s are valuable in cardiovascular effects. I can tell you (and I am not a physician, now, giving you this advice) that studies show that if you take the correct amount of omega-3s per day, your chances of dying from a heart attack or stroke are reduced by 50%. Arteriosclerotic cardiovascular disease begins at about age three, at least, and builds up; so, that is something that holds true for everyone who is in this room.

They are also important, apparently, in development, that is, in human development. The state of North Carolina has four major medical schools. At the same time, the state of North Carolina has one of the highest infant mortality rates in the nation, equivalent to sort of a high-class developing country. The leading cause of death among infants who do not have congenital difficulties, is pre-term pregnancies. Mothers who take the correct amount of omega-3s reduce pre-term pregnancies to zero. Omega-#3s also have been shown to be absolutely necessary for the full and complete development of the infant, the central nervous system, brain function and retinal function, in prenatal administration to the mother and postnatal administration to the infant for three months. This was done in primate studies and the human studies are now underway at the University of Tennessee. So, they are important in effectively shaping the individual right from the first.

They are also important in a group of diseases called auto-immune diseases that include those of our aging population, such as arthritis. They have been shown, because the molecular mechanisms for these are known, to moderate the effects of arthritis, rheumatism, asthma, multiple sclerosis, and other diseases that are collectively called the auto-immune diseases. So, we believe that they are going to be very important substances and they are natural substances that everyone eats every week, particularly in the form of fish or shellfish, etc.

In conclusion, I would note that we need more substantive effort, not only on the part of the state government, which is coming around to this now, but on the part of the federal government to support marine research that is applied marine research. I said this last week as one of a five-member review panel for the only algal biotechnology programs sponsored by the federal government: it is only $1.7 million. The algal species are some of the most important species for producing high-volume chemicals which would lead to a more productive economy. $1.7

million is the only major federal program on this; we need more federal support.

DUKE/UNIVERSITY OF NORTH CAROLINA OCEANOGRAPHIC CONSORTIUM

Presented by Dr. Len Pietrafesa on behalf of
Dr. Thomas C. Johnson, Director
Cooperative Oceanographic Program
Duke University Marine Laboratory
Beaufort, North Carolina

The topic is "The Duke/UNC Oceanographic Consortium: Where Are We Going?" The ship operations are going well with the CAPE HATTERAS. The schedule for 1988 is approximately 180 days, which includes a 60-day expedition in March and April to the western Caribbean, between Jamaica and Nicaragua. The remainder of the year it will be off the east coast extending as far as Bermuda.

The second thing is about the status of instrumentation aboard the vessel. The ship is going into the shipyard in Norfolk, Virginia, this week and will have an acoustic doppler current profiling system installed. This is manufactured by RDI located in San Diego, California. The instrument will look down from the hull of the vessel and actually will profile currents every several meters through the entire water column while the ship is underway. The CTD system that is presently aboard is restricted to the upper thousand meters but now has the capability of measuring water turbidity via transmissometer as well as fluorescence via fluorometer; both have been attached to the CTD system. The hopes that are expressed for 1988 are that a deep-water CTD system will be installed with the capabilities of going to 6000 meters. Also, there is the hope of a multi-channel seismic profiling system.

Long-term plans are to expand the role of the Consortium beyond the ship operations; that is to serve as a body that brings the representatives from all the UNC campuses that are involved in the sciences, along with Duke University, together and the hope is that this unit that combines all these resources could serve in other capacities and not just in dealing with the CAPE HATTERAS ship schedule perhaps, development of a national facility for specific analysis, such as multi-channel seismic work, perhaps a deep current meter array facility, perhaps an accelerator or mass spectrometer facility.

There exists amongst many of the scientists who regularly use the CAPE HATTERAS and amongst those who have not but would like to, a physical expansion of the CAPE HATTERAS. A 20 or 25 foot stretch would expand the scientific complement from 12 personnel to 20 personnel, for example. It would expand the working deck area by 300 square feet and it would offer an expansion and improvement of the lab space. It would not increase the operating costs, it turns out, to increase the size of the CAPE HATTERAS, but it might, and these are Tom's words, "might convince Len Pietrafesa and other scientists with bigger ship needs, to start using the CAPE HATTERAS on a regular basis." Some of us have instrumentation needs just in storing the equipment as we are about to go to sea and upon retrieving the instrumentation to be able to bring it back, which exceeds the fantail and deck space of the HATTERAS, and, so, it has restricted our ability to use it.

NORTH CAROLINA AQUARIUM - PROSPECTS AND POTENTIALS

James Lanier
North Carolina Aquarium, Kure Beach, North Carolina

When the Aquarium first opened in 1976 we were called a number of things. At one point we were known as the New Hanover Marine Center or the New Hanover Ocean. Finally, we ended up with the name of the North Carolina Marine Resources Centers at Manteo, Bogue Banks and at Fort Fisher. In 1976, the prediction was that, if we were lucky, eventually we would have about 300,000 visitors a year, 100,000 for each facility. This actually sounded ambitious to the people who had planned those facilities.

About three years ago, we surpassed the one million mark. This is comparable to all the large aquariums in the country. We do not do it in one facility; it is about equally split between the three. Here at Fort Fisher we will probably surpass 400,000 visitors. We had 250,000 visitors in the month of July alone.

This expansion is happening throughout the country, not just in North Carolina. This is probably going to be the "great decade" for aquariums. The Shedd Aquarium in Chicago, one of the great classic aquariums in this country, had a visitation last year of about 900,000. The Monterey Bay Aquarium, the National Aquarium in Baltimore and the New England Aquarium in Boston, all have a visitation that is about the same as our combined visitation in the North Carolina Aquariums. We have had a hard time keeping up with the predictions; our history of visitations has been very different from the other aquariums. The other aquariums were complete to start with, and had tremendous initial visitation. They were fully staffed, they had all their transparencies in place, all their fish IDs, all their aquariums were all ready to go when they opened their doors. They started off with a "bang" and tapered off. We started out with very little and have built essentially every year.

Every year I have felt that visitation was ready to level off, and every year I have been wrong. Rather than attempt another prediction I would like to spend just a little time telling you about some of our plans. At least, we can influence that a little bit more. I do not pretend that we have a tremendous influence over our visitation. I hope that the improvements that we have made have made a difference and that the name change has made a difference. At least people know what we are now. They used to think that we were primarily a research institution. Many of the people involved with the early development of the Aquarium hoped that scientists from around the State would use us very extensively as field stations. In my opinion, that was not a realistic belief from the beginning because most of the big programs have their own labs.

What we have gotten is "spill-over" from people who did not have room at UNCW to do their research, who wanted to come down and use us if they needed salt water or aquariums. The MIT weather study project used us for a radar installation and office spaces for about two months, winter before last. We will continue to do that sort of thing but it will continue to be a very small part of what we are all about. We are a public facility. We were funded with Coastal Plains money that was designed to improve the economics of the area. We feel we are making a major impact on the tourism industry and look forward to continued improvement and expansion in that area.

Chaper 10. Gulf of Mexico

Chairperson - Dr. Robert Y. George

A MODEL FOR ESTUARY/SHELF INTERACTIONS

Rezneat M. Darnell and Steve E. Lochmann
Department of Oceanography
and
John D. McEachran
Department of Oceanography and Wildlife & Fisheries Sciences
Texas A & M University, College Station, Texas 77843

ABSTRACT

Along the south Atlantic and northern Gulf coasts the estuarine and continental shelf ecological systems are in many respects quite similar. The prevailing climatic and hydrographic regimes foster habitat diversity and high levels of productivity by communities of similar species. Many theoretical and applied problems are common to the two areas. A conceptual model of the total coastal system is presented showing internal compartments and pathways of exchange as well as relationships with the external environments. Types of large scale studies recently completed or underway on the northern Gulf coast are described and discussed. These include the ecosystem approach, downstream series approach, emphasis upon the passes, broad seasonal picture of the continental shelf, long term time-series data sets, multidisciplinary approach, and mathematical modeling approach. These examples serve to illustrate the relevance of northern Gulf studies to problems of the south Atlantic states. Management agencies which must solve ecosystem level problems have a major responsibility for addressing research activities to these large-scale problems and for developing and financing the teams necessary to carry them out.

INTRODUCTION

The North Carolina coast has historically been known for the richness and diversity of its estuarine and marine resources. The tidal marshlands, mud flats, bay waters, barrier islands, and continental shelf have long provided fishery and other maritime resources and recreation areas for the citizens of North Carolina and neighboring states. During the past few decades the coastal resources of the State have been subject to mounting pressures so that they are now in danger of being severely diminished. The basic problem lies in the expansion and coastalization of the human population, increased technology, and the rising demand for seafood and recreational resources. This pressure is mediated through such factors as chemical pollution of river water entering the estuaries, local habitat destruction, and intense fishing pressure. Such problems are not unique to North Carolina. They are shared in common with most coastal states, but they are most closely akin to the problems of adjacent states and of the northern Gulf coast. The present article discusses some of the recent and current studies carried out in the northern Gulf coast area and addresses the relevance of these studies to the North

Carolina coastal problems.

Similarities of the Northern Gulf and South Atlantic Coasts

Careful examination of a world map reveals that most of the major world estuaries are located along the south Atlantic and Gulf coasts of the United States. This coastline is a treasure of marine resources common to and largely unique to the two areas. Reference to Table 1 reveals that the climatic and hydrographic regimes are quite similar, and this has resulted in the creation of long barrier islands, or outer banks, fronting major coastal estuaries and saline lagoons. Such low salinity areas provide a great variety of habitat types and extensive coastal marshlands dominated by emergent *Spartina* marshgrasses. These are areas of extremely high biological productivity, and they serve as nursery areas for many important coastal species. Seaward lie broad continental shelves paved by fine, riverborne sediments composed primarily of sand, silt, and clay. Occasional rocky outcrops occur. The two areas are characterized by similar coastal faunas including American oysters; brown, pink, and white shrimp; blue crabs; menhadens; porgies; drum fishes; and flounders. Offshore there are bluefishes, snappers, groupers, mackerels, and billfishes. Many of the inshore fishes and shellfishes of commercial and recreational importance are estuary dependent. Because of the physical and biological similarities, knowledge gained in one area has considerable applicability in the other, and methods of investigating the coastal resources and processes are also broadly applicable.

Table 1. Relevance of Gulf of Mexico margin studies to the South Atlantic Coast

1. The two areas have somewhat similar climatic regimes.
2. The two areas have somewhat similar hydrologic regimes.
3. Both areas have large estuaries characterized by great habitat diversity and extensive *Spartina* marshes.
4. Both have broad continental shelves with predominantly sand/silt/clay bottoms.
5. Many of the estuary-related species are common to the two areas.
6. Life history patterns of individual species appear to have geographic similarities.
7. Knowledge gained in one area must have considerable applicability in the other.
8. Methodology for investigating the problems should be broadly applicable in both areas.

Conceptualization of the Coastal System

For many years research workers have tended to focus upon one aspect or another of the coastal system. Particular attention has been concentrated upon the estuaries which are easier to reach and to examine. Lesser effort has been devoted to the continental shelf, and only a limited amount of investigation has been directed to the passes which connect estuaries with the continental shelf. Management efforts have likewise tended to focus upon a limited portion of the system with heaviest attention being directed toward the estuary. However, it is becoming increasingly clear that both research and management efforts will be more effective if carried out within the context of the larger picture.

A conceptual model of the complete coastal system is presented in Figure 1. The three main parts of the system are the estuary, pass, and continental shelf. Considering the importance of exchange processes, all three components may be viewed together as forming a single functional system with interactive components, as discussed in detail by Darnell and Soniat (1979). The system is influenced by external factors, including atmosphere, land, upstream freshwater, and the open ocean. The system imports water, dissolved and particulate inorganic materials, dissolved and particulate organic materials, and living organisms. It exports the same categories of materials. This model provides a perspective on the total coastal system and its internal and external relationships, and it serves as background for the discussion of relevant Gulf of Mexico studies.

Gulf of Mexico Studies

The Ecosystem Approach

As noted earlier, most of the studies carried out on the North Carolina coast have been concerned with smaller aspects of the larger systems. However, there are considerable advantages to the holistic approach where the various components and processes of an estuary, pass, or shelf are examined simultaneously. For example, studies on the growth rates of a single species of fish without knowledge of food availability and competitive interaction with other species does not provide a complete picture. The same reasoning applies to studies of nitrogen and phosphorus loading of an estuary if information is not available concerning potential reservoirs and rate-limiting pathways of exchange, uptake, and release. On the northern Gulf coast early efforts were made to address the estuarine ecosystem by Darnell (1958, 1961). More recent and more thorough studies have been carried out by Livingston and coworkers in Apalachicola Bay, Florida (Livingston, 1976; Livingston, et al., 1975; Meeter, Livingston and Woodsum, 1978). Definition of the larger system provides a context within which the more specific studies may be interpreted. Ecosystem studies provide an invaluable baseline

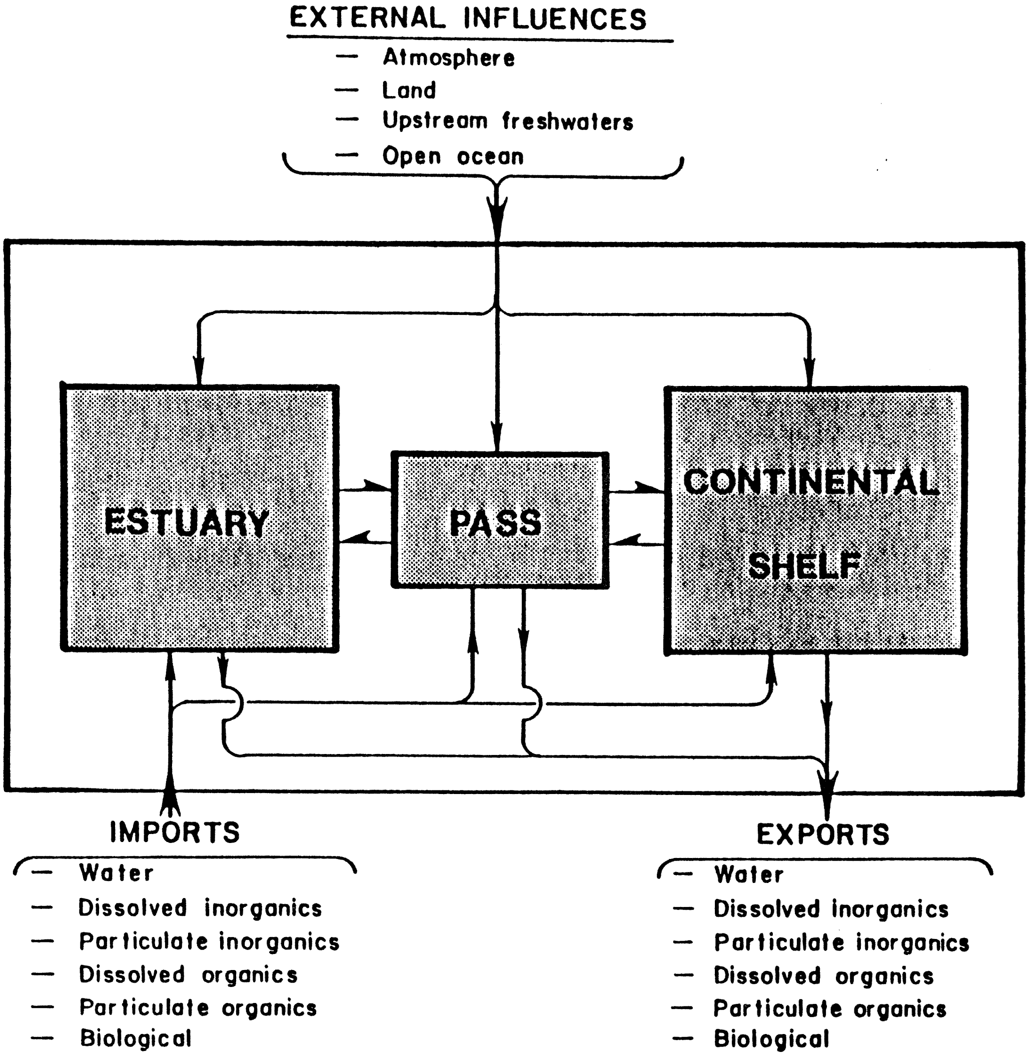

Figure 1. Conceptual model of the estuary/pass/shelf system.

against which future changes in the system may be measured. Furthermore, management efforts, which must often relate to total systems, are far more effective when the potential effects upon the systems may be fairly assessed in advance.

Downstream Series Approach

Rivers bring materials to estuaries which export materials through passes to the continental shelf. The shelf, in turn, exports materials through the passes to estuaries, and in some cases, to the rivers. Thus, it is extremely important to design and carry out studies which provide information on the downstream chain of events. This problem was placed in excellent perspective by Windom (1975) who proposed the following formula to describe the downstream flux of chemical materials:

$$K_i + (K_p - K_1) = K_o$$

where K_i is the rate of input (from a river to an estuary), K_p and K_1 are, respectively, the rates of local production and loss (within the estuary), and K_o is the final rate of output (from the estuary to the continental shelf). Obviously, the exchange could go in either direction. For example, the same equation could apply to the recruitment of american eels from the shelf through the estuaries to the rivers. Export phenomena in the downstream series have been investigated on the Gulf coast by Odum and Heald (1975), Happ, et al. (1977), and Copeland (1965), among others. Some nutrients and pollutants move passively through the systems, whereas others may involve complex biological, chemical, and physical interactions along the way. The life histories of all estuary related species involve continental shelves, passes, and estuaries and can only be assessed properly when considered in the context of the total system. The importance of downstream series studies is obvious.

Emphasis Upon The Passes

All exchanges between the estuary and the continental shelf are mediated by the interconnecting passes. Through these bottlenecks flow massive amounts of water in response to forcing by tidal pumping, wind stress, and freshwater outflow. The physics of water movement through the passes is only partially understood, and the load of dissolved and particulate materials carried passively by the water has seldom been quantified. Through the passes also come eggs, larvae, and juveniles of fishes shrimp, and crabs which are spawned on the continental shelf and which must undergo their early growth stages within the estuaries. Some of the very young stages may be transported passively. Others exhibit behavior patterns in response to water movement and salinity changes so that their transport patterns result from interactions between physical factors and biological responses. Detailed knowledge of the dynamics of the pass systems is critical to our understanding of the larger picture and, in particular, of the life histories of the estuary dependent species. Investigations on the dynamics of the passes are currently underway in Louisiana and Texas, but such studies are largely in their infancy.

Broad Seasonal Picture of the Continental Shelf

The continental shelf is a major component of the larger coastal system. With some notable exceptions, shelf studies have tended to be local in context, devoted to smaller aspects of the system, and restricted in time. Thus, there is a real need for broadscale, comprehensive, seasonal studies to place the shelf systems into perspective so that knowledge of the shelves can be more closely coordinated with what is known about the estuaries and passes. A good beginning has been made in the northern Gulf of Mexico through the works of Darnell (1985); Darnell, Defenbaugh and Moore (1983), Darnell and Kleypas (1987), Defenbaugh (1976), Rogers (1977), and others. For example, Figures 2 and 3 depict the seasonal density distribution patterns of a penaeid shrimp and a fish species on the shelf off the coast of Mississippi and Alabama. Both species are estuary related and of considerable commercial importance. Such data can be translated into numbers of individuals and weights of a species exported to the shelf in the annual crop. Similar maps are now available for about four hundred species of shrimp and fishes extending the entire length of the U.S. Gulf coast, from the Rio Grande to the Florida Keys. Such a broadscale picture provides an overview of the total shelf ecosystem, it establishes a context for the more local shelf studies, and it lays the foundation for more process-oriented investigations of the functional shelf system. Such a picture is also invaluable for management purposes since it identifies species stocks and seasonal concentrations which need protection, particularly during spawning periods, and it provides guidance for future research activities.

Long Term Time-Series Data Sets

Studies in the coastal area typically run for short time spans, and with the exception of certain tide gauge and water run-off records, coherent sets of more than three years' duration are quite rare. However, Livingston and coworkers, studying the Apalachicola River and Bay system of northern Florida, have amassed a large ecological data base extending over a dozen years or more. Included are standardized physical, chemical, and biological measurements (Dugan and Livingston, 1982; Livingston, 1982; Livingston, et al. 1976). The importance of such a long and detailed data base is that it permits sophisticated analysis of the natural variation within the system in response to the physical forcing factors, primarily those associated with climatic variation and river flow levels. Once these relationships are well understood, it becomes possible to predict ecological changes associated with physical variables and to sort out natural ecosystem changes from those due to human disturbance.

Multi-Disciplinary Approach

There is still a need for the individual scientist to carry out specific studies in the coastal environments. However, during the past few decades there has progressively developed the need for larger and more complete coastal system studies involving data collected simultaneously by scientists representing several disciplines. In dealing with coastal ecosystems it is a fact of life that the physics, chemistry, geology, and biology are closely bound together and that all are dramatically affected by meteorological phenomena. "Multi-disciplinary approach" has become a catch-phrase of our time, but is entirely appropriate and bears emphasis within the present context. Although fairly expensive, such studies provide the only means of obtaining answers to certain critical environmental problems, especially

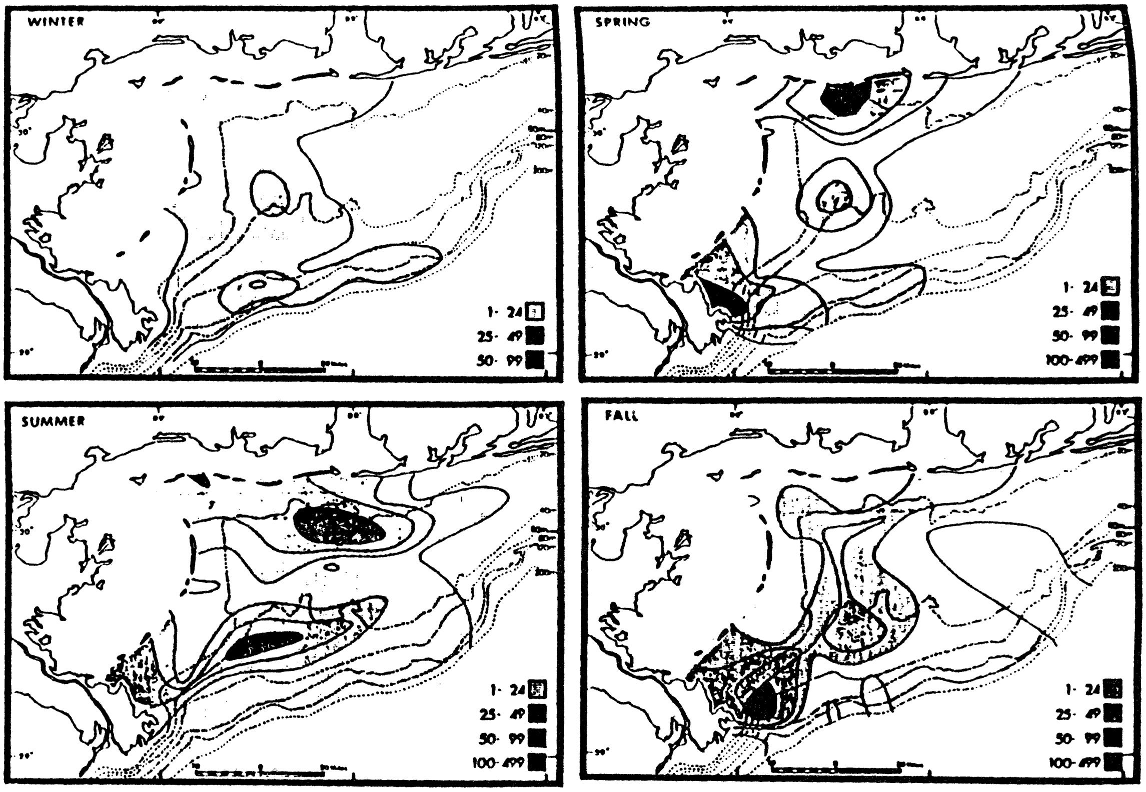

Figure 2. Seasonal distribution patterns of the brown shrimp, Penaeus aztecus, on the continental shelf of the Mississippi Bight area. Number of individuals per hour of trawling.

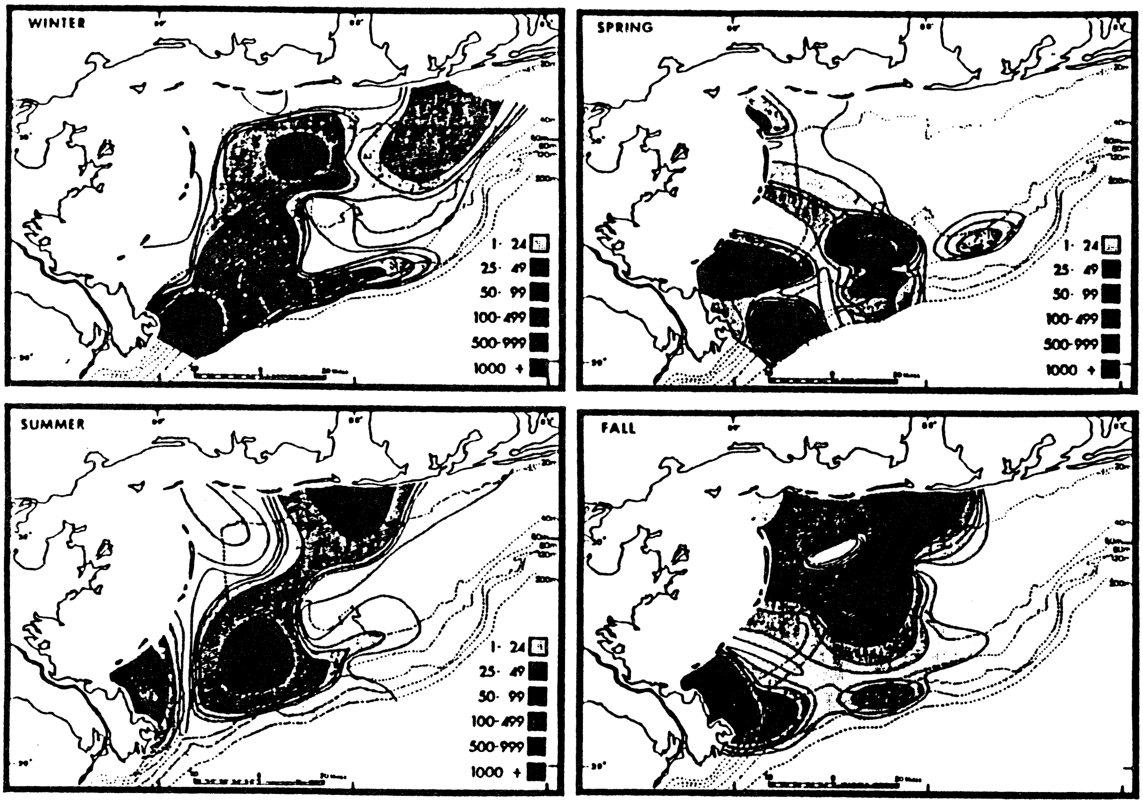

Figure 3. Seasonal distribution patterns of the Atlantic croaker, Micropogonias undulatus, on the continental shelf of the Mississippi Bight area. Number of individuals per hour of trawling.

those dealing with large-scale ecosystem function. Results of such studies are particularly relevant to the missions of management agencies. During the past dozen years extensive multidisciplinary studies of the continental shelf of the northern Gulf of Mexico have been funded by the Minerals Management Service of U.S. Department of the Interior, NOAA of the Commerce Department, and the U.S. Department of Energy. Results of these studies are included in the technical reports of these agencies, but unfortunately, much of the information has not been published in the regular journal literature.

Mathematical Modeling Approach

We have entered an age in which sophisticated mathematical tools and computational facilities are accessible to most research scientists, and as a result we are now capable of dealing effectively with natural processes involving multiple components and complex interrelationships. In many parts of the world, including the northern Gulf coast, natural phenomena are being simulated through the use of mathematical models. In some cases data input comes from remote sensing satellites. All of the types of investigations listed above yield vast quantities of information, and this may be reduced to mathematically defined depictions of the flow diagrams representing ecosystem structure and function. Of particular significance is the linkage of the physical with the biological data. Properly defined, mathematical models can provide deep insights into the functional relationships of large and complex natural systems, and they are of great value to the manager who must weigh the potential results of alternative management decisions.

CONCLUSIONS

In the foregoing discussion we have outlined some of the major types of recent studies being carried out in the northern Gulf of Mexico. These include the ecosystem approach, downstream series approach, emphasis upon the passes, broad seasonal picture of the continental shelf, long-term time-series data sets, multidisciplinary approach, and mathematical modeling approach. It is not meant to imply that such studies are unknown to investigators of the south Atlantic states. In fact, in some cases, the south Atlantic studies are well ahead of those in the northern Gulf. What is being emphasized is that studies in each of these categories carried out in the northern Gulf have great relevance to problems of the south Atlantic states, and that such studies are of both theoretical and applied nature. The ultimate goals in both areas are to describe and understand the functional relationships of the natural systems and through managerial action to preserve the basic integrity of the natural systems and their exploitable biological resources in the face of mounting human pressures. These are formidable tasks, and the need for solutions is becoming ever more urgent. We need all the help we can get, and closer ties and more rapid information exchange between workers on the Gulf and south Atlantic coasts would be to the definite advantage of all parties, especially considering the similarity of our ecological contexts and the nature of our common problems.

Since most of the approaches outlined above involve "big science" in the sense that they must be implemented by teams of researchers, managerial agencies which fund such studies have a special responsibility to see that the studies are designed to provide answers to questions of basic ecosystem function and that they are carried out by the best available combination of scientific talent. Such agencies must also recognize the values of long term data sets and be willing to provide long term funding for some projects. Short-term, brushfire approaches do not provide an adequate basis for long term coastal management needs.

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Appendix 1

ADVISORY COUNCIL

Dr. B.J. Copeland, Director
UNC Sea Grant Program
North Carolina State University
Box 8605
Raleigh, N.C. 27695
(919) 737-2454

Dr. John Costlow, Director
Duke University Marine Laboratory
Beaufort, N.C. 28516
(919) 728-2111

Dr. Dirk Frankenberg, Director
Marine Sciences Program
University of North Carolina at Chapel Hill
Venable Hall
Chapel Hill, N.C. 27514
(919) 962-1252

Dr. Robert Y. George
Institute for Marine Biomedical Research
7205 Wrightsville Avenue
Wilmington, N.C. 28403
(919) 256-3721

Dr. William Hogarth, Director
N.C. Division of Marine Fisheries
P.O. Box 769
Morehead City, N.C. 28557
(919) 726-7021

Dr. Paul Hosier
Assistant Vice Chancellor for Academic Affairs
University of North Carolina at Wilmington
601 S. College Rd.
Wilmington, N.C. 28403
(919) 395-3540

Dr. Tom Johnson, Director
Cooperative Oceanographic Program
Duke-UNC Oceanography Consortium
Duke University Marine Laboratory
Beaufort, N.C. 28516
(919) 728-2111

Appendix 2

CHAIRPERSONS

Dr. Joseph Bonaventura
Duke University Marine Laboratory
Beaufort, N.C. 28516
(919) 728-2111

Dr. Dirk Frankenberg, Director
Marine Sciences Program
UNC-Chapel Hill
Venable Hall
Chapel Hill, N.C.
(919) 962-1252

Dr. Robert George
Professor of Oceanography
UNCW
601 S. College Rd.
Wilmington, N.C. 28403
(919) 256-3721

Dr. Courtney Hackney
Associate Professor of Biology
UNCW
601 S. College Rd.
Wilmington, N.C. 28403
(919) 395-3487

Dr. William Hogarth, Director
N.C. Division of Marine Fisheries
P.O. Box 769
Morehead City, N.C. 28557
(919) 726-7021

Dr. Thomas Johnson, Director
Duke-UNC Oceanography Consortium
Duke Marine Laboratory
Beaufort, N.C. 28516
(919) 728-2111

Dr. Lisa Levin
Assistant Professor of Oceanography
N.C. State University
Raleigh, N.C. 27607
(919) 737-3721

Dr. Jesse H. Meredith, Chairman
Bowman Gray School of Medicine
Wake Forest University
Winston-Salem, N.C. 27103
(919) 761-5000

Dr. Douglas N. Rader
Program Coordinator
Albemarle/Pamlico Estuarine Program
Dept. of NRCD
Box 27687
Raleigh, N.C. 27602
(919) 733-4984

Appendix 3

PANEL MEMBERS

Dr. Charles Brown, Chairman
Geology Department
East Carolina University
Greenville, N.C. 27858-4353
(919) 758-6229

Dr. B.J. Copeland, Director
UNC Sea Grant Program
N.C. State University
1235 Burlington Labs
Raleigh, N.C. 27607
(919) 737-2454

Dr. Rez Darnell
Professor of Oceanography
Texas A & M University
College Sta., Texas 77843-3146
(409) 845-3211

Dr. William Hogarth, Director
N.C. Divison of Marine Fisheries
P.O. Box 769
Morehead City, N.C. 28557
(919) 726-7021

Dr. Alan W. Hulbert, Program Director
The NOAA National Undersea Research Program
UNCW
7205 Wrightsville Avenue
Wilmington, N.C. 28403
(919) 256-5133

Mr. Donald Johnston
Environmental Science and Engineering
Res. Triangle Park, N.C. 27709
(919) 541-6884

Dr. Will Kirk
LaQue Center for Corrosion Technology, Inc.
P.O. Box 656
Wrightsville Beach, N.C. 28480
(919) 256-2271

Dr. James Lanier, Director
N.C. Aquarium
P.O. Box 130
Kure Beach, N.C. 28449
(919) 458-8257

Dr. Tom Long, Director
Maricultra Inc.
Wrightsville Beach, N.C. 28480
(919) 256-5010

Ms. Donna Moffitt
Office of Marine Affairs
Dept. of Administration
417 N. Blount Street
Raleigh, N.C. 27601
(919) 733-2290

Mr. Mark Messura
N.C. Board of Science & Technology
116 W. Jones Street
Raleigh, N.C. 27603
(919) 733-7232

Dr. Michael K. Orbach, Chairman
N.C. Marine Science Council
East Carolina University
Greenville, N.C. 27858-4353
(919) 733-2290

Dr. Ray Zwycewicz
N.C. Biotechnology Center
4501 Alexander Drive
Res. Triangle Park, N.C. 27709
(919) 541-9366

Appendix 4

LIST OF AUTHORS

Dr. Larry P. Atkinson
Dept. of Oceanography
College of Sciences
Old Dominion University
Norfolk, VA. 23508-8512
(804) 440-4285

Dr. Brad M. Bebout
Institute of Marine Sciences
Morehead City, N.C.28557
(919) 726-6841

Dr. Larry B. Cahoon
Dept. of Biological Sciences
UNCW
601 S. College Rd.
Wilmington, N.C. 28403
(919) 395-3706

Dr. Robert R. Christian
Dept. of Biological Sciences
East Carolina University
Greenville, N.C. 27834
(919) 757-6718

Dr. Robert Y. George
Professor of Oceanography
Inst. for Marine Biomedical Research
UNCW
7205 Wrightsville Ave.
Wilmington, N.C. 28403
(919) 256-3721

Dr. William C. Hamlett
Medical College of Ohio
C.S. 10008
Toledo, Ohio 43699
(419) 381-4109

Dr. Eugene Huntsman
National Marine Fisheries Service
Beaufort Laboratories
Beaufort, N.C. 28516
(919) 728-8724

Dr. Thomas Johnson, Director
Duke-UNC Oceanography Consortium
Duke University Marine Laboratory
Beaufort, N.C. 28516
(919) 728-2111

Dr. Donald F. Kapraun
Dept. of Biological Sciences
UNCW
601 S. College Rd.
Wilmington, N.C. 28403
(919) 395-3484

Dr. William Kirby-Smith
Duke-UNC Oceanography Consortium
Duke University Marine Laboratory
Beaufort, N.C. 28516
(919) 728-2111

Dr. David G. Lindquist
Dept. of Biological Sciences
UNCW
601 S. College Rd.
Wilmington, N.C. 28403
(919) 395-3474

Dr. James Oliver
Dept. of Biology
UNC-Charlotte
Charlotte, N.C. 28213
(704) 597-4049

Dr. Hans W. Paerl
Institute of Marine Sciences
Morehead City, N.C. 28557
(919) 726-6841

Dr. Leonard J. Pietrafesa
Professor of Oceanography
N.C. State University
Raleigh, N.C. 27607
(919) 737-3721

(List of Authors con't)

Mr. Hugh Porter
Institute of Marine Sciences
UNC-Chapel Hill
Morehead City, N.C. 28557
(919) 726-6841

Dr. Stan Riggs
Dept. of Geology
East Carolina University
Greenville, N.C. 27834
(919) 757-6360

Dr. William M. Rizzo
Dept. of Biological Sciences
East Carolina University
Greenville, N.C. 27858-4353
(919) 757-6718

Dr. Frank J. Schwartz
Institute of Marine Sciences
UNC-Chapel Hill
Morehead City, N.C. 28557
(919) 762-6841

Dr. Ronald K. Sizemore
Dept. of Biological Sciences
UNCW
601 S. College Rd.
Wilmington, N.C. 28403
(919) 395-3478

Dr. Scott Snyder
Dept. of Geology
East Carolina University
Greenville, N.C. 27858-4353
(919) 757-6360

Dr. Donald M. Stanley
Dept. of Biological Sciences
East Carolina University
Greenville, N.C. 27858-4353
(919) 757-6718

Dr. Joseph St. Jean
UNC-Chapel Hill
Mitchell Hall 029 A
Chapel Hill, N.C. 27514
(919) 966-4516

Dr. Joan D. Willey
Dept. of Chemical &
Physical Sciences
UNCW
601 S. College Rd.
Wilmington, N.C. 28403
(919) 395-3459