

A Component of the U.S. Global Change Research Program

Northwest Atlantic Implementation Plan

U.S. Global Ocean Ecosystems Dynamics

Report Number 6

June 1992

U.S. GLOBEC

Global Ocean Ecosystems Dynamics

A Component of the U.S. Global Change Research Program

Northwest Atlantic Implementation Plan

Report Number 6

June 1992

Produced by

U.S. GLOBEC
Scientific Steering Committee Coordinating Office
Division of Environmental Studies
University of California
Davis, CA 95616-8576
Phone: 916-752-4163
FAX: 916-752-3350
Email: T.POWELL (Omnet)
hpbatchelder@ucdavis.edu (Internet)

Additional copies of this report may be obtained from the above address

IMPLEMENTATION PLAN

for the



16 June 1992

Implementation Plan for U.S. GLOBEC NW Atlantic/Georges Bank Study
TABLE OF CONTENTS

1. EXECUTIVE SUMMARY	1
2. ACKNOWLEDGEMENTS.....	4
3. INTRODUCTION	5
4. BACKGROUND	6
4.1 The Georges Bank Ecosystem.....	6
4.1.1 General Description.....	6
4.1.2 Criteria Used in Selecting Georges Bank.....	6
4.1.3 Space-Time Boundaries of Georges Bank Study.....	9
4.2 Rates of Birth, Growth, Mortality and Exchange Processes Controlling Population Abundance.....	9
4.3 Physical Oceanography of Georges Bank.....	12
4.4 Target Species.....	17
4.4.1 Overview of Cod and Haddock on Georges Bank.....	17
4.4.2. Overview of Georges Bank Plankton.....	24
4.4.3. Larval Fish/Plankton Interactions on Georges Bank.....	28
4.5 Physical/Biological Interactions on Georges Bank.....	29
4.6 Main Hypotheses of Georges Bank Study.....	33
5. PROGRAM IMPLEMENTATION.....	35
5.1 Major Components of the Georges Bank Study.....	35
5.1.1 Program Objectives	35
5.2 Experimental Program.....	36
5.2.1 Broad-scale Studies.....	36
5.2.1.1 Shipboard Surveys (1994 - 1998).....	37
5.2.1.2 Physical/Biological Moorings (1994-1998)	38
5.2.1.3 Satellite Surveys (1994-1998).....	41
5.2.2 Fine-scale process studies.....	42
5.2.2.1 Vertical mixing and stratification (1994).....	42
5.2.2.2 Study of Source/Retention/Exchange of Plankton (1996)	45
5.2.2.3 Cross-Frontal Exchange (1998).....	48
5.2.2.4 Population/Cohort Studies of Target Species (1994-1998).....	48
5.2.3 Modeling and Historical data analysis	49
5.2.3.1 Theory and Modeling.....	49
5.2.3.2 Historical Data Sets.....	51
5.3 Methodology and instrumentation needs and development.....	52
5.4 Schedule	58
6. DATA MANAGEMENT AND SYNTHESIS.....	61
7. RELATION TO OTHER PROGRAMS.....	63
7.1. Connections between the Georges Bank Study and Other U.S. GLOBEC Programs ...	63
7.2. Relation to other National and International Programs.....	63
8. REFERENCES.....	66

1. EXECUTIVE SUMMARY

Rationale for the U.S. GLOBEC NW Atlantic/Georges Bank Study: The primary objective of the U.S. GLOBal ocean ECosystem dynamics program is to understand the underlying physical and biological processes that control the population dynamics of key populations of marine animals in space and time (Peterson and Powell, 1991). Most of the ecological work will be conducted on recruitment of zooplankton and fish. It is assumed that changes in the recruitment of fish and zooplankton populations are rooted in the early stages of life. Thus, we can understand the links between recruitment and climatic change only if the relationships between the physical and biological parameters affecting those early stages are described and understood.

The first intensive U.S. GLOBEC field study will be conducted in the Georges Bank region of the Northwest Atlantic starting in 1994 (GLOBEC, 1991c). Reasons for selecting this area are: Georges Bank is thought to be highly sensitive to climatic change because it is positioned in a faunal, climatic and oceanic boundary region; the primary and secondary production on Georges Bank support a large and commercially valuable fisheries; Georges Bank is a region predicted to be more heavily impacted by climate change than other areas in the North Atlantic Ocean; and Georges Bank is of sufficient size and has a physical circulation pattern which enables distinct, trackable populations to develop and persist for long periods that are amenable for time-series study.

The target taxa to be studied include pelagic stages of cod (Gadus morhua) and haddock (Melanogrammus aeglefinus), and the copepods Calanus finmarchicus and Pseudocalanus spp., which are prey for early life stages of the fish larvae. The focus of the Georges Bank Study is to determine how biological and physical processes interact to control the population dynamics of these target species on the Bank. Information obtained can be used to assess the potential fate of these populations under various plausible global climate change scenarios.

This study is both a part of the international GLOBEC Program sponsored by SCOR and IOC, and the Cod and Climate Change Program of the International Council for the Exploration of the Sea. In addition, the study will complement many other national and international programs including the NOAA Atlantic Climate Change Program, the NOAA Coastal Ocean Program, the Canadian Ocean Production Enhancement Network (OPEN), and the Northern Cod Science Program (NCSP). Cooperation with OPEN, NCSP and Cod and Climate Change Program will provide the opportunity to compare results of similar studies from different bank and coastal systems of the North Atlantic Ocean.

Hypotheses: Specific hypotheses developed to address how physical processes affect the population dynamics of the target organisms on Georges Bank are:

- the horizontal and vertical structure of the circulation of water around Georges Bank leads to a circulation gyre; the residence time of water is long relative to biological time scales so that in situ growth rather than lateral exchange is the dominant process controlling the abundance of animals on the Bank;
- seasonal density stratification over the southern flank of the Bank causes prey aggregation in the pycnocline and thus increased survival of predator populations;
- temporal changes in mixing and stratification may control the abundance and species composition of phytoplankton which in turn may result in different rates of growth and production of herbivorous copepods in well-mixed, frontal, and stratified regions of the Bank;

- the occurrence of large, episodic exchanges of water and organisms on/off the Bank contributes to variability in population abundance;
- seasonal density stratification and the processes of turbulent mixing influence predator-prey encounter rates and thus the growth and survival of individual organisms;
- predation rather than starvation is the dominant source of mortality of fish larvae; predation rather than advective loss is the dominant source of mortality of copepods.

Implementation: The Georges Bank Study has four major components: broad-scale field studies, fine-scale process studies, modeling studies, and methodology/instrumentation development. The broad-scale studies will include ship board surveys, moored instrumentation and analysis of satellite data. These studies will determine the distribution and abundance of the target organisms in relation to their physical environment over the December to August pelagic period of the gadid larvae. Experimental work on living animals will be carried out during these surveys as well, and will be directed at measuring vital rates of individuals relating to population dynamics, and at gaining new information on basic biology of the target species.

Fine-scale process studies will be nested within the broad-scale observations to investigate specific biological and physical processes. The approach anticipated to be used in most of these studies is to follow a drogoue while investigating the physical-biological interactions. Processes associated with vertical mixing and stratification, and with cross-frontal exchange will receive the greatest attention. With respect to biological work, a vigorous field sampling program will be coupled with experimental work on living animals. Close cooperation and interaction will be required between the broad-scale and fine-scale components of the program in the execution of field sampling, with experimental work, and in analysis of the data.

Modeling studies will assist in the formulation and interpretation of the field studies, as well as in providing the context for integration of the results. U.S. GLOBEC already has some modeling studies underway and additional modeling studies may be required. Our goal of integrating the results of modeling with field sampling and experimental studies cannot be overemphasized.

As for methodology and technology, if we are to achieve the full objectives of the Georges Bank Study, we will require the application of recent developments in methodology and technology, both in the sampling systems used and in the analysis techniques applied to samples. Instrumented net systems, multi-frequency acoustical samplers, bio-optical and optical imaging systems, and moored instrumentation will measure the physics and biology on scales relevant to the controlling processes. Biochemical analysis of copepods to indicate growth rate and physiological state, otolith analysis to determine birth date and growth rate of fish larvae, and genetic analyses to determine possible sources of Georges Bank copepod populations are among the techniques that could be considered in this study.

With these different components the specific program objectives are:

- 1) Quantify abundance of target species in time and space on Georges Bank over the December/August period.
- 2) Measure vital rates of target species relating to population dynamics.
- 3) Quantify the physical processes that influence the vertical mixing and seasonal stratification of the water column; determine if the vertical distribution and vital rates

of target species are correlated with mixing processes. Examine effects of mixing-driven changes in the phytoplankton food environment on copepod growth rates.

- 4) Quantify the rates of physical exchanges of water and biota across the boundary of the Bank; determine how these exchange processes are affected by vertical migration behavior and how they influence population abundance.
- 5) Determine how microscale turbulence interacts with micro-patchiness to affect predator-prey interactions and vital rates.

The field program is structured to have alternate years of intensive study (1994, 1996, 1998). The broad-scale studies will be conducted in each of the intensive years. The focus of the process studies, however, will change in each intensive year. In 1994, the priority will be on fine-scale studies of the vertical mixing and stratification processes; in 1996, the focus will be on processes controlling the inflow, retention and exchange of water and organisms from the bank; and in 1998, on frontal exchange processes. Depending upon funding constraints, some work in each process area may be undertaken in each year. A modest broad-scale program will be conducted in the intervening years (1995 and 1997) to maintain continuity of observations through the entire period of the program.

A number of data sets already exist which could help address some objectives of the Georges Bank Study. Analysis of these data sets is encouraged and could be supported as part of this program.

All data collected during the Georges Bank Study should be managed through a central site, combined with existing data sets for the region and made available to the program participants. Real-time telemetry of data from shipboard measurements and moored instruments, as well as preliminary model results will be made available to investigators in the field to aid in program response to events and unusual observations. Final data sets will be archived and made available to the scientific community. All participants must adhere to the data management distribution and exchange policies of U.S. GLOBEC and the U.S. Global Change Research Program.

2. ACKNOWLEDGEMENTS

This report was developed largely by an Implementation Team in early 1992 (in alphabetical order - R. Beardsley, A. Bucklin, C. Davis, L. Incze, J. Irish, G. Lough, D. Mountain, and P. Wiebe) and is based on extensive prior discussions by larger groups of U.S. and Canadian scientists at meetings held in Halifax, Nova Scotia in June 1990 (GLOBEC, 1991c) and Cambridge, MA in July 1991. Useful input and review of early drafts of this report was provided by: G. Gawarkiewicz, M. Huntley, G. Paffenhöfer, T. Powell, C. Peterson, W. Peterson, and S. Smith and by the U.S. GLOBEC Steering Committee. The final draft was reviewed externally by K. Frank, M. Grosslein, P. LeBlond, J. Loder, W. Michaels, D. Olson, I. Perry, P. Shelton, and K. Thomson, and three additional anonymous reviewers. The final version was edited by W. Peterson, F. Schwing, and the Implementation Team. The U.S. GLOBEC Scientific Steering Committee gratefully acknowledges all of these significant contributions.

3. INTRODUCTION

The primary objective of the GLOBAL ocean ECOSYSTEM dynamics program is to understand the underlying physical and biological processes that control the abundance of key populations of marine animals in space and time (Peterson and Powell, 1991). The ultimate application of this knowledge is to understand the marine ecosystem as it relates to marine living resources and to understand how fluctuations in these resources are driven by climate change and exploitation (GLOBEC, 1991b). It is assumed that changes in the recruitment of fish and zooplankton are rooted in the early stages of life. Thus, we can understand the links between recruitment and climatic change only if the population parameters in those early stages are described and understood. To begin this long-term program, the initial U.S. GLOBEC effort focuses on understanding and quantifying of present day physical forcings and their effects on the population dynamics of selected target species.

The first intensive U.S. GLOBEC field study will be conducted in the Georges Bank region of the Northwest Atlantic starting in 1994 (GLOBEC, 1991c; Figure 1). This area was chosen because: Georges Bank is of sufficient size and has a physical circulation which enables distinct trackable populations to develop and persist for long periods amenable for time-series study; Georges Bank supports a very productive fisheries and is thought to be highly sensitive to climatic change because it is positioned in a faunal and physical boundary region; and Georges Bank is in a region predicted to be more heavily impacted by climate change than other areas in the North Atlantic Ocean (Manabe et al., 1991). Target taxa to be studied include pelagic life stages of cod and haddock and their major prey and predator species. The overall goal of the Georges Bank Study is to determine how biological and physical processes interact to control abundance of these target species populations on Georges Bank in space and time. This information then can be used to assess the potential fate of these populations under various plausible global climate change scenarios.

This report presents a conceptual plan for the implementation of the U.S. GLOBEC Northwest Atlantic/Georges Bank Study. The report begins in Section 4 with a brief review of the Georges Bank ecosystem, giving the specific characteristics of this region which make it suitable for intensive study. Then the physical oceanography of the Bank and the target species are described. Section 4 ends with a discussion of the key physical/biological interactions occurring on the Bank and the main scientific hypotheses of the study. The main components of the study are then presented in Section 5. These include an experimental program of both broad-scale and smaller-scale process studies, methodology and instrument development, modeling, and historical data analysis. Requirements for program management and data management are discussed in Section 6, and the relationships between this study and other national and international programs are described in Section 7.

The framers of this report hope that the proposed implementation plan represents a valid attempt to craft a sound scientific program, and that further planning by the larger scientific community will find this initial plan a useful starting point. It should be obvious that the magnitude of the program will be driven by availability of funding. Despite the realization that not all of the scientific issues discussed here can be (or ever will be) funded, we felt that it was better to outline an ambitious program than a more limited one which lacked vision. When initiated, the Georges Bank study will be a complete program in the sense that it will address physical-biological objectives which are judged to have the greatest relevance to the issue of climate change. The challenge to all prospective investigators is to demonstrate convincingly that their work leads to a new level of understanding of the links between the atmosphere, ocean physics, and population dynamics of marine organisms, in the context of climate change.

4. BACKGROUND

4.1 *The Georges Bank Ecosystem.*

4.1.1 General Description.

Georges Bank is a shallow submarine bank lying along the outer continental shelf about 180 km east of Cape Cod, Massachusetts (Figure 2). Along with Browns Bank, Georges Bank forms the southern sill of the Gulf of Maine with its many basins. Georges Bank is bounded on the east and west by the Northeast and Great South Channels, respectively. The Bank is roughly elliptical in shape with a very steep flank along its northern edge and a more gently sloping flank out to the shelf break at 100 m along its southern edge. The Northeast and Great South Channels have sill depths of about 230 and 60 m, respectively, and the Northeast Channel is the primary conduit for slope water flowing into the Gulf of Maine. Formed by glacial action during the last Ice Age, the Bank has a rough crest covered with large sand waves and shoals which cause the bottom depth there to vary from 10-40 m. Currents over the Bank are dominated by strong semidiurnal tidal components and a mean clockwise gyre that intensifies with increasing stratification in the summer. During the summer period, the gyre becomes partially closed with water parcels recirculating around the Bank with an approximate period of 50 days (Flagg et al., 1982). Bank waters exhibit a large seasonal temperature variation, typically increasing from 5°C in late winter to 15°C in late summer (Flagg, 1987). The biology of the Bank is characterized by high plankton and fish biomass, and high primary and secondary production. Extensive background information on the physical oceanography and biology of Georges Bank is given in Backus (1987), yet fundamental questions remain about the dynamics of populations living on the Bank and their coupling to the physical environment.

4.1.2 Criteria Used in Selecting Georges Bank.

The criteria for selection of this region as the first U.S. GLOBEC study site are outlined in the U.S. GLOBEC Initial Science Plan (GLOBEC, 1991c; pp. 8-10). These reasons include the following:

a) An analysis of historical data collected since 1951 shows that the Georges Bank area has experienced some of the North Atlantic's largest changes in sea surface temperature (Gordon et al., 1992). Georges Bank is an area that coupled ocean-atmosphere climate models suggest will be subject to larger change than other parts of the North Atlantic Ocean (Manabe et al., 1991). The most significant regional changes are expected to be in temperature and precipitation associated with changes in surface pressure and wind stress patterns.

The flow of water along the shelf from Newfoundland to the Mid-Atlantic Bight is largely buoyancy-driven from local and distant freshwater sources including Hudson Bay runoff and glacial or sea-ice melt from the Labrador Sea. Climatic changes in the net precipitation minus evaporation patterns between 40-65°N could alter both local runoff and the strength and relative freshness of the along-shelf flow entering the Gulf of Maine and Georges Bank. Changes in the magnitude of the subtropical Gulf Stream and subpolar Labrador Current transport due to differences in wind forcing, air temperature, and salinity could significantly impact the position and dynamics of ocean fronts, rings, and other features in the Georges Bank area. Such changes may also affect the timing, intensity and location of stratification on the region's submarine banks. Other important processes, including water formation in the Labrador Sea (Lazier, 1981) and sea ice development (Hill and Jones, 1990), may be linked to climate change and other long-term fluctuations.

b) The ecosystem on Georges Bank is also sensitive to climate change (Frank, et al., 1990). Georges Bank is located in a faunal transition zone, with colder boreal water fish and plankton

species to the north and warmer water species to the south (Figure 1). With the large annual cycle of water temperature on the Bank, it is both the northern limit for many of the warm water organisms and the southern limit for many of the cold water species. A climate-induced change in mean water temperature of 2°C or more could cause a significant latitudinal shift in the faunal transition zone and thus in the seasonal occurrence of different organisms on the Bank. This is in addition to the ecological consequences of other potential climate change effects on the environment, as discussed above.

c) Changes in the timing and intensity of seasonal stratification due to a changing climate could effect on cod and haddock populations differentially. Cod larvae may be less sensitive to water column stratification (because they are winter spawners), whereas haddock larvae are highly sensitive to stratification (because they are spring spawners), and survive best in stratified waters.

d) Important target species are present on Georges Bank and are entrained in the clockwise circulation which increases the residence time of the populations on the Bank (Walford, 1938; Clarke, et al., 1943; Davis, 1987b; Lough and Bolz, 1989). These species exhibit substantial in-situ population growth and development on the Bank because of enhanced retention and elevated food concentrations.

e) A variety of physical processes including tidal mixing, stratification, frontal dynamics and storm events, together with definable populations of dominant target species allow generic physical/biological mechanisms and interactions to be studied. Another comparison made possible on Georges Bank that has broad application is a comparison of the phytoplankton food environments in well-mixed vs. stratified water columns, and concomitant study of the effects these different environments might have on the rates of growth and production of herbivorous zooplankton.

f) A significant historical research and data base exists for the biology and physics of the Bank and the surrounding region. While much of this work is summarized in Backus (1987), new studies have been (and should be) undertaken on smaller-scale physical and biological processes and circulation modeling.

g) Although this area has been extensively sampled in the past and a substantial base of information is available about the resident populations, the level of understanding is still not sufficient to enable predictions about the response of the populations to climate change to be made with any accuracy or confidence. This is because integrated and coupled physical/biological measurements either have not been made or not made with sufficient resolution. New instrumentation and techniques that are being developed, integrating both biological and physical measurement, should be readily adapted to the spatial and temporal requirements of a comprehensive study of physical/biological interactions of the Bank.

h) A significant opportunity exists for comparative research through international collaboration with several programs, including the Canadian Ocean Production Enhancement Network (OPEN) program, Northern Cod Science Program (NCSP) and the International Commission for the Exploration of the Sea (ICES) Cod and Climate Change Program (CCC). In particular, the OPEN program is focussed on understanding the physical and biological interactions on bank systems on the Scotian shelf. Comparison of results between these ecosystems and Georges Bank should benefit both programs. Also, since cod has been an important fishery throughout the North Atlantic fishing grounds, coordination of the Georges Bank Study with the ICES program should improve our ability to predict broader-scale climatic influences on fisheries.

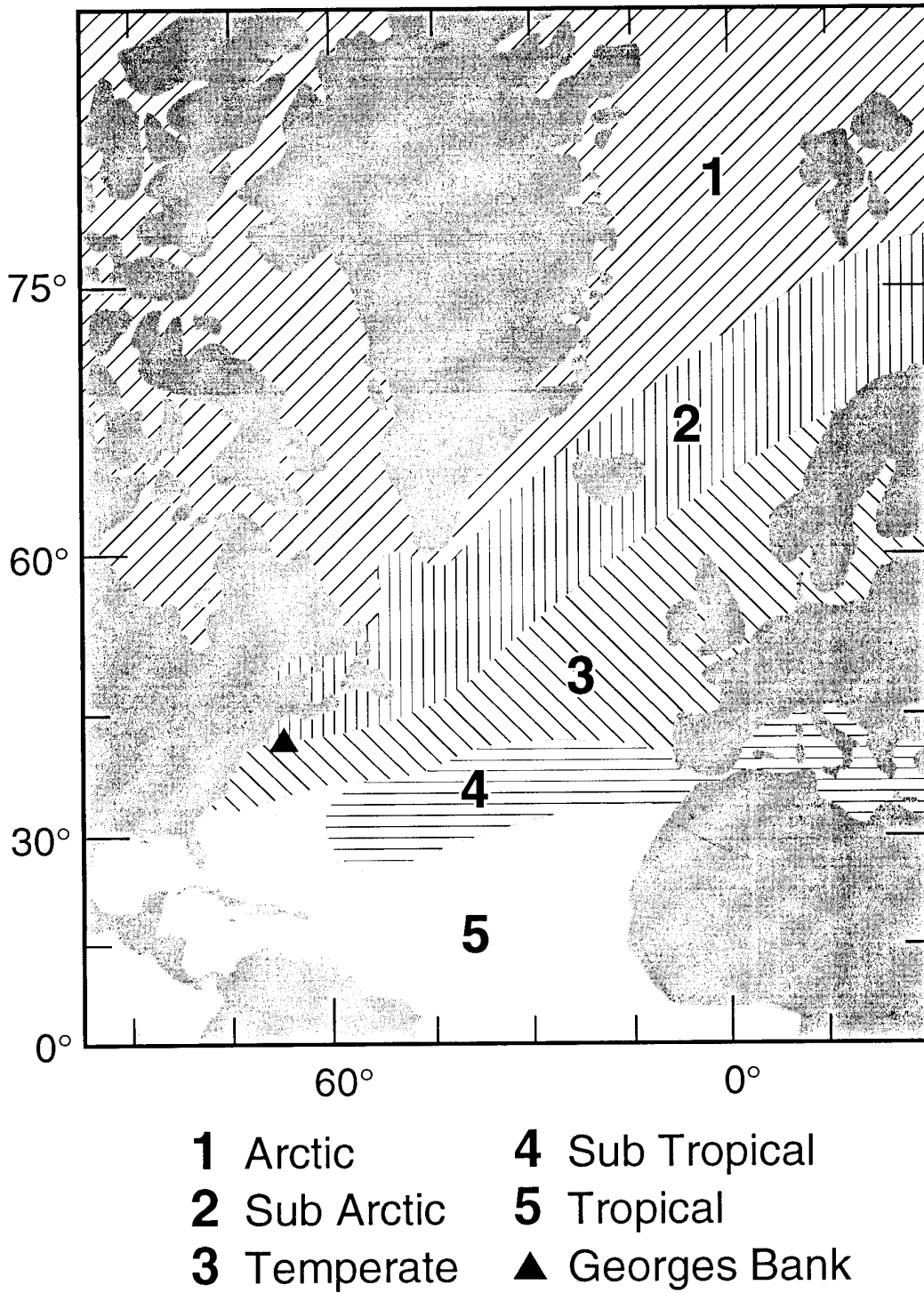


Figure 1. Biogeographic plankton boundaries in north Atlantic in relation to Georges Bank (modified from Herman, 1979).

4.1.3 Space-Time Boundaries of Georges Bank Study.

A working definition of the geographical boundary of Georges Bank is useful to place a space and time focus in the Northwest Atlantic/Georges Bank Study. The target fish species, cod and haddock, spend much of their early life history - from egg to demersal stages - within the shelf waters covering the Bank from winter through summer. The target zooplankton populations, which are prey for the cod and haddock larvae, also reside for most or all of their life cycle in the Bank waters. We therefore define the Bank as the area within the 100 m isobath with the western boundary located near 69°W along the center of the Great South Channel (Figure 2). The Northwest Atlantic/Georges Bank Study will focus on the key processes controlling population dynamics of the target species within the Bank during the period from December to the following August. Additional sampling in the regions around the Bank (e.g., the Gulf of Maine and Slope Water) and during the rest of the year will be necessary to better understand the physical and biological properties of the water flowing onto and off the Bank. Most or all of this will be accomplished using moored instrumentation.

4.2 Rates of Birth, Growth, Mortality and Exchange: Processes Controlling Population Abundance

To provide a conceptual framework for studying physical/ biological interactions, we first outline the factors controlling population abundance. Within a region, the biomass of a species is regulated by birth, growth, death, and exchange processes operating in each life stage (Figure 3) and given by the mass balance equation:

$$\frac{\partial}{\partial t} M_i = \alpha_{i-1} M_{i-1} + I_i - E_i - R_i - P_i - S_i - \alpha_i M_i + PE$$

where M_i is the biomass of stage i , α_i is the recruitment rate out of stage i , I is ingestion, E is egestion, R is respiration, P is predation, S is starvation, and PE is physical exchange (includes advection and diffusion). For adult and egg life stages, the equation must also include loss and input terms, respectively, for egg production (Figure 3). The left-hand side of the equation can be obtained directly from field data on abundance, and the size distribution and/or age structure of individuals within a population. On the right-hand side, individual growth rate can be measured in lieu of ingestion, egestion, and respiration (Figure 3). Measurements of growth rate (and/or development times) also can provide indices of starvation potential, as well as estimates of transfer rates (i.e., recruitment rates) between life stages (Figure 3). For adult female holozooplankton, egg production rates should be measured as functions of food availability, condition factors, and spawning behavior. Measurements of body size may be important for some holoplanktonic taxa where fecundity is related to adult size. If growth rate and starvation are found to significantly limit population growth, the components of growth can be examined in further detail.

Given that phytoplankton abundance (and probably phytoplankton species composition as well) differs greatly in well-mixed vs. stratified regions of the Bank (shown later in this document in Figure 10), copepod egg production, development and growth rates also may differ between well-mixed, frontal and stratified regions of the Bank. Thus, studies that focus on spatial variations in growth rates could lead to a better understanding of environmental control of copepod population dynamics. Physical processes that control phytoplankton dynamics should be studied because whichever physical processes directly control phytoplankton growth rates may indirectly control copepod population dynamics.

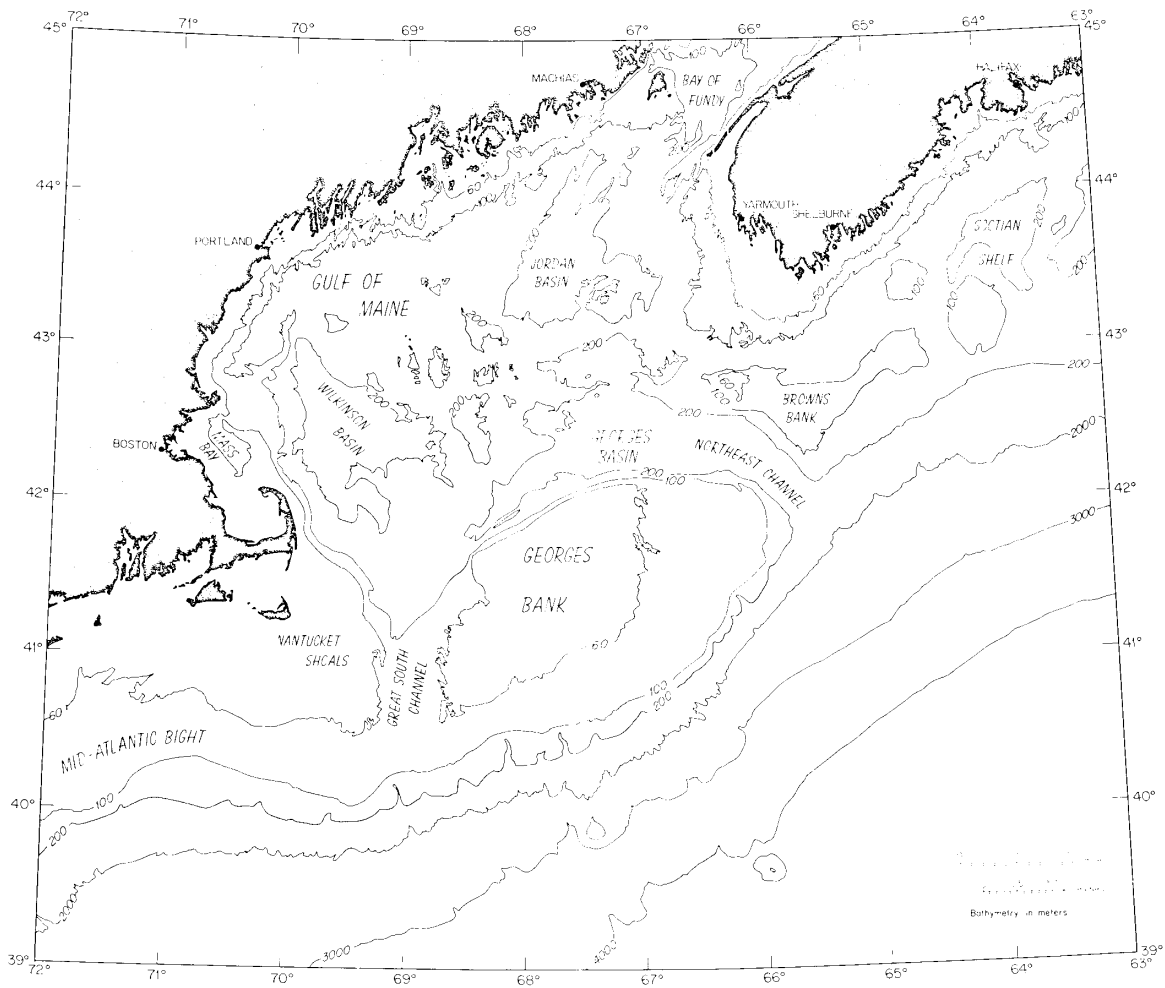
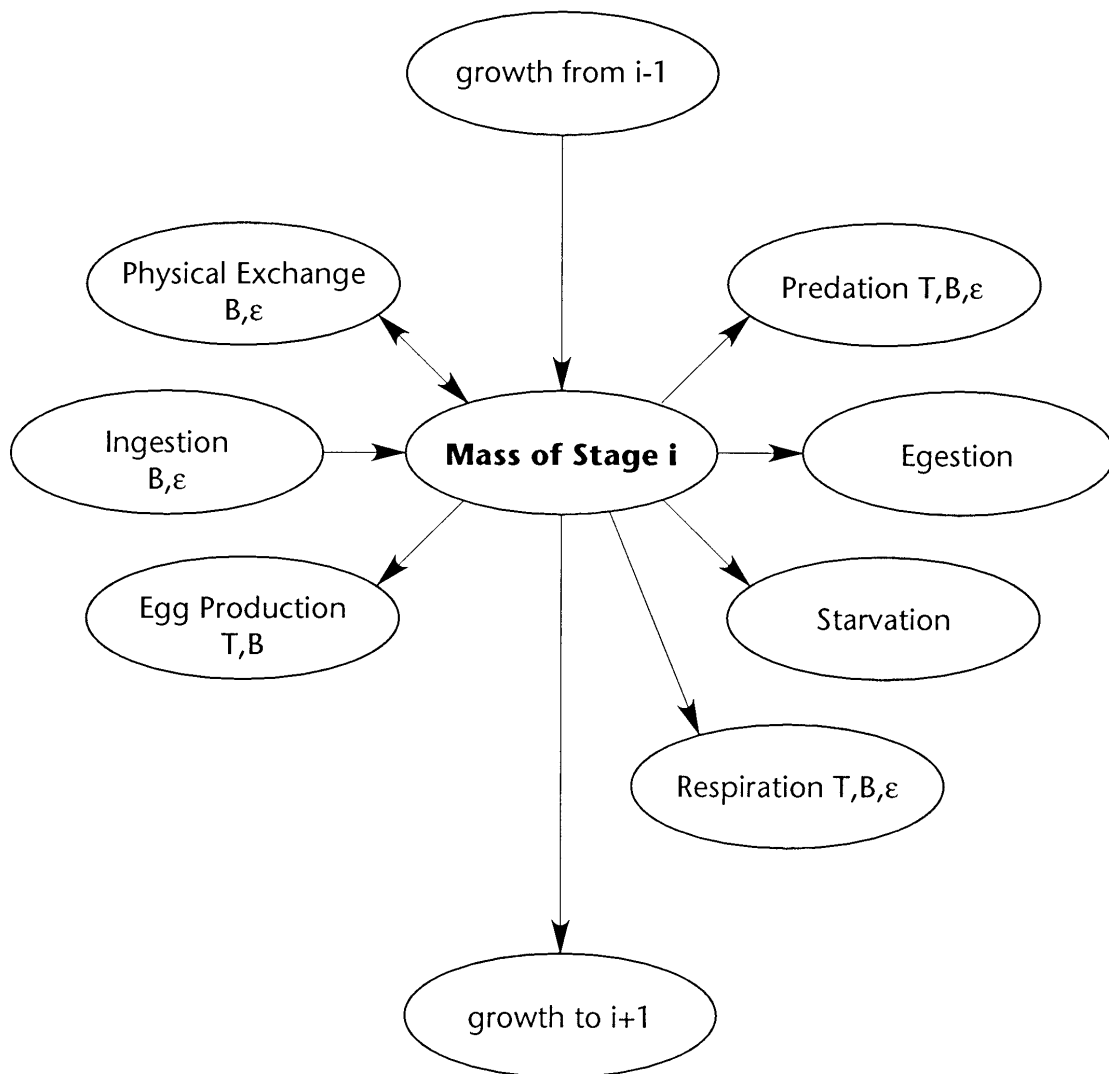


Figure 2. Bathymetry of Georges Bank, the Gulf of Maine, and the adjacent continental shelves. Depth contours are in meters.



T - Temperature
 B - Behavior (swimming, feeding)
 ε - Turbulence (heat and momentum flux, predator/prey interaction)
 Physical Exchange = mean circulation, storms and rings, frontal exchange

Figure 3. Schematic illustration of factors affecting populations biomass.

Swimming and feeding behavior of the target species could be studied in relation to prey abundance, nutritional quality, and avoidance behavior as well as in relation to microscale patchiness, turbulence, and predation rates (Figure 3). These behavioral activities affect rates of ingestion and respiration (and therefore growth and starvation) as well as susceptibility to predation. Study of these behaviors could provide one of the keys to understanding the relationship between physical processes and population response.

Mortality rates can be estimated from field studies which show abundance of a given developmental stage along with measurements of stage-specific development times, following Steele and Mullin (1977) and Kimmerer (1987). Mortality rates for eggs can be derived from equations in Kiørboe et al., (1988). Also required will be estimates of physical exchange of animals on and off the Bank from detailed information on the flow field, spatial gradients in animal abundance, and estimates of the time rate of change in abundance. Mortality rates can also be estimated from predator abundances and consumption rates, and prey abundance and prey growth rates.

Physical factors which may directly affect animal abundance include temperature effects on biological rates (Figure 3), microturbulence effects on ingestion, respiration, and predation, and advective losses or gains from the study area. This latter category includes both horizontal advection by mean and episodic currents associated with steady forcing (e.g., buoyancy and tidal) and transient forcing (e.g., storms and mesoscale eddies and rings), and the effective horizontal movement of zooplankton caused by their vertical swimming behavior in a time-dependent vertically sheared current field. Given the apparent long residence time of animals on the Bank, we hypothesize that individuals of some species have evolved behavior patterns which serve to retain them on the Bank. We know little about these behaviors. Also included here is consideration of sources of animals found on the Bank; although larval fish are probably produced locally on the Bank during winter and spring, copepods at that time of the year almost certainly recruit from somewhere else.

At present, we have only a limited understanding of how physical processes interact with the dynamics of dominant zooplankton species on Georges Bank. Local physical processes are of course important, however the effects of large-scale (and remote) physical forcing on ecological efficiency and the consequences for recruitment at higher trophic levels are poorly understood. Significant insight can be gained by modeling interactions between physical transport, mixing-stratification, simple food chain interactions and the population dynamics of dominant or characteristic zooplankton species. Each species has evolved certain characteristics which are affected differently by advective transport out of favorable growth areas; some species may be highly dependent upon seasonal input onto the Bank of individuals from source populations off the Bank, and some may not.

4.3 Physical Oceanography of Georges Bank.

On the large scale, Georges Bank is part of a very long coastal current system which flows southwestward from Laborador to the Mid-Atlantic Bight (Figure 4; Chapman and Beardsley, 1989). Locally, two oceanic water masses and local air/sea interaction determine the hydrographic conditions within the Gulf of Maine and on Georges Bank (Bigelow, 1926). Cold, low salinity coastal water enters the Gulf of Maine from the Scotian Shelf (Smith, 1983) and warm, saline Slope Water enters through the Northeast Channel (Ramp et al., 1985). Both of these inflows to the Gulf exhibit significant seasonal and inter-annual variability. The two water masses plus local runoff mix during a generally cyclonic (counterclockwise) movement around the Gulf which may slow down or even reverse in part during winter (Brown and Irish, 1992). During the summer, this basin-scale movement may be comprised of smaller-scale cyclonic flows around Jordan, Wilkinson, and Georges Basins (Brooks, 1985, Butman and Beardsley, 1991). In the western Gulf of Maine, near-surface waters flow both southward around Nantucket Shoals into the Mid-

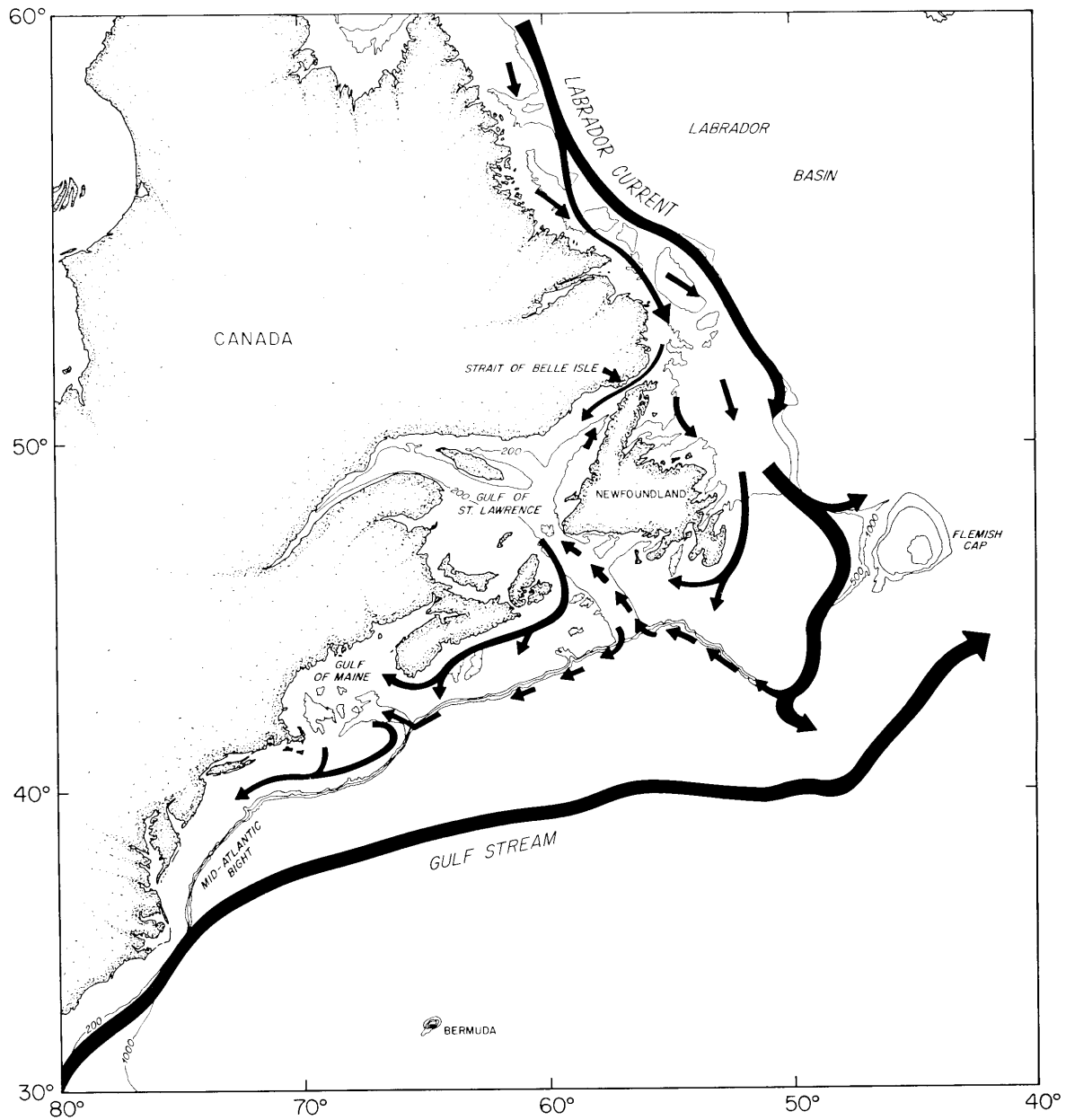


Figure 4. General circulation over the northwestern Atlantic continental shelf (from Chapman and Beardsley, 1989). Also shown is the mean position of the Gulf Stream (from Auer, 1989 and Kelly, 1991). Broader arrows denote regions of higher current concentration, and broken arrows along margin correspond to deeper flows.

Atlantic Bight and eastward onto the northwest flank of Georges Bank (Hopkins and Garfield, 1981; Limeburner and Beardsley, 1982; Beardsley et al., 1991). On the northwest flank, the interaction of strong tidal currents and steep bottom topography results in a strong horizontal density front and a narrow, jet-like current flowing eastward along the northern edge of the Bank (Loder, 1980; Magnell et al., 1980; Butman, 1982). The flow then turns clockwise and slows to move southwestward along the southern flank of the Bank. The strength of this anticyclonic (clockwise) circulation increases with increasing stratification in the spring and summer (Butman et al., 1987). A permanent hydrographic front along the southern edge of the Bank separates the shelf water over the Bank from the more saline Slope Water offshore (Flagg, 1987). Much of the shelf water flowing southwestward along the southern flank of the Bank continues westward into the Mid-Atlantic Bight (Beardsley et al., 1985). During stratified conditions, some of the shelf water on the southern flank of the Bank moves northward through the Great South Channel, forming a partially closed gyre (Butman and Beardsley, 1987).

Instantaneous water movements on the Bank are dominated by strong tidal forcing and wind events associated with storms. The Gulf of Maine/Bay of Fundy basin system is near-resonance at the semi-diurnal tidal frequency, which amplifies the semidiurnal tidal amplitude in the Bay of Fundy and the currents across Georges Bank (Garrett, 1972; Greenberg, 1979; Brown and Moody, 1987). The tidal currents are rotary with maximum velocities (and tidal excursions) increasing from about 30 cm/s (4.3 km) near the shelf break on the southern flank to 75 cm/s (10.7 km) and larger over the crest (Bumpus, 1976; Moody et al., 1983). Due to bottom friction, tidal currents exhibit a large decrease in magnitude and some veering in direction near the bottom (Brown, 1984). This vertical shear generates strong turbulence and vertical mixing over the shallow top of the Bank (Garrett et al., 1978). Wind driven currents, although transient, can be much larger than the mean velocities (Noble et al., 1985; Brink et al., 1987). Storm events potentially can exchange large amounts of water on/off the Bank. In addition, along the southern edge of the Bank, warm-core Gulf Stream rings can influence the flow field and entrain large amounts of shelf water off Georges Bank and into the Slope Water offshore (Flagg, 1987; Garfield and Evans, 1989).

The balance between the tendencies for recirculation of water around the Bank and for advective exchanges of water from the Bank result in an average residence time of about 50 days for a near-surface water parcel within the 100 m isobath on the Bank (Flagg et al., 1982; Loder et al., 1982; Beardsley et al., 1991). Estimates of residence time are somewhat shorter in winter and somewhat longer in summer. The increase in residence time in summer appears to result from a greater tendency for water to recirculate around the Bank during stratified conditions.

Water properties on the Bank exhibit characteristic seasonal cycles. In winter, atmospheric cooling and wind mixing keep the entire Bank region vertically well-mixed (Figure 5a). During spring, increasing solar insolation and decreasing wind mixing (Figure 6a-b) cause the water column on the southern flank to become stratified in temperature and density (Figure 5b, Figure 6c-d). Over the shallow, central region of the Bank, turbulent tidal mixing is sufficiently strong to keep the water column well mixed year round. Tidally mixed fronts develop near the 60 m isobath, separating the central Bank from the stratified waters to the north in the Gulf of Maine and to the south on the flank of the Bank (Loder and Greenberg, 1986). Seasonal warming and increasing stratification continue through the summer. In autumn and winter, cooling and increasing wind mixing again lead to well mixed conditions over most of the bank in the winter.

The seasonal range in temperature is about 12°C at the surface in the well-mixed region, and about 8°C at the bottom over the southern flank of the Bank. The currents on the southern flank of the bank also exhibit a seasonal cycle, with mid-depth (45 m) along-bank values of about 5 cm/s in March increasing to a maximum of about 11 cm/s in September. The seasonal increase in along-bank velocity is consistent with the geostrophic shear associated with the increasing across-

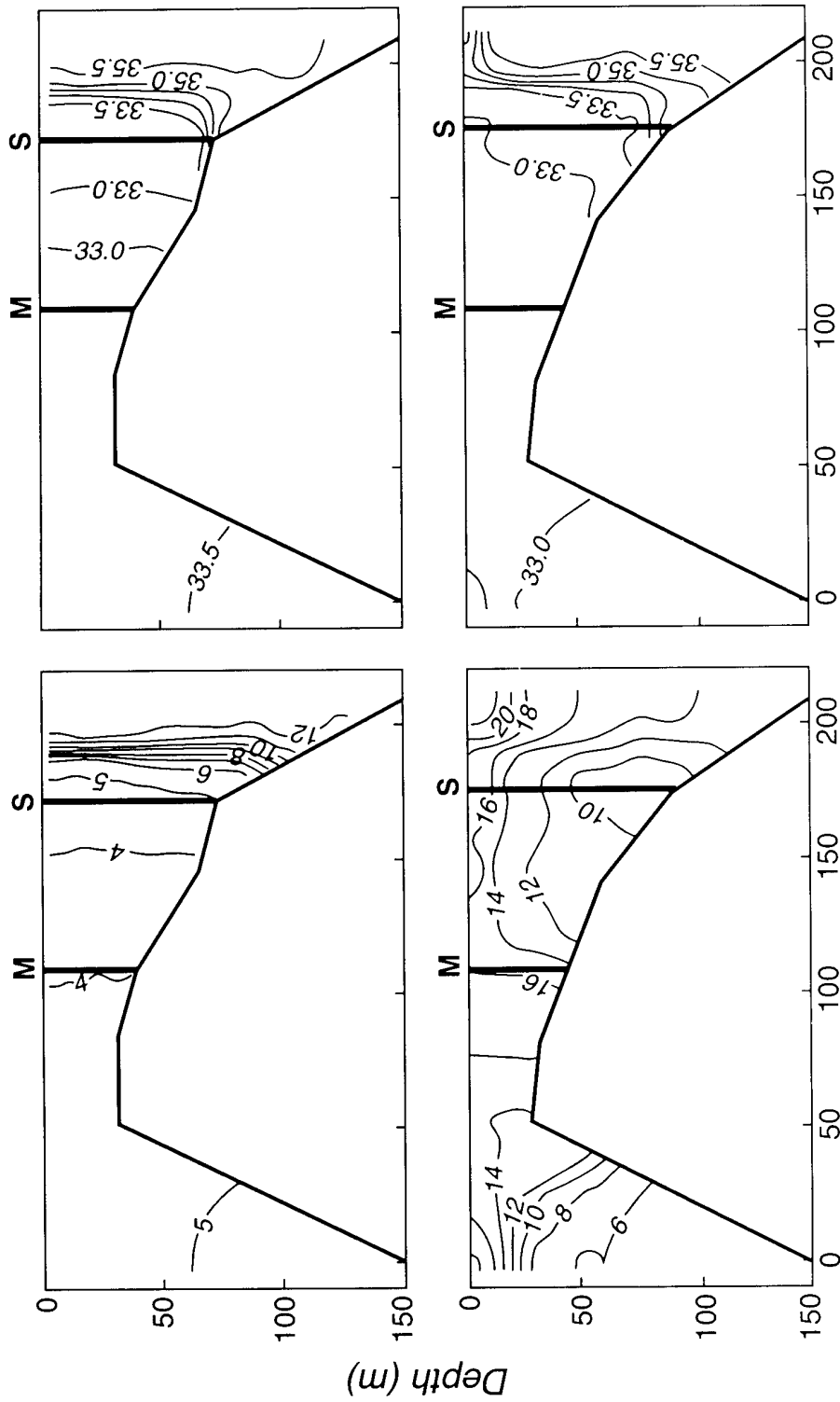


Figure 5. Cross sections of water properties across Georges Bank: a) winter temperature, b) winter salinity, c) summer temperature, and d) summer salinity. The winter data are from March 1980, the summer data from August 1980. Locations of stations in the well-mixed region (M) and the stratified region (S) used in Figure 6 are indicated. Distance along the x-axis is from the northern edge of the Bank.

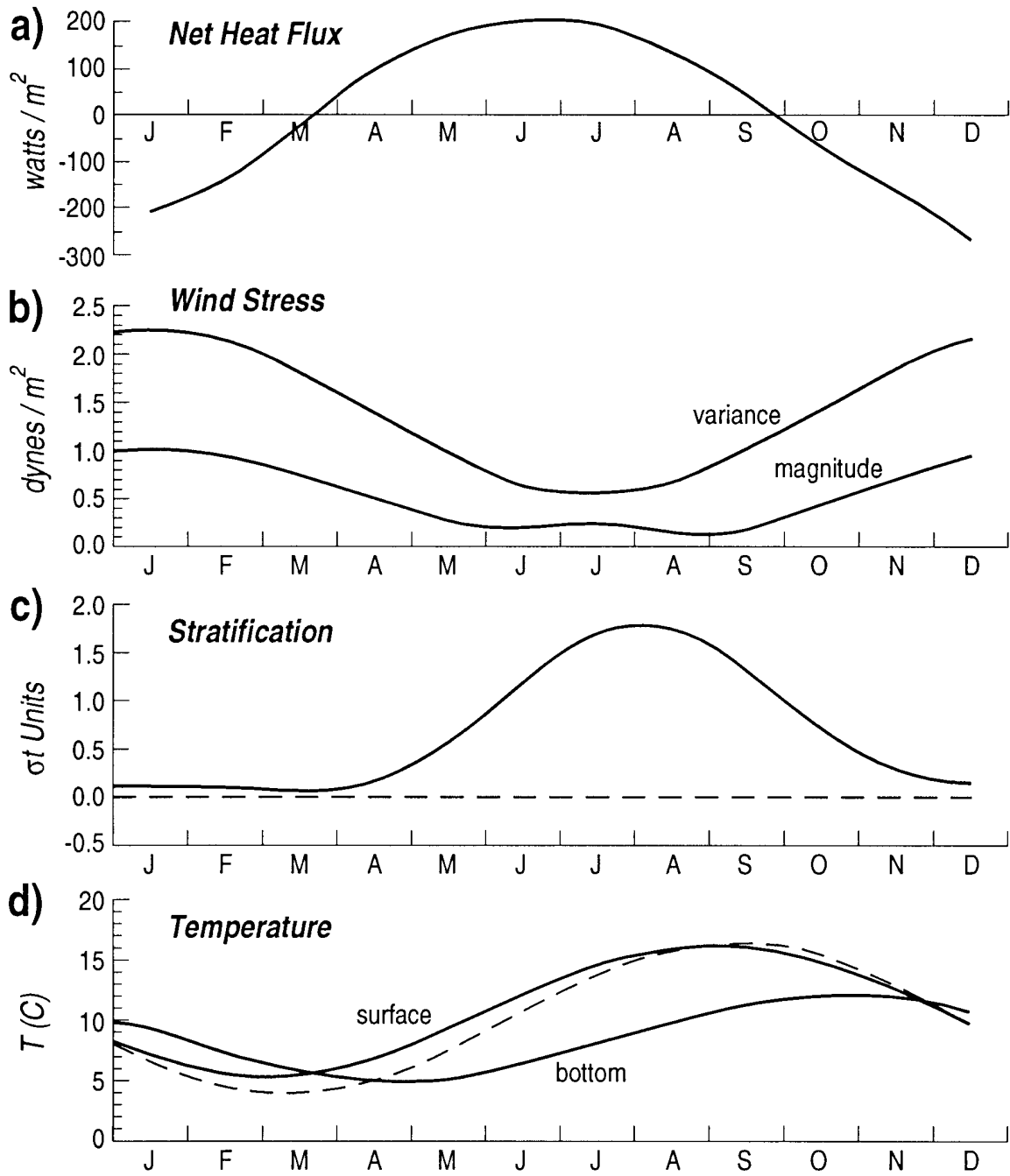


Figure 6. a) Annual cycle of net surface heat flux in the Georges Bank region; b) annual cycle of the magnitude and variance of the wind stress in the Georges Bank region; c) annual cycle of density differences between surface and bottom at the well-mixed site (- -) and the stratified site (—) on the southern flank of Georges Bank indicated in Figure 5; d) annual cycle of water column temperature at the mixed site (- -) and the surface and bottom temperature at the stratified site (—).

bank density contrast between the well-mixed and stratified regions (Butman and Beardsley, 1987).

The role of inter-annual and longer fluctuations in the North Atlantic on the oceanography of Georges Bank must be noted. Recent observations show that Georges Bank has experienced some of the North Atlantic's largest changes in sea surface temperature (Gordon et al., 1992). A global analysis shows that the North Atlantic experiences the second highest amplitude variations in large-scale inter-annual surface pressure patterns (Wallace and Gutzler, 1981). These variations, identified as the North Atlantic Oscillation (Walker, 1924; Walker and Bliss, 1932), have a period of about 7 years (Rogers, 1984) and are associated with the observed pattern of wind strength, SST anomalies, changes in water masses, Labrador Sea water formation, and sea-ice coverage. There is also evidence that such variations covary with cod stocks in the Northwest Atlantic that are otherwise unrelated to fishing pressure. Longer time-scale climate fluctuations, based on the geological record and model simulations, also appear linked to swings in the dynamics of the North Atlantic and related large shifts in fisheries potential.

4.4 Target Species.

Target species were chosen to represent key elements of the holoplanktonic and ichthyoplanktonic assemblages on Georges Bank (Figure 7). The suggested target species include pelagic life stages of cod and haddock, and the holoplanktonic copepods of the genera Calanus finmarchicus and Pseudocalanus (both moultoni and newmanii). These copepods are major prey of the larval fish (Kane, 1984). The population dynamics of these target species will be studied in depth, focussing on those processes discussed in section 4.2 (Figure 3).

Other species which are thought to be important in the life cycle of the target species, but are not designated for in depth population dynamics study, include: copepods, (Centropages, Paracalanus, Oithona), chaetognaths (Sagitta elegans), amphipods (Monoculodes edwardsi, Gammarus annulatus, Themisto gaudichaudi), mysids (Neomysis americana), and euphausiids (Thysanoessa inermis, Meganctiphanes norvegica). Gelatinous predators of copepods and fish larvae also are suggested for study; these include medusae (Staurophora mertensii, Aglantha digitale, Cyanea capillata) and the ctenophore Pleurobrachia pileus. Non-target species should be studied in relation to their impact on the target species, focussing on such factors as distribution, abundance, and predation rates. Information on these species should be collected collaterally with data on the target species.

Criteria for selecting target species are outlined in the U.S. GLOBEC Initial Science Plan (1991b; pp. 38-39) and in the U.S. GLOBEC Northwest Atlantic Program report (1991c; pp. 12-20). In short, cod and haddock are commercially important species whose population dynamics are known to be sensitive to physical variability including temperature, mixing, and advection (e.g., Buckley and Lough, 1987). In addition, a long historical data record exists for these species and, in the case of cod, there is a current international ICES program (Cod and Climate Change) to study the potential effects of climate change on their population dynamics. The target holoplanktonic species, Calanus and Pseudocalanus, are dominant members of the zooplankton community on Georges Bank during the late winter, spring, and summer when the planktonic stages of cod and haddock are in the water column. Study of the physical and biological factors affecting their population dynamics will provide information on mechanisms of dispersal and recruitment of marine planktonic populations in general as well as on processes controlling food availability to and predation on the target fish species.

4.4.1 Overview of Cod and Haddock on Georges Bank.

Atlantic cod (Gadus morhua) and haddock (Melanogrammus aeglefinus) are demersal gadoid species distributed on both sides of the Atlantic; in the western North Atlantic they range

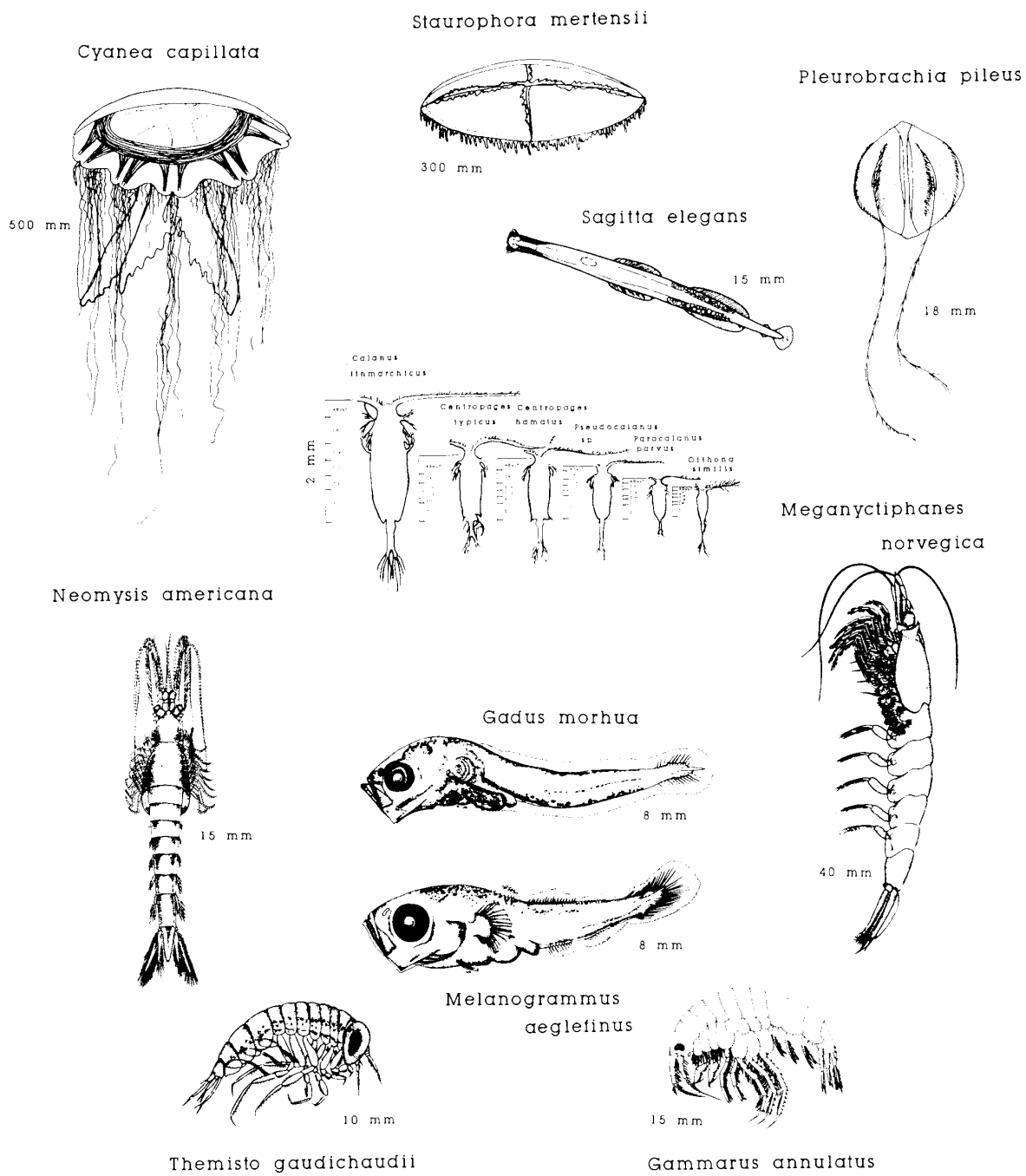


Figure 7a. Drawings of representative target species and other important members of the plankton.

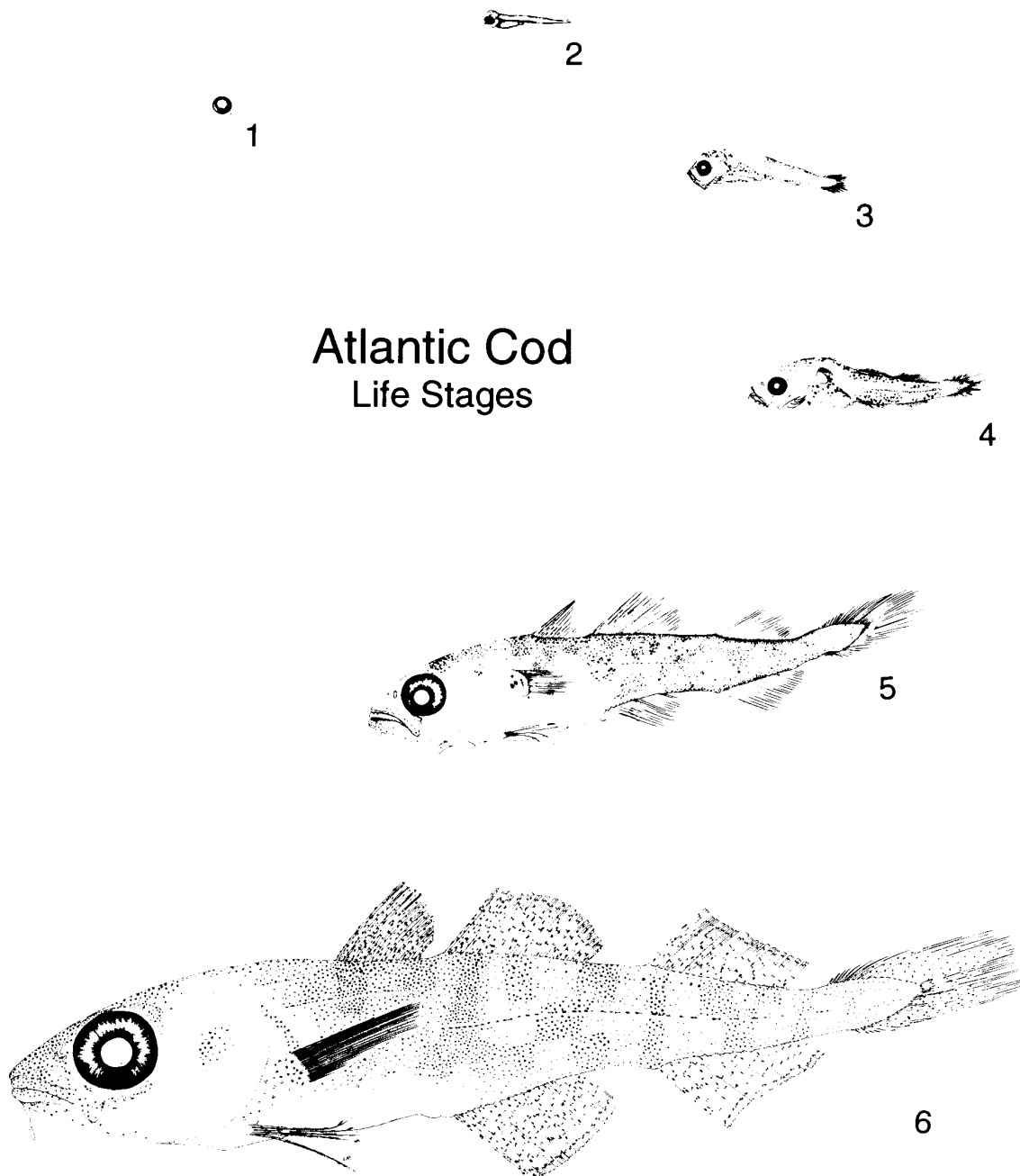


Figure 7b. Stage development series of Atlantic cod, *Gadus morhua*, illustrated from specimens collected on Georges Bank (drawn by E.A. Broughton, NEFSC, Woods Hole Lab.). Stage 1: Egg, 1.5 mm. Stage 2: Early Larva, 3 mm. Stage 3: Late Larva, 10 mm. Stage 4: Early Pelagic Juvenile, 15 mm. Stage 5: Late Pelagic Juvenile, 35 mm. Stage 6: Recently-settled Juvenile, 65 mm.

from Greenland to North Carolina (Brown, 1987). The Georges Bank cod stock is the most southerly cod stock in the world (Wise, 1958). Historically high concentrations of both species have occurred on Georges Bank. Commercial fisheries have existed since the 1700's. Both cod and haddock populations on Georges Bank are depleted to the point that their future as a viable fishery is in doubt (NOAA/NMFS, 1991). The abundance of other demersal species, particularly the elasmobranchs (e.g., small sharks and skates) which are only now undergoing limited harvesting and which are important predators on the gadoid juveniles, have increased dramatically in the last decade.

Peak spawning for cod normally occurs between February and March, but the peak can vary from year to year (Smith, 1983). In warm to moderate winters, peak spawning can occur as early as December but, during unusually harsh winters, it can be delayed until the end of March (Smith et al., 1981). Optimum spawning and hatching temperatures are between 5-7°C (Heyerdahl and Livingstone, 1982). Haddock spawning occurs during late March or early April (Overholtz, 1987) although the onset and duration of spawning appears to be associated with increasing water temperature (Marak and Livingstone, 1970). On average, peak spawning probably occurs around the first week in April. Although spawning is widespread in shoaler waters, the northeastern part of Georges Bank is an important spawning area for both species (Figure 8). Eggs generally drift south and west in the clockwise gyre (Lough, 1984) and the larvae hatch in 2-3 weeks at typical early spring temperatures (Laurence and Rogers, 1976). Developmental rate is similar for both species as they grow through larval and juvenile stages (Fahay, 1983). The transition from pelagic to predominantly demersal life normally occurs by mid-summer, 3-4 months from hatching, when they attain a size of 4-6 cm (Lough et al., 1989). Juveniles typically are associated with pebble-gravel substrate which probably reduces predation and provides an abundance of epibenthic prey (Lough et al., 1989). Growth is rapid for the 0-group fish and sexual maturity commences at age 2 at approximately 40 cm (Overholtz, 1987; O'Brien, 1990). Year-class strength appears to be set by the end of their first year of life; however, the timing and causes of first-year mortality for a given year class are difficult to determine and consequently our understanding is limited (Fogarty et al., 1987).

The early life history of cod and haddock has been divided into six stages (Figures 7b, 8, 9) based on our knowledge of their timing and location on Georges Bank, vertical distribution, growth, principal prey, and selected environmental factors. The six stages are: (1) Egg, 1.5 mm diameter, (2) Early Larva, 2-8 mm, (3) Late Larva, 9-13 mm, (4) Early Pelagic Juvenile, 14-29 mm, (5) Late Pelagic Juvenile, 30-49 mm, and (6) Recently Settled Juvenile, 50-69 mm. Peak spawning for cod occurs about a month earlier than haddock, but overlaps with that of haddock. Haddock spawning is more discrete in time and space and their larvae develop when stratification begins and the bank gyre intensifies. The mortality rate of cod eggs has been reported to average 22%/day (Daan, 1981). Upon reaching Stage 6, cohort abundance has decreased about 4-5 orders of magnitude at an average mortality rate of 6-8%/day (Lough, 1984). Growth for both species has been described by Gompertz-type curves based on daily growth increments of otoliths (Bolz and Lough, 1988). Growth rate increases from 0.13 mm/day at hatching to about 1.0 mm/day at age 100 days. In well-mixed waters during early spring, eggs and larvae (stages 1-3) are broadly distributed throughout the water column with their vertical distribution centered at mid-depth (20-30 m ; Lough and Potter, in press). Late pelagic juveniles (stage 5) are located progressively deeper in the water column; near 40 mm, most juveniles are associated with the bottom. Larvae tend to be found deeper by day and shallower by night; the larger fish have a greater vertical range. Recently-settled juveniles (stage 6) remain on the bottom by day and migrate 3-5 m into the water column at night (Lough et al., 1989). While the diel vertical migration of cod appears to be strongly related to the light-dark cycle, haddock behavior can be more complex.

Egg, larval, and juvenile patches have been identified on Georges Bank. They have been tracked and studied as they were advected along the southern flank in a sheared flow field (Lough and Bolz, 1989). Some variable part of the population is recirculated around the western end of

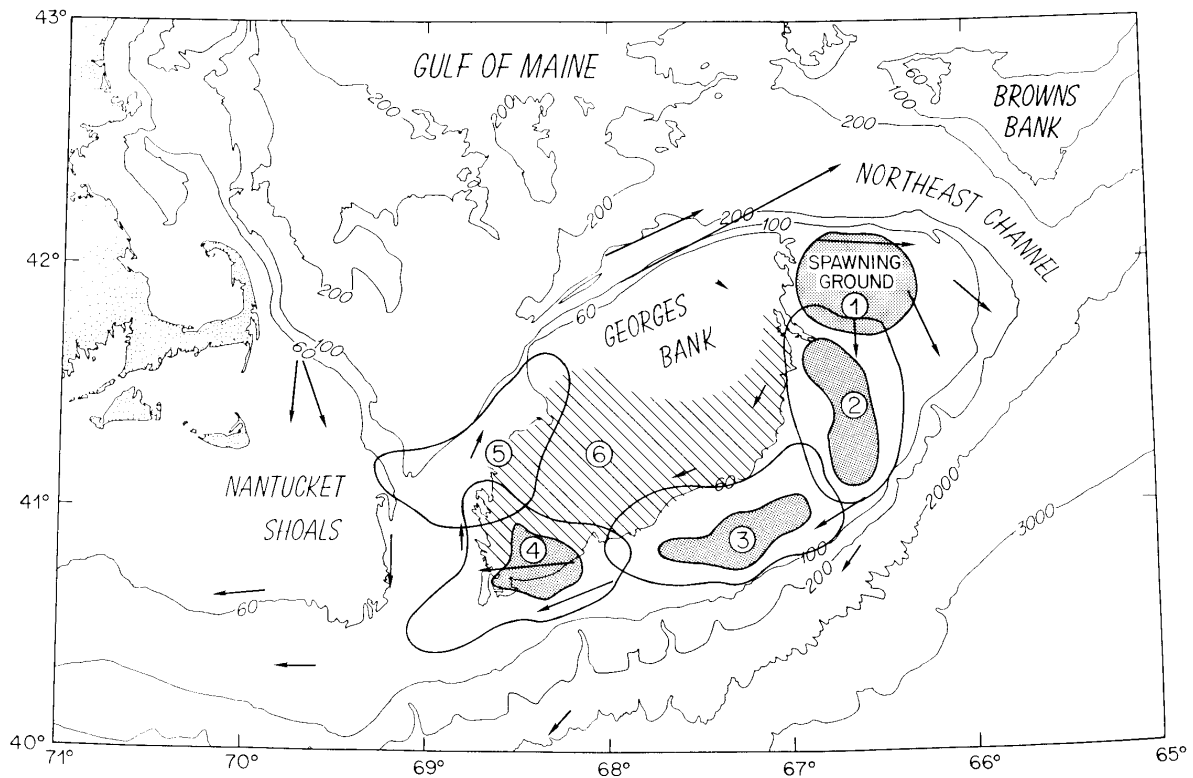


Figure 8. Generalized distribution of cod/haddock eggs (1), larvae (2, 3), and pelagic juveniles (4, 5) during their first 3-4 months of life in the clockwise circulation over Georges Bank. Cross-hatching indicates where highest abundance of recently-settled juveniles (6) may be found in mid-summer. The arrows represent the direction and relative speed of mean subsurface flow.

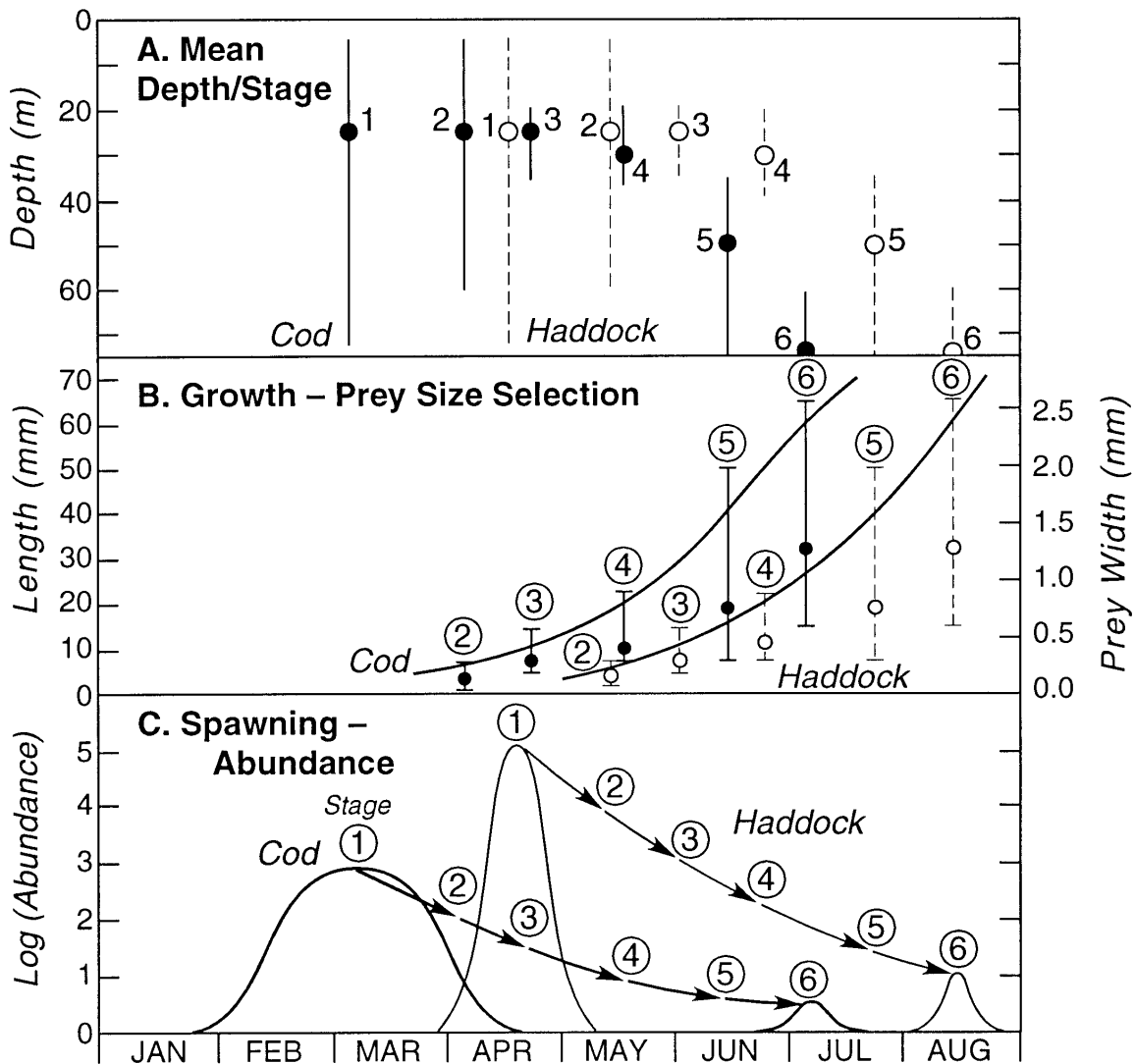


Figure 9. A. Generalized mean depth and range of the six life stages of cod and haddock on Georges Bank from eggs through recently-settled juveniles. B. Growth curves of standard length for cod and haddock on Georges Bank from hatched larvae through recently-settled juveniles. Their mean prey width and range is superimposed on the growth curves for each of the larval and juvenile life stages. C. Generalized cod and haddock spawning on Georges Bank and their development through six early life history stages: (1) Egg, (2) Early Larva, 2-8 mm, (3) Late Larva, 9-13 mm, (4) Early Pelagic Juvenile, 14-29 mm, (5) Late Pelagic Juvenile, 30-49 mm, and (6) Recently-settled Juvenile, 50-69 mm. Arrows trace the population decline through stage development.

the Bank through the Great South Channel, but in unusual years, a large portion of the larvae may be transported westward into the Mid-Atlantic Bight (Polacheck et al., 1992). Nevertheless, Lough and Bolz (1989) found evidence for continuous recruitment of cod and haddock to the shoal central part of the Bank. Retention appears to be enhanced by residing near bottom in areas less than 70 m deep and interacting with cross-isobath currents. The shelf/Slope Water front intersects the bottom at about 80 m and Gulf Stream warm-core eddies moving near the southern edge can play an important role in the movement of water on and off the shelf, and the entrainment and transport of organisms (Lough, 1982; Joyce and Wiebe, 1983; Wroblewski and Cheney, 1984; Joyce et al., 1992). The southeast flank of Georges Bank is particularly vulnerable to advective exchange/loss during periods of strong southward wind stress (Walford, 1938; Cohen, et al., 1986). The generalized gyral pattern for the six life stages best fits haddock. The distribution pattern of cod is more widespread since their spawning is more protracted and earlier in the winter, when there is more wind mixing and advection, and the mean circulation gyre is weaker. Some surveys appear to show a resident larval cod population on eastern Georges Bank.

Water column stratification over the southern flank of Georges Bank has been shown by Buckley and Lough (1987) to have a significant influence on the feeding, growth, and survival of cod and haddock larvae. In May 1983, larvae and their prey were found concentrated in the thermocline region. A comparison of well-mixed versus stratified sites showed that recent growth based on RNA/DNA ratio analysis was higher at the stratified site. At the well-mixed site where prey biomass was lower, 50% of the haddock were in a starved condition. Cod collected at the same site were in better condition and growing faster than haddock. Cod larvae appear to be better adapted as a winter species when prey densities generally are lower; haddock larvae, better adapted to spring conditions, require higher prey densities which are concentrated by spring stratification (Lough, 1984). However, on eastern Georges Bank, Perry and Neilson (1988) found that in late June 1985, prey zooplankton biomass was lower at a stratified site compared to a well-mixed site. This may have been due to differential rates of local growth caused by different food environments in well-mixed vs. stratified conditions.

The prey of larval cod and haddock consist of the developing zooplankton on Georges Bank. Yolk sac and first-feeding larvae (Stage 2) prey primarily on small plankton such as copepod nauplii, phytoplankton, and lamellibranch larvae (Kane, 1984; Buckley and Lough, 1987; Auditore et al., 1992). Both species of fish eat diatoms and Peridinium although these items represent a larger percentage of the diet of haddock than cod. With the exception of the yolk-sac stage, both cod and haddock feed on the same species of prey throughout their early life and select prey that are numerically dominant. Prey size plays an important role as larger size prey generally are selected as the fish grow larger. During the spring on Georges Bank, larvae (stages 2 and 3) prey on the increasing populations of copepod nauplii, copepodites, and adults of Calanus finmarchicus, Pseudocalanus spp., Oithona similis, and Centropages typicus. As pelagic and recently-settled juveniles (stages 4-6), they shift prey selection to epibenthic, swarming populations that also undergo diel vertical migrations such as mysids (Neomysis americana), amphipods (Gammarus annulatus, Themisto gaudichaudii, T. compressa), chaetognaths (Sagitta elegans), and euphausiids (Meganycitophanes norvegica) (Auditore et al., 1988; Perry and Neilson, 1988; Lough et al., 1989).

Predation on pre-recruit stages can substantially reduce both absolute recruitment levels and the resilience of the population to exploitation (Fogarty et al., 1987). Its importance as a dominant source of pre-recruit mortality in many fish populations is now widely appreciated (Hunter, 1981; Sissenwine, 1984; Houde, 1987, 1989; Bailey and Houde, 1989). Further, predation can play a critical role in compensatory processes through several possible pathways including: (1) density-dependent growth coupled with size dependent predation (Beverton and Holt, 1957; Shepherd and Cushing, 1980; Werner and Gilliam, 1984; Miller et al., 1988; Anderson, 1988; Beyer, 1990); (2) density-dependent predation (i.e., predator switching and selective predation on abundant prey); and (3) directly through cannibalism. The Georges Bank fish community has undergone profound

changes during the last three decades (Fogarty et al., in press). As the traditionally harvested species of principal groundfish and flounders declined sharply under intense exploitation, the abundance of other demersal species (small sharks and skates) have increased dramatically in the last decade. Spiney dogfish now may have replaced silver hake as the primary fish predator (Sissenwine and Cohen, 1991). Dogfish, silver hake, and squid also are known to prey on juvenile fish (Edwards and Bowman, 1979). Pelagic fish species, notably mackerel and herring, have increased in abundance so that Georges Bank is currently considered a predator-controlled system (Michaels, 1991; Fogarty et al., in press).

Recent studies have shown that a significant biomass of mackerel (and possibly herring) migrate along the southern flank of Georges Bank during late-April through early-May (the same time and place as identified in this document for intense study of advection and stratification). Significant mortality of larval cod and haddock may result from predation by mackerel at this time (Michaels, 1991). It is hypothesized that in years with warmer temperature anomalies on southern Georges Bank during spring, the mackerel migration could proceed across the southern portion of the Bank (rather than around the Bank as in cool years), resulting in a greater probability of encounter with the drift of cod and haddock larvae from the northeastern region of the Bank. Therefore, climatic warming could possibly result in the poor recruitment of Georges Bank cod and haddock due to shifts in the distribution and migrations of planktivorous fish.

There are not sufficient data to adequately identify and quantify egg and larval mortality due to predation, let alone partition mortality rates among the various predator groups on Georges Bank. Numerous studies document the consumption of fish eggs and larvae by a wide variety of invertebrates and fish. Hunter (1984) summarized mortality rates of pelagic eggs and concluded that 98% of cod eggs in the North Sea probably are consumed by predators before hatching. Möller (1984) provides evidence that the jellyfish *Aurelia aurita* caused a significant decline in the larval herring population of the Kiel Fjord. Fish eggs and larvae can comprise a large part of the natural diet of other passive predators such as medusae and ctenophores (especially *Pleurobrachia*) (Fraser, 1962; Purcell, 1985). More active invertebrate predators such as chaetognaths, large copepods, amphipods, isopods, and euphausiids may contribute to egg and larval losses. Older cod larvae and pelagic juveniles are likely predators of larval cod (Laurence et al., 1981). Hunter (1984) concluded that herring and other planktivorous fishes were major consumers of fish eggs and larvae.

4.4.2. Overview of Georges Bank Plankton.

The plankton ecology of Georges Bank has been reviewed extensively in Backus (1987) and can be summarized as follows. A spring diatom bloom occurs in March in the well-mixed region (<60 m) and April in deeper areas (60-100 m); diatoms remain dominant in the well-mixed region all year while dinoflagellates dominate the stratified deeper area during summer and fall, with maximum abundance near the seasonal pycnocline (Figure 10; O'Reilly et al., 1987; O'Reilly and Busch, 1984). High biomass and productivity in the well-mixed area are maintained through tide-induced vertical mixing together with physical input of new nitrate (Walsh et al., 1987). About half the nitrogen demand of the primary production is supplied as nitrate input along the edges of the Bank, but the physical exchange mechanisms are poorly understood. Recycling accounts for about 1/3 of the phytoplankton demand during winter and spring and about 2/3 during summer and fall (Walsh et al., 1987; Loder et al., 1982). Recent studies by Canadian researchers on the northeast flank suggest that tidal mixing processes may be the dominant physical factor controlling cross-frontal exchange in the well-mixed area (Harrison et al., 1990).

On an annual basis, there is a low ratio of secondary to primary production compared to the North Sea, but a high ratio of fish production to secondary production (Cohen and Grosslein, 1987). It has been suggested that differences in apparent transfer efficiencies between trophic levels in the different ecosystems may be due to advective loss of zooplankton (Cohen and

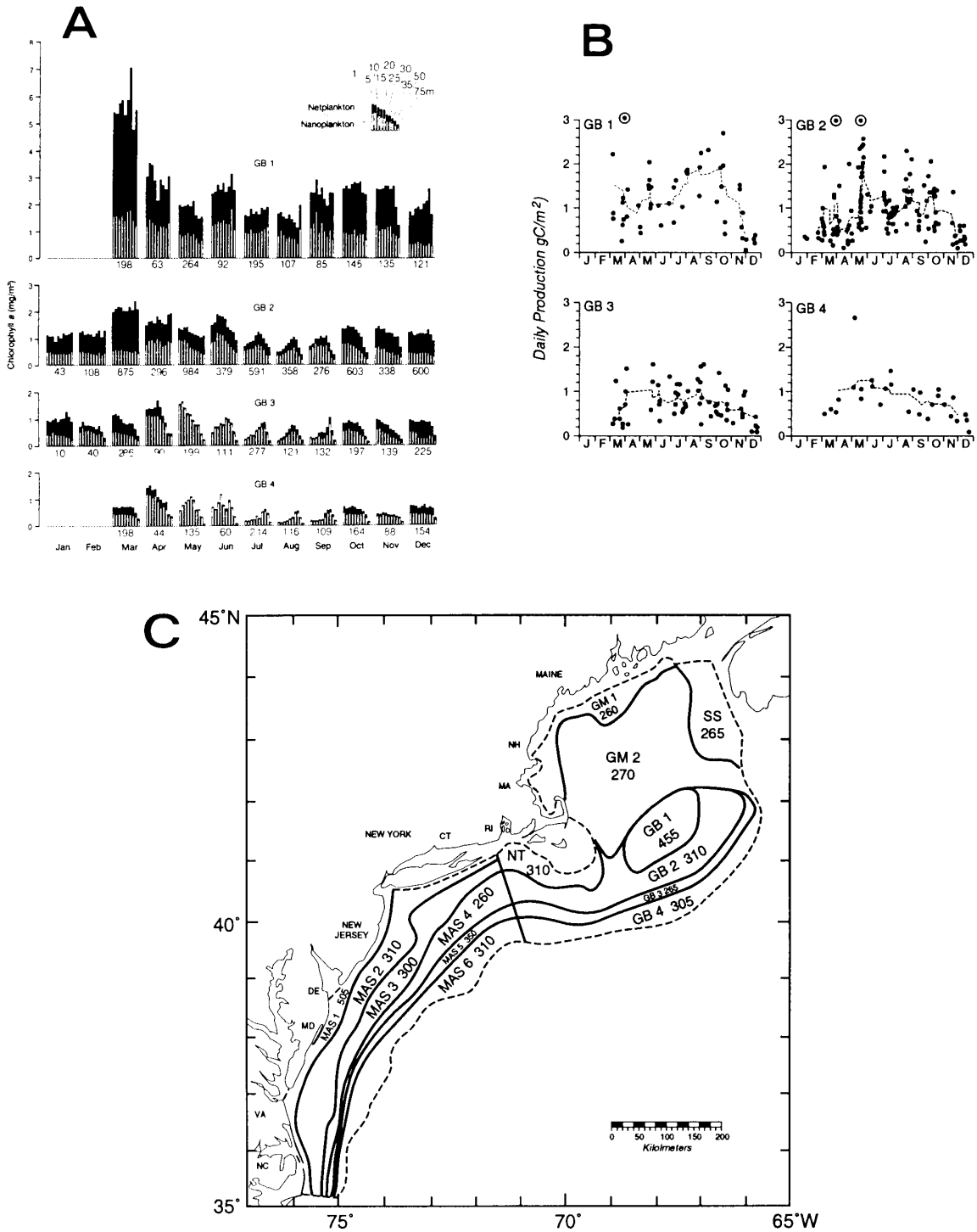


Figure 10. Seasonal chlorophyll abundance and seasonal primary productivity in well-mixed and stratified areas on Georges Bank (from O'Reilly et al., 1987). Numbers at base of histograms in (A) are samples in each month. Circled points in (B) are offscale; dashed line is running average (N = 7). Numbers in (C) are primary production in gC/m²/yr.

Grosslein, 1987). Estimates for seasonally averaged turnover rates of the Bank water mass support this view (Mountain and Schlitz, 1987), but the time dependence on sub-seasonal scales is not known. In particular, the impact of storms and Gulf Stream rings on Georges Bank trophodynamics has not been examined (Mountain and Schlitz, 1987; Klein, 1987). Klein (1987) used a simple nutrient-phytoplankton-zooplankton model coupled to a kinematic model of circulation in the well-mixed region of the Bank. His model showed large loss rates of plankton from the region which were comparable to those found by Walsh et al., (1987). Klein also noted that his physical loss rates were long term averages of short term events including storms and rings. Klein further discussed the need for more realistic zooplankton models which include population dynamics and spatial distributions outside the well-mixed area. Lacking any direct measurements of secondary production disallows anything more than speculation about the relative importance of in situ growth vs. advective exchanges (gains and losses) as factors controlling copepod population size.

The annual cycle, spatial distribution and production of zooplankton on Georges Bank are analyzed in Davis (1984a,b,c; 1987a,b). The zooplankton is dominated in numbers and biomass by the copepods Calanus finmarchicus, Pseudocalanus newmanii, Pseudocalanus moultoni, Centropages typicus, Centropages hamatus, Paracalanus parvus, and Oithona similis. Calanus and Pseudocalanus are winter-spring species, while Centropages and Paracalanus are dominant during fall. O. similis is abundant throughout the year. Very little is known about their growth rates, but since they are small in size their growth rates are probably high. Because of this, their contribution to total production may be higher than one might guess from knowledge of their biomass alone. Zooplankton production is highest during late summer and early fall due to rapid growth of warm-water species that are small in size. Most of the production is thought to go into predation by the chaetognath Sagitta elegans, the ctenophore Pleurobrachia pileus, and the omnivorous copepods Centropages spp.

Each of the dominant species has its own characteristic life cycle (Davis, 1987a) and therefore may be impacted differently by advective gain of individuals from surrounding regions to the Bank and loss from the Bank (Figure 11). Questions about the isolation of Bank populations from contiguous areas (e.g., Gulf of Maine, Slope Water) and the importance of local recruitment vs. immigration of new recruits from any "source" regions are unresolved. Stephenson and Kornfield (1990) concluded that recruitment of herring on the Bank resulted from reproduction of the indigenous population following a ten-year period of very low population density, because the pre- and post-crash populations were genetically indistinguishable. Population genetic and life history analysis of the target species will be required to address questions of the degree of reproductive isolation and the source(s) of immigrants to Bank populations .

Calanus finmarchicus is a large boreal copepod which reaches maximum abundance in June, accounting for the major portion of the spring zooplankton biomass peak. It enters diapause as fifth-stage copepodid in mid-summer and spends the warm stratified months at depths of 50-300 m in the Gulf of Maine (Bigelow, 1926; Clarke, 1933, 1934; Mullin, 1963) and 200-500 m in Slope Water (Miller et al., 1991). C. finmarchicus spawns on Georges Bank in February and produces two generations during its spring appearance there. During its growing season Calanus abundance is higher in the deeper regions of the Bank (60-100 m) than in the well-mixed area, Gulf of Maine, or Slope Water. Calanus undergoes diel and seasonal vertical migration which depend on life stage. The life cycle of Pseudocalanus moultoni is similar to Calanus in that it begins its population growth during the winter when it is carried onto the northwestern edge of Georges Bank by prevailing currents. Pseudocalanus (including P. newmanii, Frost, 1989) reaches maximum abundance in spring (May-June). Pseudocalanus spp. abundance decreases markedly after June as it gives way to Centropages hamatus, C. typicus, and Paracalanus parvus. The latter two species, during peak abundance, inhabit the warm surface layer on Georges Bank and the Gulf of Maine, undergoing little or no diel migration. Their distributions are less restricted to the Bank as is the case for their spring counterparts. P. parvus is not likely to be food limited on

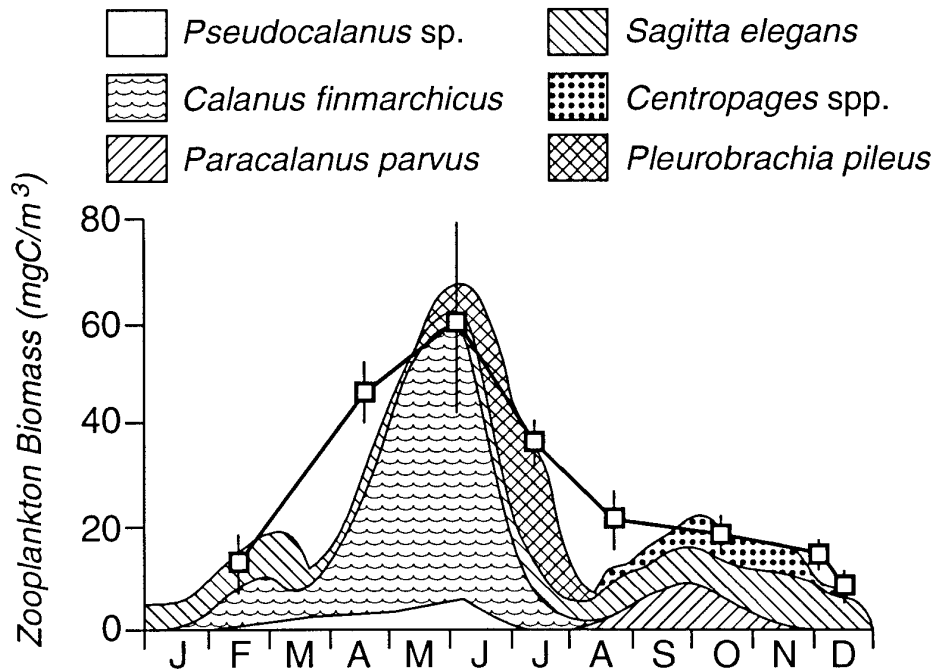
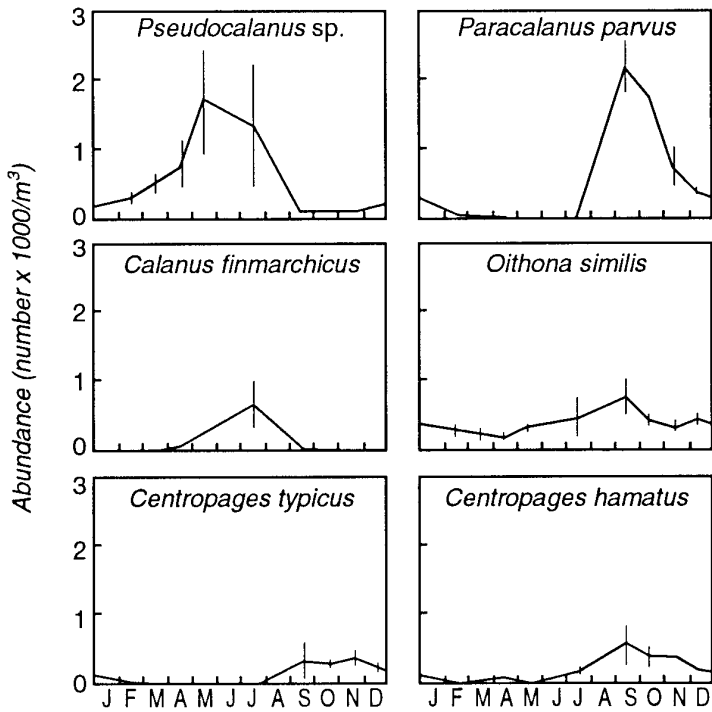


Figure 11. Zooplankton seasonal cycles on Georges Bank; squares with error bars are carbon biomass estimated from MARMAP displacement volumes (from Davis, 1987b).

Georges Bank whereas C. typicus growth and reproduction are inhibited at mean Bank food levels (Davis and Alatalo, in press). C. hamatus lays bottom resting eggs which overwinter in the sediments and hatch out from August-September, giving rise to a large fall population. This species, like other species which produce resting eggs, has a well defined distribution restricted to the well-mixed region.

Other larger crustacean zooplankton, including the mysid, Neomysis americana, the amphipods, Monoculodes edwardsi, Gammarus annulatus, and Themisto gaudichaudi, and the euphausiid, Meganyctiphanes norvegica, can serve as prey of late stage cod and haddock larvae (Lough et al., 1989), as well as predators on early stages. The role of these larger zooplankton as predators on the copepod populations may be important based on their abundance and large size. These species are all benthoplanktonic and are known to undergo pronounced diel vertical migration (Whitely, 1948). M. norvegica and the two amphipod species are more abundant in the deeper regions (60-100 m; Davis, 1987b). Very little is known about the life cycles of these species on Georges Bank (see review in Davis, 1987b).

Gelatinous species of zooplankton including medusae and ctenophores can be important predators on copepods and fish larvae, and larvaceans (Fritillaria borealis and Oikopleura dioica) may be important grazers of phytoplankton on the bank. Gelatinous predators thought to be important on Georges Bank include the scyphomedusa Cyanea capillata (250-1200 mm), the large hydromedusa Staurophora mertensii (100-200 mm), the trachymedusa Aglantha digitale (20-40 mm), and the ctenophore Pleuorbrachia pileus (20-40 mm) (Davis, 1987b). Commensal associations of pelagic juvenile haddock with the hydromedusae Cyanea capellata have been reported (Lough and Potter, in press). Data on the abundance of these species in time and space on Georges Bank is limited due to a general lack of quantitative sampling methods for these delicate forms.

Species of zooplankton targeted for study include those which are dominant on Georges Bank and also have an important impact on the life cycle of larval cod and haddock. These species include the copepods Calanus finmarchicus and Pseudocalanus spp. As mentioned above, other copepods, larger crustaceans, chaetognaths, mysids, and gelatinous predators should be studied at the same time.

4.4.3. Larval Fish/Plankton Interactions on Georges Bank.

Cod and haddock spawn during the early spring and growth of their larvae appears linked closely to the seasonal development of their prey populations (Sherman et al., 1984; Figures 9b, 11). Energetic demands of a fish larva increase as the larva grows so that the highest rations are required at the end of the larval stage. Both cod and haddock spawn prior to the peak in zooplankton biomass on Georges Bank (Figures 9b, 11), suggesting that food limitation during the larval stage may be important in regulating their population cycles. The timing of spawning such that the late larval stages coincide with the peak in zooplankton biomass has been suggested recently as a mechanism that enhances recruitment success; this is an extension of Cushing's (1972, 1975) match-mismatch hypothesis (Bollens et al., in press). The decline of the zooplankton mass in July-August coincides with the settling of larval cod and haddock and development of their benthic feeding habits.

In addition to the coincidence of larval fish food demand and the peak in total zooplankton mass, the size distribution of prey found in the stomachs of larval cod and haddock matches closely the size distribution of the developing zooplankton assemblage. In late winter/early spring (March-April) when the fish larvae are of small body size (2-8 mm - Stage 2), the zooplankton is dominated numerically by the small copepod Pseudocalanus spp. (1 mm prosome length), whereas later in spring (May-June) when the larvae have higher energetic demands and are capable of ingesting larger prey, most of the biomass consists of the larger Calanus finmarchicus (2.5 mm

prosome length) (Davis, 1987b). By early summer (July), the larger crustaceans, including mysids, amphipods, and euphausiids, reach peak abundance coinciding with the mean prey size ingested by the late larvae and pelagic juveniles. By mid-summer (August), the zooplankton biomass has declined due to increases in predatory gelatinous species in the water column, and the juveniles seek refuge on the bottom.

4.5 Physical/Biological Interactions on Georges Bank.

Physical processes exert important influences on the biological processes which control the distribution and abundance of populations on the Bank (see Tables 1, 2). Understanding the connections between these physical and biological processes is the primary focus of the Northwest Atlantic/Georges Bank Study. For each of the six life stages of cod and haddock, physical and biological factors may have different effects on a cohort's survival, depending upon its location, degree of aggregation, behavior, and coincidence with planktonic prey and predators (Tables 1,2). The principal spawning time and location of cod and haddock have evolved so that developing larvae coincide with developing plankton populations in the spring. These populations are advected along the southern flank of the Bank and arrive at the western end just as recirculation intensifies, further serving to retain these cohorts on the Bank. Examples of the important physical processes are:

Advection - The mean inflow of water onto the Bank from the Gulf of Maine brings nutrients, which support the high primary production on the Bank (Schlitz and Cohen, 1984), and younger stages of zooplankton, which seed the spring increase in some of the zooplankton species on the Bank (Davis, 1984a). For Calanus finmarchicus, a key aspect of their seasonal biology is lateral transport on and off the Bank. The main stocks must come onto the Bank from the Gulf of Maine, Scotian Shelf, and/or from Slope Water to the south, in late-winter/spring. The stock which builds up on the Bank during spring and early summer must either die off, or lateral flow carries them over deep water where they once again enter diapause. The ultimate population size achieved by Calanus in late-spring may depend initially upon the size of the colonizing propagule of females.

The tendency for the around-bank circulation to become closed with increasing stratification provides a mechanism for retaining planktonic organisms on the Bank and is believed to be important for survival of larval fish populations on the Bank (Iles and Sinclair, 1982; Bolz and Lough, 1984). In contrast, storm events and warm-core ring entrainments which remove water from the Bank represent potentially important mechanisms for episodic exchanges of organisms from the Bank.

Turbulent Mixing - Tidally-induced turbulent mixing over the shallow areas of the Bank provides for rapid availability of regenerated nutrients within the photic zone and promotes the high rate of primary production observed in the Bank's central area (O'Reilly and Busch, 1984). Surface wind stress and waves also can produce significant turbulent mixing over the Bank, and the combined effects of surface and horizontal buoyancy fluxes and tide- and wind-induced mixing determine the location of the tidal mixing front found around the top of the Bank (Loder and Greenberg, 1986). Secondary circulation associated with the tidal-mixing front may cause surface convergence, which may act as a concentrating mechanism of organisms (Loder et al., 1992). Turbulent mixing, due to either surface or internal tides or winds, also can affect the contact rate between planktonic organisms (Rothschild and Osborn, 1988). Variability in turbulent intensity may have an important influence on the feeding success of zooplankton and larval fish populations (e.g., Sunby and Fossum, 1989; Davis et al., 1991).

Stratification - Springtime development of density stratification on the southern flank of the Bank is associated with increased concentrations of chlorophyll and zooplankton in the pycnocline. This concentrating of food organisms is believed to be an important factor in the growth and survival of larval fish on Georges Bank (Buckley and Lough, 1987). Disruption of the density structure and

Table 1. Assessment of physical and biological factors that can potentially impact early life stage abundance of cod and haddock on Georges Bank.

Stage-	PHYSICAL FACTORS							BIOLOGICAL FACTORS											
	Temperature	Adective Loss	Frontal Processes	Tidal Mixing	Stratification	Surf. Boundary Layer	Botl. Boundary Layer	Calanus	Pseudocalanus	Oithona	Centropages	Demersal Epifauna	Planktonic	Cannibalism	Large Pelagics	Large Demersals	Disease	Endoparasites	Parasites
1. Egg	H	H	H	H	H	H	L	-	-	-	-	-	H	L	L	L	H	?	L
2. Early Larva	H	H	I	H	H,I	H	L	H	H	I	L	L	H	L	L	L	H	L	H
3. Late Larva	I	L	H	I	H,I	I	L	H	L	H	L	L	L	L	I	L	L	L	H
4. Early Pelagic Juvenile	L	I	H	I	I	L	I	H	L	H	I	I	L	I	H	L	L	I	H
5. Late Pelagic Juvenile	L	I	I,H	I	I	L	H	I	I	L	I	H	L	H	H	H	L	I	I
6. Recently settled Juvenile	I	L	L	H	L	L	H	L	L	L	L	H	L	H	I	H	I	H	L

H=High Potential Impact
I=Intermediate Potential Impact
L=Low Potential Impact

Table 2. Assessment of physical and biological factors that can potentially impact the abundance of the copepods, Calanus and Pseudocalanus, on Georges Bank. The first letter in a cell corresponds to Calanus; the second to Pseudocalanus.

Stage	PHYSICAL FACTORS							BIOLOGICAL FACTORS																
	Temperature	Advective Loss	Frontal Processes	Tidal Mixing	Stratification	Surf. Boundary Layer	Bot. Boundary Layer	Prey					Predator				Parasites							
								Diatoms	Dinoflagellates	Protozoans	Other copepods	Detritus	Chaetognaths	Larger Crustaceans	Fish	Gelatinous forms	Disease	Endoparasites	Ectoparasites					
1. Eggs	H ⁴ H	H ⁴ H	I ¹	I ¹	I ¹ L	??	L ¹ L	-	-	-	-	L ¹ L	L ¹ L	L ¹ L	??	??	??	??	??	??	??	??	??	
2. Early nauplii	H ⁴ H	H ⁴ H	I ¹	I ¹	H, H	??	L ¹ L	H ⁴ H	H ⁴ H	??	L ¹ L	??	H ⁴ H	H ⁴ H	??	??	??	??	??	??	??	??	??	??
3. Late nauplii	H ⁴ H	H ⁴ H	I ¹	I ¹	H, H	??	L ¹ L	H ⁴ H	H ⁴ H	??	L ¹ L	??	H ⁴ H	H ⁴ H	??	??	??	??	??	??	??	??	??	??
4. Early copepodids	H ⁴ H	H ⁴ H	I ¹	L ¹ L	H ⁴ H	??	L ¹ L	H ⁴ H	H ⁴ H	??	L ¹ L	??	H ⁴ H	H ⁴ H	??	??	??	??	??	??	??	??	??	??
5. Late copepodids	H ⁴ H	H ⁴ H	I, I	L ¹ L	H ⁴ H	??	L ¹ L	H ⁴ H	H ⁴ H	??	L ¹ L	??	H ⁴ H	H ⁴ H	??	??	??	??	??	??	??	??	??	??
6. Adults	H ⁴ H	H ⁴ H	I ¹	L ¹ L	H ⁴ H	??	L ¹ L	H ⁴ H	H ⁴ H	??	L ¹ L	??	H ⁴ H	L ¹ L	??	??	??	??	??	??	??	??	??	??

the associated concentration of larval prey organisms by storm events could have significant negative impacts on year-class recruitment.

Frontal Exchange - Exchange across the fronts along the edges of the Bank can transfer properties and organisms across the Bank. Along the northern flank, a tidally induced internal hydraulic jump and internal waves are believed to enhance mixing and cross-frontal exchange during stratified conditions (Loder et al., 1992). The frontal zone has a zooplankton composition that is transitional between the well-mixed area and the stratified waters in the Gulf of Maine. The trajectory of the current jet across the northeast region of the Bank acts to retain both zooplankton and phytoplankton on the Bank and contribute to their accumulation in the well-mixed area (Perry et al., in press). Along the southern flank, shear instabilities in the shelf/Slope Water front can result in the removal of water and organisms from the Bank (Ramp et al., 1983).

Bottom-boundary Layer Processes - The bottom-boundary layer plays an essential role in the generation of tidally induced turbulence and mixing, and thus in determining the structure of the temperature and density fields. The large near-bottom shear in the oscillating current field allows for the differential movement of a vertically migrating organism relative to the average horizontal motion of the water column. The interaction of current shear and vertical migration is believed an important mechanism for organisms to maintain their location or enhance their residence time on the Bank (e.g., Lough and Trites, 1989). An on-bank (shoalward) component to the flow near bottom in late spring and summer may contribute to the retention of older cod and haddock larvae on the Bank (Lough and Bolz, 1989).

Control of Phytoplankton Abundance and Species Composition by Mixing Processes. In shallow water columns, both wind and tidal mixing are significant processes in resupplying nutrients to the photic zone after the spring bloom and during summer months, thus enhancing primary production during months when high productivity would not normally be expected (Pingree et al., 1976). Spatial variations in tidal mixing can lead to ecological zonation along a gradient determined by levels of turbulence and water depth; a well-mixed shallow water column is often separated from deeper stratified water by a marginally stratified transition (or frontal) zone. Phytoplankton (and copepods) tend to be uniformly distributed with depth within well-mixed water columns, but concentrated at or above the pycnocline in stratified columns (Holligan and Harbour, 1977; Holligan et al., 1984a). Primary production tends to be highest in the frontal zones (Holligan et al., 1984b).

The phytoplankton community is often characterized by a dominance of diatoms in the well-mixed and frontal zones, and flagellates in the stratified waters (Holligan and Harbour 1977). As noted earlier in this document, this is known to be true for Georges Bank (O'Reilly et al., 1987; O'Reilly and Busch 1984). Highest phytoplankton biomass is often associated with a mixed water column (see Figure 10). Such variations in food web structure could influence the egg production, growth and recruitment rates of herbivorous zooplankton. This was one of the key hypotheses of "Foodweb I", the final CEPEX experiment (Grice et al., 1980). A recent attempt to study the effects of a well-mixed vs. stratified water column on copepod dynamics was carried out at the Marine Ecosystems Research Laboratory at the University of Rhode Island. Sullivan (in press) compared zooplankton abundance and community structure in well-mixed and stratified tanks. She found that copepods were much more abundant in the stratified tanks, and that dominance in the two tanks shifted from Eurytemora and Acartia tonsa in the well-mixed tanks to Oithona colcarva in the stratified tanks. It is intriguing that these changes in abundance and species composition were remarkably similar to those described by Holligan et al., (1984a) for well-mixed and stratified waters of the English Channel. How (or if) a larger species like Calanus finmarchicus would respond to a spatial gradient in water column mixing is not known. For any species, it is not known whether a response is due to solely to physical disturbance resulting from to increased turbulence or to biological differences resulting from the increased mixing (i.e., differences in phytoplankton biomass and species composition).

4.6 Main Hypotheses of Georges Bank Study.

Since the goal of the Georges Bank Study is to understand how physical processes affect population dynamics, the general hypotheses of the study reflect this focus. Based on the background material given above, the major physical processes affecting abundance of the target species lead to the following hypotheses:

LOCAL GROWTH vs. RETENTION/EXCHANGE

- 1) Due to the circulation gyre, the residence time of water over the Bank is long relative to biological time scales so that in situ growth rather than lateral exchange is the dominant process controlling population abundance on the Bank.
- 2) Fine-scale horizontal exchange causes significant leakage of nutrients, plankton, and fish larvae across the frontal boundaries of the Bank, thus causing a chronic input and exchange/loss of nutrients, plankton and fish larvae.
- 3) Secondary circulation associated with the tidal mixing front causes a surface convergence near the well-mixed area boundary, providing a mechanism for concentrating target species in the tidal front zone. Transport towards the center of the Bank should be greatest for plankton in the upper layer of the water column in this zone, or for those species which undertake vertical migrations.
- 4) Periodic vertical migration of zooplankton and juvenile fish into and out of the sheared bottom-boundary layer can lead to horizontal movement against the mean horizontal flow.

STRATIFICATION

- 5) Seasonal density stratification over the southern flank of the Bank causes prey aggregation in the pycnocline and increased survival of predator populations.
- 6) Differences in phytoplankton abundance and species composition mediated by differences in water column stability result in measureable differences in copepod recruitment and growth rates. This leads to greater abundances in one region over another, due solely to high growth rates in situ.
- 7) Turbulent mixing, generated by wind and tidal forcing, has a significant impact on rates of ingestion, respiration, and predation; the processes of turbulent mixing and seasonal density stratification influence predator-prey encounter rates and thus growth and survival of individual organisms.

EPISODIC GAINS and EXCHANGES/LOSSES

- 8) The residual mean flow is important in horizontal transport of zooplankton and fish larvae onto and off of Georges Bank, thus causing major sources and sinks for Bank populations.
- 9) The seeding of copepod populations from the Gulf of Maine during winter has a significant impact on the level of prey biomass for larval fish during late spring and early summer. A corollary is that the population genetic makeup of the prey on Georges Bank reflects the genetic makeup of the source populations.

- 10) Storms, especially during winter and early spring, as well as impingement of warm-core rings, can cause large exchanges/losses of zooplankton and fish larvae from Georges Bank, thus increasing the apparent mortality rate of Bank populations.
- 11) Population size is continuously regulated by incremental rather than episodic events, i.e., the time scale of the variability of the driving forces is of the same order as the generation time of the population.

MORTALITY

- 12) Predation rather than starvation is the dominant source of mortality of fish larvae; predation rather than advective exchange is the dominant source of mortality of copepods.

These hypotheses provide the foundation from which the implementation plan for the Georges Bank Study was developed, and upon which it will continue to be developed. In the next section, program components, and specific objectives and strategies for accomplishing them are presented.

5. PROGRAM IMPLEMENTATION.

This implementation plan was developed to address the problems and questions concerning the dynamics of planktonic populations on Georges Bank and adjacent waters, as governed by the hypotheses presented above. It is recognized that there are finite resources available to support this scientific endeavor and the plan reflects the need to marshal the resources wisely. The program is envisioned to begin with start-up funding in 1993. Major field programs will be conducted in 1994, 1996, and 1998, with a different set of processes being focussed upon in each of these years. This section begins with the program goals and then provides a general discussion of the scientific and logistic elements associated with major components which are viewed as essential to the success of the program. A schedule which reflects the temporal relationships of the components and the major events concludes this section.

5.1 Major Components of the Georges Bank Study.

The Georges Bank Study has four major components:

- 1) Broad-scale field study of the distribution and abundance of the target organisms and their physical environment;
- 2) Distinct, but well integrated field studies of smaller-scale processes known or thought to be important in regulating the occurrence and abundance of target species;
- 3) Modeling studies designed to assist in the formulation and interpretation of the field studies, as well as to provide the context for integration of the results;
- 4) A methodology and instrumentation development program required to enable fundamental portions of the Georges Bank Study to be achieved and to add to our ability to conduct such studies elsewhere in the ocean.

The blending of these components into an integrated program will require cooperative research efforts involving biological and physical oceanographers, and strong multidisciplinary leadership, both within the scientific community and between scientists carrying out the work and scientists at the Joint NOAA/NSF U.S. GLOBEC office.

The plan to implement the Georges Bank Study is focussed on five specific program objectives.

5.1.1 Program Objectives

- 1) Quantify abundance of target species in time and space on Georges Bank over the winter/spring period using spatially and temporally nested sampling to cover a broad range of time and space scales. [Components 1, 2, and 4].
- 2) Measure vital rates of target species relating to population dynamics (i.e., Figure. 3; feeding, swimming, respiration, egestion, growth, fecundity, predation, starvation). [Components 2 and 4].
- 3) Quantify the seasonal stratification of the water column, and those physical processes which strongly influence its variability, in relation to (a) the vertical distribution and (b) vital rates of the target species, and in relation to control of nutrient and phytoplankton dynamics and the translation of these effects on zooplankton population dynamics [Components 1, 2, and 3].

- 4) Quantify rates of physical exchanges of water and biota across the boundary of the Bank due to cross-frontal flows, residual mean flow, and episodic wind and ring events. Determine how these exchange processes are affected by vertical migration behavior, vertical current shear, and the bottom boundary as a refuge. [Components 1, 2, 3, and 4].
- 5) Determine how microscale turbulence interacts with micro-patchiness to affect predator-prey interactions and vital rates. [Components 2, 3, and 4].

5.2 Experimental Program

The experimental program will have three components; broad-scale studies, smaller-scale process studies and modeling. Each component will address specific hypotheses, but should be designed so that the information from each component will assist the interpretation of data from the other components.

The broad-scale studies will involve both bank-wide surveys and moored instrumentation. The broad-scale surveys will identify changes in the abundance of populations between survey periods and document the spatial extent of biological and physical conditions monitored on a finer temporal scale by moored instruments. The surveys also will provide the link between satellite imagery and the sub-surface oceanography. Mechanistic explanations for the biological and physical changes occurring on a bank-wide basis must come from interpretation of complementing biological and physical process studies. These interpretations will be supported by the development and use of models. The broad-scale information will guide the placement and allocation of effort in the smaller-scale process studies and will be needed a posteriori to interpret the relative influence of the various processes on the population as a whole.

5.2.1 Broad-scale Studies

The objective of this component of the program is to provide a basic description of the primary physical and biological properties of the Bank and the surrounding waters, as well as their spatial and temporal variability. This will be accomplished through a combination of ship surveys, moored instrumentation, and satellite observations. Of particular importance is documenting the life histories of the target species (cod, haddock, Calanus, and Pseudocalanus) in relation to the physical oceanographic conditions on the bank (Figure 3).

Two approaches exist to study the life history and population dynamics of the target species. First is life table or cohort analysis in which the abundance of successive stages in the life history of the population is determined. Mortality rates can be calculated directly (calculated as recruitment rates and/or development times are known). These rates can be compared to likely mortality mechanisms (e.g., predation, starvation, advective loss/ exchange). This approach requires frequent, intensive sampling, along with measurements of development time. The second approach, which requires less intensive sampling, is survivorship analysis in which the characteristics of individuals are measured in several life stages to determine the characteristics which favored survival (e.g., birthdate, growth rate, genetic parentage). Both cohort and survivorship analysis can be used in this study because of: 1) the relatively discrete nature of the cod/haddock spawning on Georges Bank (in both space and time); 2) the relatively higher abundance of Calanus and Pseudocalanus on Georges Bank than in surrounding waters; 3) the general retention of plankton within the confines of the Bank; 4) the relatively small size of the Bank; and 5) the high probability of a cohort age structure for Calanus finmarchicus driven by a large, discrete egg production "event" associated with the spring bloom.

5.2.1.1 Shipboard Surveys (1994 - 1998)

Shipboard surveys of the bank must be conducted to collect samples for cohort and survivorship analysis of the target fish and zooplankton populations. These surveys should also include the collection of data on hydrography, primary production, size-fractionated chlorophyll, and possibly phytoplankton species composition in order to provide a description of the biological and physical environment in which the target species reside.

Questions: The broad-scale shipboard sampling should address the following questions:

- 1) What are the broad-scale distributions of the target species and their predators and prey in relation to physical variables, and how do these change from winter to summer conditions?
- 2) How are the broad-scale distributions of measurements/indices for growth, fertility, respiration, and starvation in the target species related to the distributions of food supply and environmental conditions?
- 3) How are predator populations spatially and temporally distributed with respect to their prey (target species) and environmental conditions?
- 4) How does the birthdate and/or life stage frequency distribution of surviving individuals change during the drift around the Bank?
- 5) Is cohort mortality chronic or dominated by episodic events?
- 6) Is the probability of survivorship associated with individuals originating from discrete stocks?

Strategy: To determine adequately the mortality curve between successive early life stages of cod and haddock, bank-wide sampling will be required at intervals of no more than 30 days for the period December to August. Monthly sampling is needed to encompass the life stage durations and to provide quantitative estimates of their population abundance and areal distribution (See Figures 8, 9). Although the monthly interval of these surveys is insufficient to resolve the population dynamics of target copepods because the generation time is less than 60 days, the data will provide broad-scale distributional information. When combined with data from the moored instrumentation and process studies, it is hoped that this will provide the information necessary to study the changes in population structure through time. Other ideas that will result in a time series that is better suited for study of copepod dynamics are encouraged.

The "episodic vs. chronic" question identifies the need to distinguish between the two contrasting time scales of recruitment dynamics. One hypothesis is that in the early lives of the larval fish in a retention environment like Georges Bank, chronic mortality rates that persist on the order of 100 days may be the important rates determining recruitment variability. A 2-3% per day change in mortality or growth rate may have a much bigger effect on recruitment level than an event such as a warm-core ring that sweeps > 50% of the larvae off the Bank in a single brief episode. Modeling studies could be most constructive here.

For the broad-scale surveys, the areal coverage should encompass the entire bank, and include a portion of the southwestern Gulf of Maine and Slope Water. One approach is to set up a sampling grid with a spacing of about 20 km, including approximately 100 stations, which can be completed within a 7-10 day period. Stations both on and off the Bank will be needed to compare physical and biological processes in contrasting domains. In addition, to determine the egg and

larval abundance with sufficient precision for cohort analysis, areas of high concentration characteristically observed on the southeastern or southern flank of the bank should be re-sampled with a station spacing of 5-10 km. This will require an additional 40-50 stations which can be completed within a 3-5 day period.

Statistical methods should be applied prior to any field sampling to suggest the intensity of sampling required to give the statistical power to actually reject specific null hypotheses. One problem is that the pelagic phase of a larval/juvenile fish lasts several months whereas a copepod completes one life cycle in 30-50 days. It is hoped that a sampling design can be developed that will produce information on the different requisite time scales. A mixture of point time series and occasional spatial surveys may be an alternative.

Individuals of each target species differ in size and swimming (i.e., sampler avoidance) ability, and in abundance. Large volumes of water (100's of cubic meters) need to be filtered to collect the relatively rare fish larvae; small volumes (a few cubic meters) are needed for zooplankton. Thus an array of sampling gear is required. Larger-scale sampling for ichthyoplankton and zooplankton should be conducted with a combination of 1-m multiple net systems using 150 μm mesh and bongo nets using coarse and fine mesh. A portion of the sampling should be conducted with vertically discrete opening/closing nets and acoustical profilers to provide additional information on the vertical distribution of the organisms, particularly in areas of high larval concentration. New optical and acoustical sensors may also be deployed on the multiple net systems or in an underway mode to provide high resolution distributional information on plankton and fish biomass, size, and taxonomic composition. When sampling for animals to be used in experiments, gentle techniques must be employed -- nets must sample only while the ship drifts on station and large cod ends must be employed. In April through August, both 1-m and 10-m multiple net sampling are required to sample the pelagic juvenile stages of cod and haddock. All net systems should be equipped with CTD's and fluorometers to measure simultaneously the basic hydrographic and chlorophyll distributions on the Bank. Sampling of recently-settled juvenile fish and their epibenthic prey (if carried out) will require combined pelagic and bottom gear. ROV transects may provide the best single technique for obtaining representative data on the true abundance, distribution, and activity patterns of fish and their prey (Auster et al., 1991). Fine mesh nets (64 μm) and large Niskin bottles should be used to collect copepod nauplii, protozoans, and phytoplankton.

5.2.1.2 Physical/Biological Moorings (1994-1998)

The moored array component should provide a continuous time history of the variability of the physical and biological properties occurring at select locations on and about Georges Bank. These moored observations should complement the shipboard surveys described above and the satellite surveys described below, providing the continuous time record to put these spatial surveys into temporal context. The spatial surveys should describe the horizontal structure on a scale smaller than that resolved by the moorings and thus complement the time-series observations. The sum of these various observations is required to describe adequately the important physical and biological processes occurring in the region.

The broad-scale mooring program will provide the basic description of temporal variability and provide the context for the more specific small-scale process studies discussed below. Selected mooring sites should be maintained continuously for the full 5 years of the field program. These observations will monitor the seasonal changes as well as inter-annual variability. Additional moorings should be deployed for the December through August period of concentrated study and will act as focal points for some small-scale process studies.

Questions: The broad-scale moored component should address the following questions:

- 1) What is the atmospheric forcing in the Georges Bank region (momentum, heat, buoyancy fluxes as well as available light), and how does it vary spatially over short time-scale events, seasonally, and inter-annually?
- 2) What is the temporal variability of basic physical (e.g., temperature, salinity, velocity), chemical (e.g., inorganic nutrients, oxygen), and biological (e.g., phytoplankton and zooplankton biomass) properties as a function of depth at selected sites?
- 3) What tidal and internal tidal energy is present in the sea surface elevation (bottom pressure) and current, and how does the internal wave component change with season and stratification at selected sites?
- 4) What is the subtidal current at selected sites around the Bank?
- 5) What is the temporal and spatial variability of the surface wave field over the Bank?
- 6) What is the temporal variability in the abundance of target species and associated biological indicators (e.g., dissolved oxygen, nutrient concentrations, upwelling radiance and downwelling irradiance, Photosynthetically Available Radiation, stimulated fluorescence, in situ measurement of primary production, optical transparency (beam attenuation), acoustical backscatter for biomass and video imagery for size distribution and taxonomic identification) as a function of depth at selected sites?
- 7) How does the occurrence and timing of episodic events such as storms or warm-core rings affect the physical and biological properties at selected sites on the Bank and their exchange with adjacent areas?

Strategy: These temporal observations should provide descriptions of the upstream source of water and biological populations, surface and lateral forcing on Georges Bank and time history of episodic events. Sampling is required on time scales of hourly to multi-year, and on space scales of a few meters to ten's of meters in the vertical, and ten's of kilometers in the horizontal. Mooring sites should include the edge of Wilkinson Basin as a source region for water and organisms, possibly two locations along the southern flank of Georges Bank, and possibly on the crest of the Bank (Figure 12). Information on the temporal and spatial variability in the surface wave field will be useful in calculations of bottom stress, since surface waves can make a significant contribution to bottom stress. These observations will need to be combined with the broad-scale survey, satellite imagery and drifter results as well as with feedback from the modeling effort to gain the maximum description of the broad-scale physical and biological processes.

The moored program will benefit from advances that are being made in acoustics, which not only can be used to determine the vertical structure of the water velocity field, but also can be used to study the time variations of the vertical distributions of scatterers. With shipboard survey calibration, estimates of the time variability of biomass can be made. The moorings will need the latest in meteorological technology, measuring wind speed and direction, atmospheric pressure, precipitation, atmospheric temperature, relative humidity, long and short wave radiation, and sea surface temperature. Results from a U.S. GLOBEC meteorology buoy on the Bank should be combined with coastal meteorology and data from the NOAA NDBC environmental buoys on Cashes Ledge, Georges Bank, and Nantucket Shoals to provide a comprehensive description of surface forcing over the Bank (Figure 12).

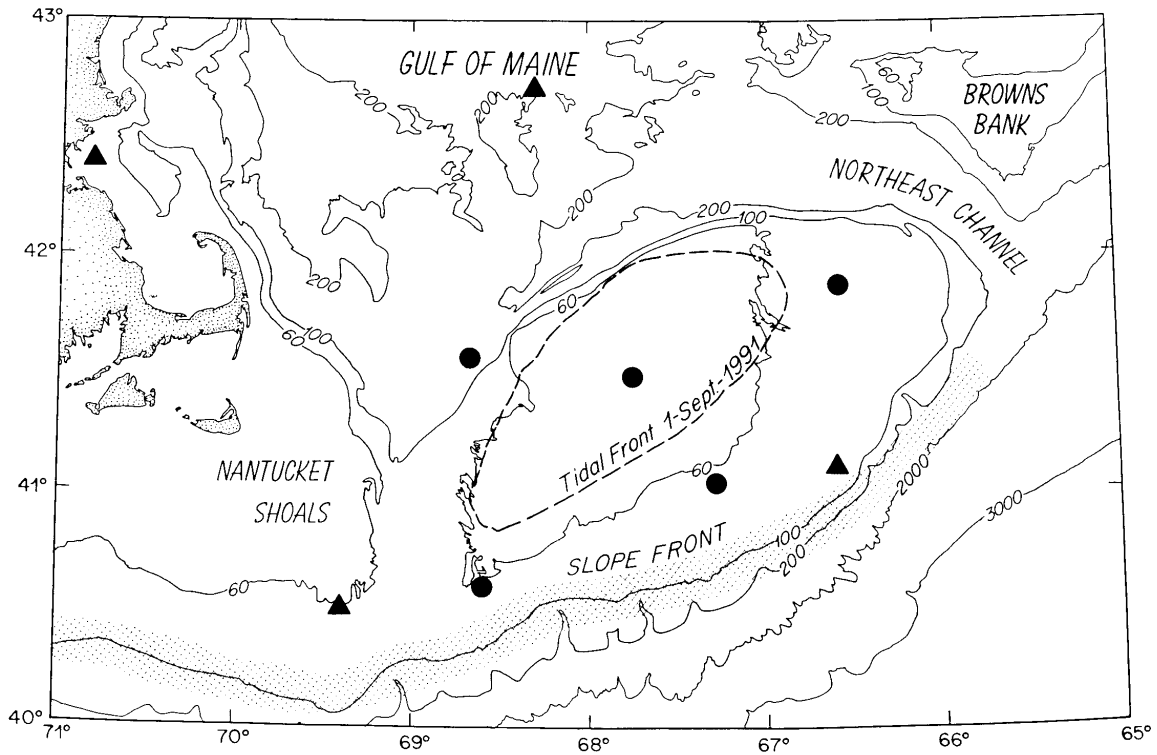


Figure 12. Broad-scale moorings on Georges Bank in relationship to the tidal mixing and shelf/slope fronts. National Data Buoy Center environmental buoys are indicated by ▲, and possible U.S. GLOBEC long-term physical/biological mooring positions by ●.

Bio-optics is the study of optical processes of the upper ocean that affect and are affected by biological processes. The time history of bio-optical and biological activity measurements listed below coupled with physical oceanographic observations are vital in studies linking primary production to upper ocean dynamics. These include the measurement of temperature, salinity, water velocity, dissolved oxygen, upwelling radiance and downwelling irradiance, PAR (photosynthetically available radiation), stimulated fluorescence, optical transparency (beam attenuation), acoustical backscatter sampling for biomass, and video imagery for species identification. New instrumental approaches to the high resolution time-series measurement of inorganic nutrients and phytoplankton production will reduce the temporal disparity that commonly exists between physical and bio-optical observations, and allow measurements of biological activities that are influenced by the physical environment.

The moored program should take advantage of real-time data telemetry to routinely transfer the data collected on the remote platform to the laboratory. These data should be processed to the first order and made available to the rest of the scientists in the program to: (1) aid in the development and verification of models; (2) ascertain that the equipment is functioning properly; (3) allow scientific analysis to start; (4) identify important and unusual conditions or events which will allow for a modification of the shipboard surveys; and (5) provide the broad-scale context for the smaller-scale process-oriented studies. Temperature from the moorings will also be used to correct AVHRR data (see below); these data may then be used in near real-time to adjust or correct sampling strategies during cruises.

5.2.1.3 Satellite Surveys (1994-1998)

Satellite data (e.g., infrared, color, altimetry, scatterometer, SAR) should be available throughout the duration of the study. These data can contribute to the analysis and understanding of many of the broad-scale and smaller-scale process oriented investigations in the overall program. They can directly assist the sampling during cruises by real time identification of major oceanographic features (e.g., fronts, rings) and changes in their location.

Questions: The satellite data collection and analysis component should address the following questions:

- 1) What is the temporal and spatial variability of the surface temperature and chlorophyll distributions in comparison with pigment related bio-optical measurements and direct primary production time-series measurements made throughout the water column during the study period?
- 2) What is the temporal and spatial variability of the tidal mixing front and the shelf/Slope Water front?
- 3) What is the temporal and spatial variability of the surface wave field over the Bank?
- 4) When, where and under what oceanographic/atmospheric conditions do episodic exchanges of water occur from the Bank across the shelf/Slope Water front, and are they associated with greater mortality of the target species?
- 5) When and how often do rings interact with the Bank?

Strategy: Satellite data should be acquired, analyzed, and transmitted to research vessels and program investigators (including modellers) participating in the program in near real-time. Communication of imagery from shore to the ships is an important part of this strategy. Post-cruise analyses of the imagery should include quantitative comparisons with the shipboard, moored, and Lagrangian observations, determination of the major frontal features and their

behavior in time and space, resolution of the well-mixed and the stratified regions of the Bank in time and space, and time-series analysis of the surface plant pigment and phytoplankton activity fields. Satellite-based measurements will provide a detailed spatial resolution of the surface field to complement time-series measurements obtained at moorings. Satellite wave data should be ground truthed with observations from moorings. Some satellite data are dependent on the absence of cloud cover. A clear image of the Bank region generally can be obtained on a time scale of every 2-5 days during spring and summer. This frequency is sufficient for valuable guidance during sampling operations and for meaningful post-cruise analyses.

5.2.2 Fine-scale process studies

The objective of the process studies is to focus on specific physical and biological processes which are believed to control the growth and survival of the target species on Georges Bank. The study of these processes generally requires observations to be made on a relatively fine scale, in both space and time, and to be made on or in association with the same set or population of organisms. This is accomplished by following a parcel of water and sampling animals from it through time while the observations for the process studies are made. These process studies are nested within the bank-wide information on the distribution of organisms and water properties provided by the broad-scale surveys described above.

5.2.2.1 Vertical mixing and stratification (1994)

The water column conditions on Georges Bank are determined, in large measure, by the balance between vertical mixing and surface heating (see Figure 6). The balance between these competing processes shifts both seasonally and with location on the Bank. Turbulence generated by surface wind stress and by stress in the bottom-boundary layer associated with strong semidiurnal tidal currents tend to mix the water column. During spring and summer, the net surface heat flux is positive and increasing. This tends to stabilize the water column, countering the tendency for vertical mixing, and leads to thermal and density stratification over the deeper areas around the perimeter of the Bank, especially over the broad southern flank of the Bank. The transition zone between the well-mixed water over the crest of the Bank and the stratified water over the flank is called the tidal mixing front. The location of this frontal region shifts as the balance between mixing and surface heating changes seasonally.

Observations have shown that when the water column is well mixed, planktonic organisms (phytoplankton, zooplankton and fish eggs and larvae) tend to be distributed throughout the column, and when the column is stratified, the plankton tend to be concentrated within or above the pycnocline. This concentration of food particles is believed advantageous to the growth of larval fish (e.g., Buckley and Lough, 1987). Conversely, increased turbulent mixing also may be advantageous to plankton feeding (e.g., Rothschild and Osborn, 1988). The conditions under which turbulent mixing or its suppression by density stratification are beneficial or detrimental to the feeding success of the target organisms is not known.

As discussed earlier, well-mixed and stratified water columns are characterized by different concentrations of phytoplankton and different assemblages as well. These differences in food web structure may lead to different growth and recruitment rates of copepods, resulting in different zooplankton assemblages in well-mixed and stratified water columns. Of particular interest is the strong link-weak link hypothesis of Runge (1988): large copepod taxa like Calanus finmarchicus are tightly coupled to the timing of phytoplankton blooms because their growth rates are highly dependent upon food concentration, whereas smaller taxa such as Pseudocalanus or Paracalanus are not coupled to variations in food concentration because their growth rates are seldom food-limited. This hypothesis was derived because maximum egg production rates of large copepods like Calanus will only occur at chlorophyll concentrations in excess of 5-10 $\mu\text{g chl-a}$ per liter; such concentrations occur only during blooms and/or in the well-mixed regions of Georges Bank.

Growth rates of small taxa such as Pseudocalanus spp. and Paracalanus parvus are probably seldom or ever limited by food supply. Their maximum egg production rates occur at 1-2 $\mu\text{g chl-a}$ per liter, a concentration which is observed in all regions of the Bank during the spring, summer and fall.

The bottom-boundary layer plays a critical role in generating turbulent mixing and in providing an environment with strong vertical shear in the currents. The near-bottom current shear may be important to vertically migrating organisms in determining their location (i.e., their retention on the Bank), and subsequently their feeding, growth and survival.

Questions: Vertical mixing and stratification studies should address the following questions:

- 1) What processes control the seasonal development of stratification on Georges Bank, especially over the southern flank of the Bank. How does stratification vary in response to diurnal surface heating, changes in current during a single tidal cycle, fortnightly modulation in tidal amplitude and synoptic scale wind events? Is temporal and spatial variability in stratification over the southern flank of the Bank similar in the along-isobath direction?
- 2) What are the dynamics controlling the structure of the tidal mixing front? What is the spatial extent of the frontal region? How does its extent and location vary in time from winter through summer? Are there secondary circulations associated with the front that affect the location or retention of target organisms within the frontal region?
- 3) What is the structure of the bottom-boundary layer on Georges Bank? How does the boundary layer change with bottom depth and with the seasonal development of stratified conditions in the water column above? How do the mean Eulerian and Lagrangian currents differ in the bottom-boundary layer? Do surface or internal gravity waves play an important role in the dynamics of the bottom-boundary layer?
- 4) How is the vertical distribution and abundance of cod and haddock larvae and their zooplankton prey influenced by the water column structure? How do these organisms respond to the disruption and subsequent re-establishment of stratified conditions by storm events? What is the time scale of this response?
- 5) How sensitive is larval growth to water column stratification? Do wind-induced disruptions in the development of stratification significantly affect the growth and survival of larval fish?
- 6) How does the sensitivity of larval growth to stratification change as stratification develops and as the larvae grow in size during the spring?
- 7) Two mechanisms can lead to successful encounters of larval fish. Copepod prey can become concentrated in fronts or pycnoclines, or, prey can become locally abundant because of enhanced egg production by adult females in food-rich regions, leading to enhancement of naupliar recruitment. Are there situations on Georges Bank where these two mechanisms operate together, or are copepods abundant in fronts or pycnoclines due to physical mechanisms, and in well-mixed water columns because of high local growth rates?
- 8) What is the spatial and temporal distribution of turbulent kinetic energy on Georges Bank? Is turbulence suppressed in the pycnocline over the southern flank? Does

turbulent mixing affect the feeding of target organisms by increasing their contact rate with prey items?

Strategy: The processes of mixing and stratification on Georges Bank are best studied by a combination of moored and shipboard measurements of the major forcing functions and the resulting water column response, and through numerical circulation modeling. For the surface boundary layer, the primary atmospheric forcings are the surface heat and momentum fluxes. Estimation of these fluxes using bulk formulae requires measurements of the long and short wave radiation components at the sea surface, the temperature and humidity of the air above the sea surface, precipitation, and near-surface winds. Estimation of stress in the bottom-boundary layer requires current measurements which are closely spaced in the vertical, pressure measurements to determine the surface wave field and a record of the character of the sediment surface. Within the water column, temperature, salinity, and current need to be measured. Shipboard CTD/ADCP measurements will provide profile information on water structure and current with a vertical resolution of at least 1-2 m. Moored time-series measurements of water structure and current need sufficient vertical resolution to resolve the surface and bottom-boundary layers and seasonal pycnocline. The tidal mixing front or transition from stratified to well-mixed conditions occurs over a relatively short cross-isobath distance on the southern flank of the Bank. This situation provides an opportunity to make simultaneous moored measurements and shipboard transects in well-mixed, marginally stratified, and strongly stratified water columns that are exposed to essentially the same atmospheric forcing conditions. This should allow greater insight into the processes controlling mixing and stratification.

Cod and haddock larvae and their zooplankton prey also reside on the southern flank of the bank during the period when stratification is developing. Fine-scale observations of the distribution of the larvae and their zooplankton prey should be made at successive life stages: as the larvae grow in size, as their prey organisms change and as stratification develops in the water column. This study will require measurement of the micro-scale distributions of the larvae and their prey. These observations can be made by a combination of towed net systems and towed, profiling and moored acoustical and optical sampling systems. It is critical that the plankton sampling and growth rate measurements be made concurrent with the physical measurements described above. Acoustical and optical instruments should be placed on the moorings as an aid to obtaining time-series observations of the vertical distribution and abundance of chlorophyll and the zooplankton community. These continuous measurements will provide information on the physical and biological conditions between the periods of the smaller-scale ship observations. By the combination of shipboard and moored sampling, changes in plankton biomass resulting from the changing physical conditions can be determined on a range of time scales from minutes to months.

The feeding success and growth of the larvae can be determined by gut content analyses and a variety of chemical and physiological measures. RNA/DNA ratios and lipid content analysis are indicators of recent growth. The growth rates can be compared to observations of prey availability and water column conditions (temperature and density structure). Otolith increments, both in size and in chemical composition, can provide time histories of growth conditions to be compared with physical oceanographic conditions and prey abundance. Relationships between otolith increments and the time histories of physiological condition, food availability and water column properties need to be investigated. If significant relationships are found, otolith analysis could provide indications of the conditions encountered by the survivors of the larval population during different times in their early life history.

Techniques available for study of copepod growth rates are very limited. Growth rates of adult females can be estimated from measurements of egg production rates in 24-h incubations. Growth rates of the larval and juvenile stages can be estimated from measurements of molting rates in 24-h incubations. Critical for the success of this type of work is the collection of animals in as

gentle a manner as possible. See Peterson, et al., (1991) for details of how growth rates may be derived from such measurements and of some of the pitfalls associated with this type of work. The development of more precise and more rapid methods for estimation of copepod growth rates is of the utmost importance and is strongly encouraged.

A study of the dynamics of the tidal mixing front on the southern flank of the Bank will require a variety of approaches, including transects of observations across the frontal region. Towed, undulating bodies instrumented with sensors for measuring temperature, salinity and turbulent dissipation rate. Ship mounted ADCP units can provide snapshots of the structure of the front and the flow field in the frontal region at different stages of the tide. In addition, Lagrangian experiments with passive drifters or tracers should be considered to look for secondary circulations associated with the front. To indicate the influence of these physical conditions on the life history of the target organisms, concurrent observations need to be made with acoustical and optical biological instrument systems, as well as multiple opening and closing net sampling along the transect lines. Because of the near-bottom diel vertical migration of cod and haddock juveniles, both pelagic and demersal sampling gear will be needed.

The distribution of turbulent kinetic energy can be estimated by profiling and towed shear probe instruments. The recent feeding success of target organisms can be determined by the gut content and biochemical analyses mentioned above. Comparison of turbulent intensity distributions, feeding rates and prey concentration under varying conditions can indicate the degree of influence turbulent mixing has on planktonic feeding.

5.2.2.2 Study of Source/Retention/Exchange of Plankton (1996)

The primary physical processes which contribute to influx, retention and exchange of water, nutrients and plankton on Georges Bank include the buoyancy- and tide-driven subtidal mean flow, recirculation around the western end of the Bank, wind-forced off- and on-bank flows, and entrainment of Bank water by warm core rings. These advective processes have different time scales varying from an event (a few days) to fortnightly to monthly and seasonal and longer, and different length scales varying from a few kilometers to the bank-wide broad-scale. In addition, higher frequency smaller-scale phenomena such as tide-induced internal waves, internal tides, turbulent mixing and the bottom-boundary layer also may contribute to a net subtidal cross-isobath transport of water and organisms. Whether any of the target species systematically use the vertical shear of the rotary tidal currents to maintain their horizontal position or move onto the Bank is a fundamental question.

The study of these processes will require integrative approaches involving both innovative field observations and modeling. What is needed is a truly Lagrangian description of water and organism trajectories over periods of time varying from one to several tidal cycles to many days, coupled with a new level of understanding of the physical and biological processes that cause the observed Lagrangian motion. New techniques need to be developed to follow both water and key species better. This includes drifters with improved positioning, telemetry, and variable drogue depth, and new optical and acoustical sensors to obtain profiles of target species concentration, biomass, and size distribution from both fixed and moving platforms.

Population phenomena on Georges Bank will be determined in part by the characteristics of populations in the source waters (e.g., Gulf of Maine). The life history characteristics, population density, physiological state, and genetic character of immigrant individuals can be important both as predictors of population dynamics on the Bank and, for the latter two parameters, as "tags" to determine the relative contribution of each source region to production processes on the Bank. Knowledge about the genetic character of planktonic populations of the Gulf of Maine and Slope Water is important for predicting the responses of the population to disturbance, exploitation, or climate change. If the population is homogeneous across the region, re-growth of populations will

be rapid and without genetic change. If the population is heterogeneous, recolonization following a reduction in the size of the population may take longer, be less certain, and may be accompanied by genetic changes in the population, because genetically-distinct populations may provide the infusion of new recruits to Bank populations.

Questions: The source, retention and exchange studies should address the following questions:

- 1) What is the subtidal circulation over the Bank and how does it evolve in time from December to August? What physical processes (e.g., tidal, buoyancy, wind) determine the density field and drive the subtidal circulation, and do their relative contributions change with time? What time and space scales characterize these processes and the resulting subtidal circulation?
- 2) What physical processes dominate the cross-isobath transport over different parts of the Bank, both in the bottom-boundary layer and the rest of the water column? What time and space scales characterize the cross-isobath transport? Does the nature of cross-isobath transport change with stratification?
- 3) What physical processes contribute to recirculation of water around the western end of the Bank? Where and on what time scales does recirculation occur? Is recirculation primarily chronic or episodic? What processes disrupt recirculation, and how is it re-established? Does recirculation exhibit a clear seasonal cycle, with little or no recirculation in the well-mixed winter and strong recirculation in the highly stratified summer? Does recirculation occur throughout the year in the well-mixed water over the top of the Bank?
- 4) What is the on- and off-bank flow driven by different wind events? Where does this occur and on what time and space scales? Is the directly wind-driven flow concentrated in the surface boundary layer, and if so, how does this interact with the Bank topography? Is there any compensatory flow at depth and, if so, where does it occur? How does the nature of the wind-driven response change with different characteristic storms, season and stratification? Does the interaction between vertical current shear and vertical migration of the target species permit them to be retained on the Bank?
- 5) How often do Gulf Stream warm-core rings entrain shelf water from the Bank? Do rings force Slope Water onto the Bank? How large are these cross-isobath transports and are there preferential sites and times for these bank-ring interactions?
- 6) How do the physical flow processes identified above influence the retention and exchange of target species on the Bank? Which physical and biological (behavioral) processes are most important for keeping different target species on the Bank during key stages in their early life histories? Which processes are most important in causing exchange of different target species from the Bank? How do these various processes change with time from December to August? Can the exchange of organisms from the Bank be measured and quantified?
- 7) What are the life history, physiological, and genetic characteristics of target species populations in the Gulf of Maine, Georges Bank, and Slope Water? How readily can populations from these different regions be discriminated?
- 8) Is the Gulf of Maine the source region for seeding populations of major planktonic species on Georges Bank and does the source level abundance play a major role in determining the peak population size on the Bank?

- 9) How do physiological and genetic characteristics of planktonic populations in these regions change over time (generationally, seasonally, inter-annually)?

Strategy: The influx, retention and exchange of water and target species from the Bank is perhaps best studied through a combination of remote sensing, in situ Lagrangian, Eulerian, and shipboard measurements, and coupled physical/biological modeling. Remote sensing of sea surface temperature and color should monitor the existence and location of Gulf Stream warm-core rings as they pass close to the Bank, and help identify episodic exchange of Bank water along the southern flank caused by both rings and storms. Remote sensing should also help identify other on- and off-bank surface flow events which may occur around the rest of the Bank perimeter. A variety of Lagrangian studies are needed to observe the movement of water and target species both within and onto and off the Bank. These studies include the deployment of standard drifters designed to follow the horizontal water motion at selected levels, drifters which use acoustical techniques to measure remotely the vertical distribution of organism volume scattering (biomass), numbers, and target strength (size), and new drifters which mimic the vertical diel motion of different target species, and shipboard surveys which follow discrete parcels of water while measuring the horizontal currents and water properties of the surrounding fluid. Moored Eulerian measurements of physical and biological variables cited above would help establish time scales and vertical structure of different processes. Finally, physical and coupled physical/biological modeling efforts are needed to develop insight about retention and exchange processes, and to guide and complement the field measurements. More specific comments on experimental strategy follow.

Lagrangian studies are needed both a) in the western Gulf of Maine to identify source water regions which carry target zooplankton species onto the Bank in winter and early spring and b) over the Bank to help quantify the circulation there during the late winter through summer period. In particular, these studies should attempt to quantify the biological structure of the water flowing onto the Bank, including the species composition and stage structure of target species, the rates of flow, and degree to which water parcels are retained over different parts of the Bank as the seasonal stratification develops.

Lagrangian studies also are needed along the southern flank of the Bank to quantify the exchange of Bank water and target species during strong wind events. The recent development of air-deployed satellite-tracked drifters allows for an efficient seeding of Bank waters during selected storms to learn more about the response of the near-surface Bank waters to strong wind events. The availability of real-time meteorological data from moored platforms on the Bank plus regional real-time satellite infrared and color data and medium range weather forecasts should improve the ability to predict which storms to select for intensive study. These Lagrangian drifter studies can also help direct shipboard measurements of key physical and biological variables on an opportunistic basis (e.g., during a storm event or as soon afterwards as feasible). If new techniques can be developed that allow a ship to make rapid transects of target species concentrations, then this information can be combined with ADCP and CTD or Batfish data to compute horizontal fluxes of shelf water and target species, and can help researchers determine the extent to which organisms are passively transported by the flow field.

The above approach also should be applied to study the influence of warm-core rings on the retention and exchange of target species on the Bank. Remote sensing should provide good guidance to possible ring entrainment events and allow selected events to be surveyed and monitored by ship and seeded with Lagrangian drifters.

Studies of the population density, age structure, and physiological and genetic characteristics of planktonic populations will require quantitative collecting that is fully integrated with the physical characterization of the region. Depths and stations where net tows are taken need

to be carefully chosen so as to provide data on the position of the organisms in the flow field. Special collections or fixation methods may have to be employed in some cases. In most cases, it is expected that the planned plankton collections can be split following collection, and either assayed immediately or preserved appropriately.

5.2.2.3 Cross-Frontal Exchange (1998)

Georges Bank circulation can be thought of as a "leaky gyre", due to cross-frontal exchange processes as well as on-off bank mean flow and episodic forcing from storms and rings as discussed in the previous section. Cross-frontal flows potentially can cause chronic "leakage" of plankton and nutrients across the boundaries of the bank along the shelf-slope front to the south and along the Gulf of Maine/Georges Bank front to the north. Cross-frontal exchange also occurs at the seasonal tidal front positioned along the 60 m isobath and separating the well-mixed central area from the surrounding stratified region. Since nutrient level and plankton taxonomic composition in well-mixed and stratified areas are different, flows across this tidal front potentially can have significant effects on the target species populations in both areas. These flows must be better understood.

Questions: Cross-frontal exchange studies should address the following questions.

- 1) What are the exchange rates of target species from Georges Bank due to cross-frontal mixing?
- 2) What is the three-dimensional circulation associated with the shelf/Slope Water front, the northern front, and the tidal front?
- 3) How does seasonal stratification affect exchange rates at the shelf/Slope Water front?
- 4) How do biological and physical processes interact to control cross-frontal exchange of target organisms?
- 5) What are the exchange rates across the tidal front and how do these affect the nutrient and species distributions in stratified and well-mixed area?

Strategy: These questions can be addressed by process-oriented studies in each frontal system (i.e., shelf/Slope Water, northern edge, well-mixed/stratified) during stratified and unstratified periods. Quantifying cross-frontal exchange rates of target species requires rapid sampling of biological and physical properties of the frontal system in 3-dimensions over time. Abundance of target species should be quantified using depth-stratified sampling with nets, acoustics, and optical devices. Vertical migration behavior in relation to vertical shear and bottom-boundary layer flows should be determined by high frequency stratified sampling. Physical variables (salinity, temperature, advection) should be measured using "towyo" deployment of a CTD or SEASOAR and shipboard ADCP. Biological/physical moorings should be used to examine scales of variability in the frontal system. Instrumentation to be moored includes CTD, fluorometer, acoustics, and plankton pumps and video imaging systems for collection of taxonomic data.

5.2.2.4 Population/Cohort Studies of Target Species (1994-1998)

Changes in population structure of the target species should be determined in conjunction with the broad-scale surveys, stratification studies, source/retention/exchange studies, and frontal studies outlined in previous sections. Such work should proceed during all years of the study.

These studies will provide baseline information on population structure and rates of development, growth, fecundity, and mortality as populations enter the bank and are transported around the gyre.

Questions: The population/cohort studies should address the following questions.

- 1) How do populations of target copepod species respond in terms of vital rates and changes in population structure as they are transported from source waters into the relatively eutrophic environment of the bank?
- 2) What are the life history parameters (birth, development, growth, and death) of the target species populations during their drift around the bank?

Strategy: Locations and times of particular interest for the population/cohort studies include:

- 1) The inlet region of the bank north of the Great South Channel in January and February to examine changes in life history parameters of seed populations of Calanus and Pseudocalanus as they are carried onto the bank.
- 2) The northeastern Bank in March to examine life history parameters of eggs and newly hatched cod and haddock larvae which are spawned in this region, as well as the copepod populations.
- 3) The southeastern and southern flanks of the banks in April, May, and June to determine the life histories of cod and haddock mid-late larvae and pelagic juveniles as well as those of the Calanus and Pseudocalanus.

Life history data can be obtained from analysis of net samples for taxonomic, life stage, and age composition together with shipboard measurements of growth and egg production rates, physiological state and starvation. These measurements should be made in relation to key physical variables which include temperature, stratification, advection, mixing/turbulence, and time of day. Sampling should be done with high enough spatial and temporal resolution to allow life history parameters to be determined from the field data on population structure using recently developed techniques in demographic analysis (Caswell and Twombly, 1989). This will require very frequent sampling. Bearing in mind that cruises at monthly intervals will produce samples that may not be sufficient for such analysis, innovative approaches may be required to complete this task.

5.2.3 Modeling and Historical data analysis

5.2.3.1 Theory and Modeling

The development of appropriate theory and mathematical models for physical/biological interactions is an essential component of U.S. GLOBEC. This activity can provide a clear picture of the status and limitations of existing theoretical knowledge, identify areas needing additional research, provide guidance for field studies and help interpret field measurements, and hopefully lead to model verification and improved predictive capabilities. This latter step is critical since U.S. GLOBEC aims to make reliable predictions of population changes associated with future climate change. As noted earlier, much guidance will be needed in planning field studies. In particular, a sampling design needs to be developed which will give the statistical power to actually reject specific null hypotheses. Spatial sampling as well as sampling which produces a few point time series would be appropriate given the different time scales at which individuals of the target species develop.

In February 1990, U.S. GLOBEC began a program of theory and modeling research. The GLOBEC Working Group on Theory and Modeling issued a report (GLOBEC, 1991a) identifying three broad categories where theoretical work was critically needed: a) conceptual studies of simplification and predictability; b) prototype investigations of biological processes in idealized flow fields; and c) site-specific models. Based on this report, NSF issued a call for proposals; after review, a total of seven awards were made for six research projects. Four of these relate to the Georges Bank Study and will be briefly described next (see Taylor (1991) for complete descriptions of all seven modeling projects):

a) Conceptual studies:

Direct numerical simulation of homogeneous turbulence for planktonic organisms: H. Yamazaki
Project focuses on how turbulence can influence the contact rate between predator and prey. Uses direct numerical simulation to create a turbulent flow field and then conducts Lagrangian experiments with a stochastic model of plankton behavior.

b) Prototype studies:

Recruitment dynamics in event-driven bank circulations: C. Davis, G. Gawarkiewicz, D. Chapman, D. Olson, and G. Flierl
Project focuses on the effects of storms and rings on advective exchange rates of planktonic organisms from a bank like Georges Bank. Uses a numerical circulation model to study the Lagrangian response of simple flows over an isolated bank to wind and ring forcing.

Development of quantitative, hydrodynamic and biological models of settlement of planktonic larvae of benthic animals: J. Eckman, T. Gross, and F. Werner
Project focuses on the influence of velocity shear and turbulent mixing in the bottom-boundary layer on the settlement of benthic planktonic larvae. Initial effort is to use idealized one- and two-dimensional models of the turbulent bottom-boundary layer to identify and quantify key physical processes controlling larval flux at the boundary.

c) Site-specific studies:

Significance of circulation to egg and larval distributions on Georges Bank: D. Lynch, F. Werner, J. Loder, M. Sinclair, D. Greenberg, and I. Perry.
Project focuses on testing whether observed distributions of eggs and larvae can be simulated using a simple larval drift model driven by a numerical circulation model with realistic regional topography, internal density field and surface forcing.

Additional theory and modeling research in all three categories is clearly needed for the Georges Bank Study. While new conceptual studies regarding the simplification of and predictability in coupled physical/biological models will help the entire U.S. GLOBEC effort, additional site-specific modeling studies are required to understand how the different physical/biological processes described above influence the population dynamics of the target species on Georges Bank. These studies should include prototype investigations of biological processes in the following idealized flows: one-dimensional well-mixed and stratified tidal flow with a turbulent bottom-boundary layer, simplified bank gyre with and without recirculation, and simple tidal mixing and shelf/Slope Water fronts. Further development of realistic local and regional three-dimensional numerical circulation models is also needed. These models should incorporate turbulent boundary layer physics and be used to study the following problems: the formation of tidal mixing and other fronts around the Bank, the seasonal evolution of the general circulation over the Bank, the different roles of surface and lateral buoyancy forcing and tidal

mixing to establish the Bank stratification, the influence of tidal and wind forcing on mixing over the Bank, and the response of Bank waters to storms and rings. Research also is needed to incorporate basic biological processes into these new site-specific circulation models, so that state-of-the-art coupled physical/biological models for Georges Bank can become available during the course of the Georges Bank Study. Because of the complex nature of physical/biological interactions on the Bank and the need to optimize the design of field work, it is important to emphasize this theoretical work early in the Georges Bank Study. The above list of theoretical problems and issues is not meant to be inclusive, but suggestive of the types of studies to be encouraged.

Lastly, and perhaps most importantly, research is needed on how to incorporate data, both physical and biological, into models. Whether present techniques of data assimilation that have been developed for physical ocean models (e.g., Haidvogel and Robinson, 1989) are applicable to coupled physical/biological models needs to be assessed. Where lacking, new techniques need to be developed. Also, it is hoped that this exercise will ensure a good match between theory and measurement, and help identify new ways in which physical and biological data can be used to initialize, constrain, and verify coupled models.

5.2.3.2 Historical Data Sets

There are significant historical data sets which should be examined to provide an expanded time-series context for the data acquired during the Georges Bank Study. Given the relatively limited resources available for this study, it is essential that the program take advantage of past research efforts in the area. Some of these data sets are well known because of the many publications arising from them, while others have not been summarized in the open literature and are not generally known by the scientific community. They exist in various degrees of processing and public availability. In most cases, they are a combination of both biological and physical data, but were not used initially to address the specific issues that are the focus of this program. A partial list of major data sets and field survey programs includes:

- * The 1939/1940/1941 Bumpus time-series plankton study of Georges Bank
- * The 1961-present Continuous Plankton Recorder Gulf of Maine data set
- * The 1965-1966 NMFS Gulf of Maine Study
- * The 1970-1987 MARMAP study of the Gulf Of Maine, Georges Bank, and the Mid-Atlantic Bight
- * The 1978 American/Canadian Patch Study
- * The 1978-1980 New England Outer Continental Shelf Physical Oceanography Program
- * The 1979-1980 Nantucket Shoals Flux Experiment
- * The 1981 Nantucket Shoals Experiment
- * The 1981-1982 Warm-Core Ring Study
- * The 1983-1985 Southwest Nova Scotia Fisheries Ecology Program
- * The 1985-1986 Great South Channel Recirculation Experiment
- * The 1986-1987 UNH Gulf of Maine Study
- * The 1988-1989 South Channel Ocean Productivity Experiment
- * The 1978-1986 CZCS color data set and 1980-present AVHRR data set
- * Moored and coastal weather station data

In addition, other monitoring programs have provided physical and biological data for the region (e.g., 7 years of mooring records off Cape Sable, Nova Scotia before and during the Fisheries Ecology Program). There is currently a NOAA Marine Ecosystems Response-funded analysis of historical ichthyoplankton and hydrographic data from the Northeastern U.S. continental shelf region. Additional background information on some of the regions historical data can be found in O'Reilly (1987).

Researchers are encouraged to contribute to the Georges Bank U.S. GLOBEC program through analysis of historical data, especially through 1) the application of new analytical and statistical techniques to historical data sets, 2) the integration of unconnected databases, and 3) the evaluation of historical data in the context of climate and inter-annual variability.

5.3 Methodology and instrumentation needs and development

The new methods and technologies that now exist, or that are under development and being tested, will allow one to look at the physical and biological processes occurring on Georges Bank in ways not previously possible. These new developments will allow more complete spatial surveys, more detailed processes studies and longer time-series observations of the combined physical and biological parameters over Georges Bank. It is with this additional information, supplied by the combined observational data set and modeling efforts, that the complex questions outlined above can be addressed. This will aid our understanding of how physical processes influence the biological processes which control the distribution, abundance, production and population dynamics of planktonic organisms on Georges Bank.

Well established technologies such as CTDs, current meters, towed nets, and drifters should be used along with the new methods to extend our observational capabilities. Acoustical and optical instruments could be moored, towed and profiled along with established technologies to give a unique combination of biological and physical information. These new techniques are in a trial and growth period that requires additional field and laboratory testing and calibration. This development and testing program should be carried out within the context of an ongoing scientific program that can supply complementary and redundant information to evaluate and understand the performance of new instrumentation. This redundancy and overlapping data should strengthen the program considerably, as well as advance the evaluation of new technology. To be considered for funding, new instruments and methods should be in a fairly mature state of development that will allow field deployment in the early stages of the experiment. Some of the appropriate technologies and considerations are outlined and discussed below.

Integrated Shipboard Profiled and Towed Survey Platforms: The broad-scale surveys and specific fine-scale process studies will require shipboard observations made with towed and profiled instruments to resolve the horizontal and vertical structure of the physical oceanographic variables and the biological environment, and to identify the number, size and type of biological organisms present. Existing shipboard platforms should be equipped with new combined sensing capability to provide the ability to sample from the surface to the bottom in the shallow waters of Georges Bank. The broad-scale survey should provide the gross spatial structure of the physical and biological parameters into which the more detailed fine-scale process studies fit.

The vertical structure of the water column should be measured by profilers with CTD, bio-optical (Dickey, 1991), optical (Gardner et al., 1990), acoustical (GLOBEC, 1991e), and optical imaging (Davis, et al., in press) instrument suites. (Table 3 lists the various sensors included in each instrument suite.) These profiling systems should also have the ability to collect multiple water samples for shipboard or laboratory analysis of oxygen, salinity, nutrients, and chlorophyll. For biota identification, these profiling systems also should be integrated with pumped profilers. For the broad-scale shipboard surveys, 1-meter vertical spacing on most observations should be adequate. For turbulent mixing processes, centimeter or finer resolution may require free-fall microstructure (temperature, salinity and velocity) resolving instruments.

To resolve the spatial distribution, size, and number of species present, towed multiple-net sampling systems (such as the MOCNESS and bongo nets) should be employed for the broad-scale surveys as well as some process studies. CTD sensors should be added to the towed nets systems to give a record of the depth and water properties where the nets were deployed and

Table 3. Sensors and Sensing Systems

Sensor System	Measurements Made by Sensing System	Sampling Mode	Time Scale Min:Max	Resolution Vert:Horiz
CTDs	Temperature Conductivity Pressure Dissolved O2 pH	Profiled	1 hr:1 mon	0.5m:1 km
		Moored	1 min:1 yr	10 m:10 km
		Towed	1 sec:1 day	0.5 m:1 m
Current Meter	Water Velocity, Speed, & Direction	Moored	1 min: 1 yr	10 m: 10 km
Water Bottles	Water for Shipboard or Laboratory Analysis	Profiled	1 hr:1 mon	10 m:1 km
Bio-Optical	Beam Attenuation Stimulated Fluorescence PAR Upwelling Radiance Downwelling Irradiance Optical Plankton Counter	Profiled	1 hr:1 mon	1 m:1 km
		Moored	1 min:1 yr	10 m:10 km
		Towed	1 sec:1 day	1 m:1 m
In situ chemical analyzer	Inorganic nutrient; O2	Profiled Moored Towed	Continuous; 2 hr:2-3 mon	2m:100 km
In situ microbial rates (SID)	Primary production; tracer uptake	Moored Surface drifter	3-9 hr:1-3 mon (100 samples max)	10m:100 km
Optical Imaging	Video Images of Number, Size, Taxa and Biomass	Moored Towed	<1sec:3 mon 1 min:1 day	1 μ m:10 km 1 m:10 km
Nets	Species, Number & Size	Towed	1 hr:1 day	1 m:100 m
ADCP (300kHz)	Current Profiles Acoustical Backscattering	Moored Towed	1 min:1 yr 1 min:1 mon	1 m:10 km 1 m:10 m
MET	Wind Speed and Direction Atmospheric Temperature Atmospheric Pressure Relative Humidity Precipitation Long & Short Radiation Sea Surface Temperature Wave height and direction	Moored	10 min:1 yr	1 pt:50 km
		Shipboard	10 min:1 yr	1 pt:100 m
SODAR	Wind Velocity Profiles	Moored Shipboard	10 min:1 yr 10 min:1 yr	10 m:10 km 10 m:100 m
Lagrangian Drifters	GPS Position CTD & Bio-Optical	Drifting	1 hr:6 mon	10 m:100 m
Acoustical Imaging	Acoustical Backscattering Numbers & Target Strength	Profiled Moored Towed	1 hr:1 mon 1 min:1 yr 30 sec:1 day	1 m:1 km 1 m:10 km 1 m:30 m

Sampling Mode Definition:

- Profiled: instruments lowered from a ship or mounted on an ROV.
 Moored: instruments mounted on surface, subsurface, or bottom mounted platform at a fixed location.
 Towed: instruments deployed on a towed body or hull mounted on a ship.
 SID: Submersible Incubation Device.

should be of a quality to supplement the profiled and towed platform (see below) data. Some bio-optical and acoustical sensors should be included on the towed nets as appropriate. Data on species, number, size and age structure from these net tows should be used for in situ calibration and intercalibration of acoustical imaging sensors (see below).

Towed integrated biological/physical instrument platforms (such as SEASOAR) should sample the horizontal structure in more detail than shipboard profilers, as well as have the ability to sample the vertical, but with less resolution than shipboard or free-fall profiling systems. These towed platforms should have CTD, acoustical imaging, bio-optical, and optical imaging instrument suites (Table 3). They should be used in addition to vertical profilers for more detailed process studies of the spatial structure of the physical and biological environment over the Bank. For studies associated with fine-scale mixing processes, microstructure temperature, conductivity and velocity probes should be added to the towed platforms to measure the spatial structure of the turbulence and energy dissipation rates.

To determine the abundance, taxonomy and size distribution of plankton on scales from a few micrometers to centimeters, optical imaging systems (such as video cameras with magnifying optics, holographic systems and range-gated laser systems) should be used as part of the broad-scale survey as well as in specific process studies. Development of image processing systems for pattern recognition should be a critical component of this program. In addition to automating the counting of plankton samples, moored optical imaging systems could collect optical time series of plankton abundance. Data compression and processing techniques should be developed to reduce the in situ storage requirements and to allow telemetry of video data from ships and moored platforms.

For the measurement of fine-scale distributions and in situ rate processes such as swimming and feeding behaviors, and for microturbulence measurements, large Remotely Operated Vehicles (ROVs) and/or Autonomous Underwater Vehicles (AUVs) could also be used as stable remote platforms. ROVs and AUVs could be used to make process study measurements at specific locations within the water column and could be used for fine-scale three-dimensional mapping in frontal and high gradient regions as well as the bottom-boundary layer.

Acoustic Doppler Current Profilers (ADCPs): ADCPs should be used to obtain the required vertical profiles of the velocity field as either a function of position (shipboard surveys) or as a function of time (moorings). The broad-scale shipboard surveys of the velocity structure should be used to complement the moored current observations by putting them in context of the flow field, while the moorings should put the shipboard surveys in temporal context. The new broadband ADCP (Brumley et al., 1991) will provide the finer resolution in both space (3 m vertically) and time (1 min) required to resolve smaller spatial scales associated with shear, internal wave mixing and cross-frontal exchange. To address the stability of the water column and relationship to velocity shear, moored ADCP data should be utilized with the density time series. For shipboard navigation, GPS positions integrated with bottom tracking should be used in depths to 200 meters. To assure that current meter observations are adequate for monitoring the small space and short time scales required for the process studies, tests and calibrations should be done in both shipboard and moored configurations.

The broadband ADCP also monitors the amplitude of the backscattered signal and has the potential for producing profiles of scattering and biomass estimates by measuring profiles of volume scattering strength. This measurement could be used to estimate zooplankton abundance and biomass time series and profiles (see Flagg and Smith, 1989a, 1989b for results from older style, narrow-band ADCPs). When coupled with traditional biological sampling techniques on shipboard surveys, the spatial distribution of the zooplankton can be estimated. It is important that the moored time-series observations of backscatter profiles should provide qualitative time histories of biomass variations, although not as detailed as more advanced acoustical imaging instruments.

As with all acoustical backscattering instruments, calibration and intercomparison with net tows, etc., should be made before any quantitative estimates of the spatial or temporal distributions of zooplankton and biomass are made. The calibration and testing of new ADCP systems for velocity profiling, spatial resolution, bottom tracking, and acoustical backscattering need to be completed before their results can be used in the Georges Bank program. This evaluation should be done in conjunction with the acoustical imaging systems discussed below. Research may be needed on algorithm development and on measurement of target strength of individual organisms.

Acoustical Imaging: The recently held workshop on acoustical technology details the technological tools and advances required to support the U.S. GLOBEC research initiative (GLOBEC, 1991e). As indicated above, there are a variety of applications for acoustical imaging sensors where information is required about zooplankton biomass, numbers, and size information as a function of time and space. The development of acoustical imaging technology to estimate these parameters (i.e., as volume backscattering, numbers, and target strength) has increased markedly during the past several years, but there is a need for continued basic research and development to achieve a level of functionality in acoustical remote sensing of marine animals commensurate with the programmatic requirements. The Georges Bank Study will require a combination of moored, towed, and profiling acoustical instruments that use multi-frequency, dual-beam, or split-beam techniques.

In addition to the development of new sensor packages and new methods for quantitative combination of multi-frequency acoustical data, there is a need for continued development of better models of acoustical scattering from all marine organisms (e.g., various taxa of zooplankton, with special emphasis on the target species) and testing of the models through acquisition of acoustical backscatter data from single individuals, as a function of orientation, and groups of individuals. Procedures to intercalibrate the various acoustical sensors likely to be used should be established at the beginning of the program. A bio-acoustics group should be established to provide technical assistance with instruments, data processing, and calibration services and should be coordinated with the bio-optical sensor calibrations.

Integrated Moored Platforms with Adaptive Sampling and Telemetry: Time-series observations of atmospheric variables are required to measure the atmospheric forcing (momentum, heat and buoyancy fluxes) over Georges Bank. The more complete meteorological sensor suite (Table 3) on the U.S. GLOBEC mooring in the center of Georges Bank should provide the primary data for the experiment and should be used with observations made by the three NOAA NDBC buoys moored around the Bank (Figure 12) to resolve the spatial structure of the forcing. Technologies such as Doppler SODARs should be considered to improve momentum flux measurements by directly observing the vertical wind profiles rather than measuring the velocity at one height and applying bulk parameterization models to estimate stress.

Moored buoys and bottom mounted platforms should be placed at specific locations around the Bank for the broad-scale, time-series observations as well as for fine-scale process studies (Figure 12). Various sensor systems, including CTD, bottom pressure gauges, bio-optical, current meter, ADCP (for velocity profiles), systems for acoustical biological profiling, and optical imaging systems (for taxonomic identification, size and number), should be placed at various depths below the surface to give combined physical/ biological time series at critical locations. Bottom-mounted tripods should measure variables in the the bottom-boundary layer, as well as resolve the surface wave field with bottom pressure sensors.

Powering, controlling and recording data from these various sensors will require more complex data systems with higher capacity recorders and compression schemes for optimal use of the recording space and telemetry links. Power, supplied by solar panels and batteries, will have to be controlled and conditional sampling programs devised to provide long-term unalised

averages yet still sample any high frequency internal wave, turbulent mixing and biological events. Optical systems will require additional in situ image processing and compression developments (with digital signal processors) before they can be routinely used in moored applications.

Real-Time Data Management and Distribution: To take advantage of the potential for increased understanding and better utilization of ship time, a data management component should develop and utilize two-way data links to routinely relay information from instrument systems in the field to a "real-time" data base in the Georges Bank data center. This data base should be accessible by project investigators in the field as well as in their laboratories. Developments in networking ships and remote platforms together (as is now done on land by computer networks such as INTERNET) should be used to relay data (i.e., satellite imagery, moored data, and preliminary model results) from the Georges Bank data management center to the ships in the field for real-time use in planning operations. Thus, the data management office should develop and/or adapt the methodology of receiving, cataloging, and processing and distributing the real-time data (with lower data quality but faster access time) to project investigators, and at the same time deal with the slower process of editing, checking data quality, archiving and distributing the high-quality, final data sets to the project investigators and the oceanographic community. As an integrated study, this will involve time series, spatial series, optical images, physical and biological samples, satellite data, etc., in the data base with directory.

Subsurface instruments not connected directly to the surface should communicate to the data center through additional acoustical telemetry links to surface platforms. These devices have been demonstrated in test applications (Catapovic et al., 1991), and now need to be proven in general oceanographic applications. The protocol and interfacing with bottom instrumentation needs to be completed and tested. The telemetry schemes need to be reviewed, and integrated into the moored and shipboard instrumentation and into the data management plan.

Drifters: Lagrangian drifters should play an important role in illustrating water movements such as the entrainment of source water from the Gulf of Maine, the circulation around the crest of Georges Bank, the leakage of water into the North Atlantic via cross-frontal exchange, and the movement of water down the New England shelf. They should be used to "tag" water masses or regions containing a biological population to aid in following and identifying changes in the water or biology with time. Drifters should be able to be drogued at varying depths, and have GPS tracking for the accurate, closely spaced positions required for detailed process studies. Drifters need to be developed that are not influenced by surface phenomena, otherwise they may "slip" away from a subsurface patch of animals that is being studied. The drifters should be deployable from both aircraft and ships to allow the optimum deployment distributions. The drifters should be low enough in cost that using large numbers should not be prohibitively expensive. Drifter life should exceed 3 to 6 months.

In addition to position, the drifters should also measure sea surface temperature and conductivity to aid in the interpretation of the satellite surface temperature maps and shipboard surveys, and for characterization of water masses. Larger integrated drifting platforms could be constructed with the capability of carrying most of the sensors listed in Table 3. Consideration should be given to the development and use of a neutrally buoyant, subsurface drifter that can follow an isotherm or isolume to mimic the diel migration of animals, and can follow a patch of water or organisms to aid in studies of retention and exchange, and relationships between vertical distribution and current structure. These drifters should have the capacity to be tracked acoustically from ship.

Molecular Technology: Recent advances in the fields of biochemistry, molecular biology, molecular genetics, and immunology offer considerable potential to provide unprecedented insight into the feeding success, growth rate, physiological status, and genetic makeup of individual organisms collected at sea (Powers et al., 1990; Powers, 1991). Advances in molecular

technology should greatly increase our understanding of the relations among variability in the physical environment and biological responses at the molecular, organismal, and population levels.

Much basic work must be done with the organisms of interest in order to put molecular biological approaches to work to answer ecological questions. Nucleic acid base sequence data are fundamental to a variety of technical approaches, and should be considered a foundation of molecular ecological work on Georges Bank. Base sequence data may allow the design of species- and population-specific molecular probes, and the development of rapid means of identification and discrimination of taxa. Nucleic acid hybridization probe technology can provide information on the identity, growth rate, physiological status, and reproductive condition of individual organisms, as well as information on the genetic relationships among individuals, cohorts, and populations. The concentration of RNA and the RNA-DNA ratio have been used to estimate feeding success and recent growth in a wide variety of marine organisms including larval fish (Buckley and Lough, 1987) and crustaceans (Wang and Stickle, 1986). Detection and measurement of specific RNAs using nucleic acid hybridization probes should provide more detailed information on growth rate and physiological status.

The analysis of recruitment, production, and dispersal processes of the target species on Georges Bank may be addressed through population genetic approaches. Many fundamental population genetic processes for planktonic marine species are unknown, including effective population size, migration and gene flow patterns, population structure, and temporal stability of genetic characteristics. These questions could be addressed explicitly for the target species using current molecular and biochemical techniques. In addition, there should be a focussed effort to develop rapid and sensitive molecular techniques to enable screening of the many individuals necessary for ecological studies. While existing techniques can be used to assay molecular characteristics of formalin-preserved animals, these techniques need to be improved and enhanced so that existing collections can be utilized to develop the historical context for the population genetic information that will result from the Georges Bank Study.

The field of biotechnology is developing at a rapid pace, and the successful application of new techniques to oceanographic research will require interdisciplinary planning, research and development. *A posteriori* assimilation of published techniques will not provide tools and answers at the desired pace; an accelerated plan to address specific oceanographic goals is needed. To this end, U.S. GLOBEC convened a workshop in Fall 1990 on the application of biotechnology to field studies of the plankton (GLOBEC, 1991d), and in 1992 initiated a program of funding for biotechnology research and development. Two studies have been funded:

Estimation of recent growth and physiological condition of marine fish larvae and zooplankton using nucleic acid hybridization probes: T. Durbin, A. Durbin and L. Buckley

This project is an effort to use different roles, half-lives and properties of messenger RNA and ribosomal RNA to develop new indices of recent growth and physiological status of larval Atlantic cod (*Gadus morhua*) and the copepod *Calanus finmarchicus*. The concentration of rRNA and selected mRNAs will be determined using probes developed for these species. RNA concentrations will be determined under a variety of conditions imposed in culture.

Physiological status of zooplankton: Utilizing PCR to rapidly assess specific enzyme expression: D. Crawford and L. Incze

Molecular techniques will be developed to rapidly identify and quantify the level of expression of physiologically significant genes in the copepod *Calanus finmarchicus*. The techniques take advantage of the specificity and sensitivity of the polymerase chain reaction (PCR) to quantitatively amplify species-specific mRNAs that encode enzymes regulating metabolic fluxes. Species-specific primers will be designed using phylogenetically conserved primary sequences of several enzymes. The effect of environmental parameters

on levels of gene expression will be investigated using animals of various stages held in culture and captured at sea. The concentration of product from a physiologically invariant gene will be measured as a potential datum for normalizing results in order to perform analyses on taxonomically and developmentally complex assemblages of zooplankton.

Biochemical Techniques: Feeding success, important for growth and survival of larval fish, can be studied by stomach content observations and by analysis of the condition and chemical composition of individuals. Stable isotope analyses could be used in feeding studies to detect the origins of carbon and nitrogen in the diet (Thayer et al., 1983). Isotopic studies usually encompass several trophic levels, and suggest patterns of chemical connectedness between organisms such as phytoplankton, zooplankton and fish. This connectedness is one of the only direct ways to estimate energy flow in planktonic food webs, and is a powerful way to check trophic relations inferred from stomach content studies (Fry, 1988).

The distributional histories of larval cod on Georges Bank will be investigated during the spring and early summer period of developing thermal stratification, a time during which the intricacies of their vertical and areal distributions may hold important implications for larval survival and ultimately recruitment. The recently developed technique of otolith analysis (Sr/Ca ratios) (Radtke, 1988; Townsend, et al., 1989; Radtke et al., 1990) could be used to hindcast the temperature histories, and hence the distributional histories (from time of hatching to capture) of individual cod larvae collected in various hydrographic regimes in the Bank area. This technique could be advanced by employing electron energy loss spectroscopy, which will increase the resolution of the Sr/Ca technique to a level capable of resolving sub-daily temperature histories. These analyses could reveal diel migrations into or through the thermocline.

With any new technique, intercalibration and comparison among the new measurement systems and techniques will be critical to assure highest data quality and enhanced interpretation. Pre- and post-cruise calibrations of all sensors will be necessary, especially extensive calibrations and validations of the acoustical sensing systems. In situ calibrations and comparisons between moored and profiling instruments, and net tow samples should be used to identify and correct for sensor malfunction and drift, and will increase the data quality required for U.S. GLOBEC integrated studies. The calibrations and acceptance of new biochemical techniques may require dedicated laboratory experiments.

5.4 Schedule

A schedule for the different components of the Georges Bank Study is shown in Figure 13. The study is envisioned to begin in 1993 with the major field experiments to be conducted in 1994, 1996, and 1998. During these even-numbered years, smaller-scale process studies will be undertaken in parallel with comprehensive broad-scale studies. The decision on which process studies to emphasize in which year will depend on several factors. These include scientific rationale, status of supporting technology and methodology, and availability of resources (especially scientific personnel, instrumentation, shiptime, and funding). Some work in each process area could be undertaken in each year. The plan at present is to conduct mixing/stratification studies in 1994, source/retention/exchange studies in 1996, and cross-frontal mixing studies in 1998. In the intervening years, 1995 and 1997, less intensive broad-scale survey work should be conducted to monitor inter-annual variability. Some process-oriented work directed at measurement of vital rates affecting population dynamics may be continued as well. Some elements of the long-term physical/ biological moored array should be maintained continuously through 1993-1998 to observe conditions during the rest of each year and also to monitor inter-annual variability. Instrument and other technological developments are envisioned to proceed until 1997. Planning meetings and data analysis workshops will be convened at least once per year; a coordinating group should meet more frequently in order to manage the program effectively.

Shiptime is required for broad-scale surveys, process studies, and setting and retrieving moorings and drifters, allocated as follows:

BROAD-SCALE SURVEY

	# of Cruises	# of Days/Cruise	Total Days/Year
1994	9	16	144
1995	6	16	96
1996	9	16	144
1997	6	16	96
1998	9	16	144

PROCESS STUDIES

1994	3	21	63
1995	0	0	0
1996	3	21	63
1997	0	0	0
1998	3	21	63

MOORING AND DRIFTER CRUISES

1994	3	7	21
1995	3	7	21
1996	3	7	21
1997	3	7	21
1998	3	7	21

6. DATA MANAGEMENT AND SYNTHESIS

There is need for a program logistics office for the Georges Bank Study which should provide the support, guidance, and coordination required by a multiple Principal Investigator research program.

In a program such as U.S. GLOBEC, with investigators with many different skills and interests and from many different institutions or agencies, it will be necessary to lay out ground rules for data inventoring, preliminary exchange, and use by others. A free flow of preliminary information to all program investigators is vital in planning later cruises, data analyses, and modeling efforts, and in putting together the broad picture of the relationship between and among the various biological, physical, and chemical data which have been collected. As input to the U.S. GLOBEC data management committee, issues which must be addressed before any data are collected are the following:

- * Data inventory and acquisition by the data manager at a single location for the duration of the program
 - Cruise and mooring event logs
 - Inventory of all data acquired
 - Actual data files (core measurements versus proprietary data)
 - Historical data
 - Data from other programs in region (e.g., OPEN, Massachusetts Bay)
- * Data processing, quality control, and data merging and standardization
- * Data archiving (media/format)
- * Data distribution and accessibility
 - Data policy statement on nature and extent of proprietary data
 - Data reports and products
 - Data network
 - Software handling schemes
- * Real-time data /information acquisition and dissemination
 - Moored data (currents, T/S, zooplankton biomass from acoustics, fluorometry, etc.)
 - Broad-scale survey information
 - ADCP/CTD survey
 - Satellite data (e.g., SeaWiFS, AVHRR, SAR, etc)
 - Meteorological data
 - Drifter data (e.g., position, temperature, etc)
- * Data/modeling workshops

Considerable effort has recently been expended in the development of data management procedures and software for WOCE and JGOFS. Any data management system developed for U.S. GLOBEC should build on these ongoing efforts. As recognized by JGOFS, the data procedures must be able to accommodate biological as well as physical and chemical parameters, and this requires provisions for documenting measurement protocols and including data in a raw unprocessed form.

There are contractual obligations for data submission to national data centers such as NODC and NESDIS that accompany Federal Agency research awards. Generally, inventories of all data collected are to be submitted to a designated center within sixty days of the end of the

observational period/cruise or periodically for continuing observations. For data sets identified for submission to national centers, it is the principal investigator's responsibility to submit them within two years of the observational period/cruise. Since U.S. GLOBEC is part of the U.S. Global Change Research Program, all investigators involved in the Georges Bank Study must adhere to the data management policies of that program. All Federal regulations will be spelled out in detail for each funded investigator and deadlines for data submission, etc., will be enforced by the U.S. GLOBEC Program Manager.

7. RELATION TO OTHER PROGRAMS

7.1. Connections between the Georges Bank Study and Other U.S. GLOBEC Programs

No one study site will be suited ideally for the study of all processes and conditions of interest to U.S. GLOBEC. Indeed, no one site can command all of the resources necessary to do so. Because the themes of physical forcing, spatial and temporal variability, population dynamics and climate change prediction will pervade all study sites, a certain amount of commonality in the site-specific programs is expected. However, each site, and the teams of investigators funded to study that site, also can be expected to focus on conditions and processes that distinguish it from other sites. This will enable the U.S. GLOBEC program to be more global in its perspective and its achievements. In addition to the site-specific studies, there will be numerous funded efforts to improve upon modeling techniques, instrumentation, sampling methods and biotechnology. Most proposals to study these topics will be focused initially on a single site, but transfer of findings and developments to other studies at the earliest possible date is imperative. To maximize the accomplishments of U.S. GLOBEC within the context of multiple sites, multiple investigators and multiple research initiatives (e.g., instrument development, modeling, etc.), effective communication and coordination is needed. Thus, U.S. GLOBEC has established the U.S. GLOBEC Science Office, which will be located on the University of California - Davis campus from 1992-1995.

7.2. Relation to other National and International Programs

A number of national and international research programs are in progress that will complement the U.S. GLOBEC Georges Bank Study. This study is both a part of the international GLOBEC Program sponsored by SCOR and IOC, and the Cod and Climate Change Program of the International Council for the Exploration of the Sea. The sharing of data and results between all of these programs will be mutually beneficial. The value of the Georges Bank Study and the full interpretation of its results will be greatly increased through close interaction with these other programs. Full details of these other studies are contained in the planning documents of each. Many of these programs are in a state of development or rapid evolution; managers of individual programs should be contacted regarding their program's current status, mission and activities.

The NOAA Marine Ecological Response program is sponsoring a study of stratification variability on Georges Bank and its effect on larval fish survival. A pilot study was conducted in May 1992. Its objectives are to relate spatial and temporal variability in stratification on the southern flank of the bank to changes in food availability, growth, and survival of larval cod and haddock. This field study is scheduled to be completed prior to the onset of the Georges Bank U.S. GLOBEC program, and should provide an excellent source of information for the study developed from this plan.

The NOAA Atlantic Climate Change Program (ACCP) is focusing on the response of the global atmosphere to anomalies in the Atlantic Ocean and on the development of ocean-atmosphere models to simulate and predict the seasonal-to-decade changes over and around the Atlantic basin. The observations made by ACCP will provide information on the conditions in the deep oceanic region seaward of the Georges Bank area. Of particular use will be the basin-scale monitoring of climate variability through the 1990's, and high resolution analysis of the North Atlantic geological record. The modeling results will identify the changes in atmospheric forcing which may be expected to occur. This information is necessary to evaluate the potential effects of climate change on the target populations on Georges Bank.

Two programs being conducted in Canada are of interest. A component of the Ocean Production Enhancement Network (OPEN) is studying the physical and biological processes controlling the recruitment of cod on the Western Sable Bank region of the Scotian Shelf. It will

provide an excellent comparative data base for U.S. GLOBEC. The Northern Cod Science Program (NCSP) is focussing on the predator-prey dynamics of the cod stocks off Labrador and Newfoundland, including coastal regions as well as on a number of offshore banks. There is also a wealth of experience and data available from nearly two decades of Canadian physical and biological research in the Scotian Shelf, Gulf of Maine and Georges Bank (refer to section 5.2.3.2).

Of particular interest to the International Cod and Climate Change Program (CCC) is the varied response of different cod populations to climate changes in various regions of the cod's North Atlantic range. Differences in the regional data bases available for addressing this issue make interregional comparisons a high priority. There is also a new Scientific Committee on Ocean Research (SCOR) working group on pelagic biogeography that may provide opportunities for linking additional research activities in the North Atlantic with the Georges Bank study.

Together the OPEN, NCSP and CCC programs will provide the opportunity to compare results of the U.S. GLOBEC Georges Bank Study with similar investigations in other coastal and bank systems of the North Atlantic Ocean. It is essential that scientists and managers from these programs meet at regularly scheduled workshops to insure maximum coordination of research activities and information exchange. In addition, the lessons from regional programs, such as OPEN, are useful in the development of the new U.S. GLOBEC program. For example, U.S. GLOBEC researchers should interact with OPEN scientists, who have been dealing with the logistics of a monthly cruise strategy.

A NOAA Coastal Ocean Program-sponsored study of the predator-prey interactions of the primary fish populations in the Georges Bank ecosystem is proposed for 1994. It will consider the implications of the dramatic shift in fish biomass from groundfish and flounders to elasmobranchs over recent decades. This program will complement the U.S. GLOBEC Georges Bank Study by addressing the predation of adult fish on the juvenile stages of the target species cod and haddock. It will continue the investigation of those species after settlement to the bottom and through the rest of the first year of life.

The National Marine Fisheries Service (NMFS) has ongoing sampling programs which will contribute information to the U.S. GLOBEC Georges Bank Study. In particular, NMFS conducts annual fall (since 1963) and spring (since 1967) bottom trawl surveys to assess the abundance and distribution of the adult fish stocks from Cape Hatteras through the Gulf of Maine, including Georges Bank. The spring survey is conducted in March and April, in the middle of the period of interest to the U.S. GLOBEC Georges Bank Study. Larval cod have been collected in previous years as well, in conjunction with these surveys. The trawl survey program will provide information on the distribution, abundance, and fecundity of the important fish stocks in the region, including the target species cod and haddock.

The Coastal Ocean Processes Program (CoOP) is now being developed as a multi-agency, multi-disciplinary effort focussing on the transfer of properties in the coastal ocean. Overlap between CoOP and U.S. GLOBEC in relation to model development and testing, observational techniques, and process studies is anticipated. Other U.S and international programs, including the Joint Global Ocean Flux Study (JGOFS) and the World Ocean Circulation Experiment (WOCE), are not presently involved in research in the North Atlantic. However, the experience of these "mature" research programs, in terms of technology development, field logistics, extensive data sets, and model simulations, will be valuable in the development of the Georges Bank U.S. GLOBEC plan. For example, WOCE scientists from Canada and the United Kingdom are examining the ocean's response to the North Atlantic Oscillation, which may be related to fluctuations in the Georges Bank ecosystem. The use of long-term moorings at Bermuda by JGOFS scientists may benefit the Georges Bank program. Possible linkages between variability in the Bermuda time series and variability in the Georges Bank area should be explored. Inter-annual

variability in the North Atlantic Oscillation is correlated with changes in water temperature at Bermuda (Talley and Raymer, 1982). Much of this work is still ongoing; cooperative field and model research between this U.S. GLOBEC program and these studies is strongly encouraged.

8. REFERENCES

- Anderson, J. T. 1988. A review of size-dependent survival during pre-recruit stages of fish in relation to recruitment. *J. Northw. Atl. Fish. Sci.* 8: 55-66.
- Auditore, P. J., G. R. Bolz, and R. G. Lough. 1988. Juvenile haddock, Melanogrammus aeglefinus, and Atlantic cod, Gadus morhua, stomach contents and morphometric data, from four recruitment surveys (1984-1986) in the Georges Bank-Nantucket Shoals area. Northeast Fisheries Center, Natl. Mar. Fish. Serv., NOAA, Woods Hole Lab. Ref. 88-05, 105 p.
- Auditore, P. J., R. G. Lough, and E. A. Broughton. 1992. A review of the comparative development of Atlantic cod and haddock based on an illustrated series of larvae and juveniles from Georges Bank. NAFO Sci. Coun. Studies (Submitted).
- Auer, S.J. 1987. Five-year climatological survey of the Gulf Stream system and its associated rings. *J. Geophys. Res.* 92 (11): 11709-11726.
- Auster, P.J., R.J. Malatesta, S.C. LaRosa, R. A. Cooper, and L.L. Stewart. 1991. Microhabitat utilization by the megafaunal assemblage at the low relief outer continental shelf site-middle Atlantic bight, USA. *J. Northwest Atl. Fish. Sci.* 11: 59-69.
- Backus, R.H. 1987. (ed) Georges Bank. MIT Press, Cambridge, Massachusetts. 593 pp.
- Bailey, K. M., and E. D. Houde. 1989. Predation on eggs and larvae of marine fishes and the recruitment problem. *Adv. Mar. Biol.* 25: 1-83.
- Beardsley, R.C., D. C. Chapman, K.H. Brink, S.R. Ramp and R. Schlitz. 1985. The Nantucket Shoals Flux Experiment (NSFE79). Part I: A basic description of the current and temperature variability. *J. Phys. Oceanogr.* 15: 713-748.
- Beardsley, R.C., R. Limeburner and C. Chen. 1991. Summertime Lagrangian circulation in the Great South Channel/Georges Bank region. *Trans. Amer. Geophys. Union, EOS* 72: 260 (abstract).
- Beverton, R. H. J., and S. J. Holt. 1957. On the dynamics of exploited fish populations. UK Min. Agric. Fish., Fish. Invest. Lond. (Ser. 2) 19. pp. 533.
- Beyer, J. 1990. Recruitment stability and survival-simple size specific theory with examples from the early life dynamics of marine fish. *Dana* 7: 47-147.
- Bigelow, H.B. 1926. Plankton of the offshore waters of the Gulf of Maine. *Bull. Bureau Fish.* 40: 1-509.
- Bigelow, H.B. 1927. Physical oceanography of the Gulf of Maine. U.S. Dept. of Comm. Bur. Fish. 40: 511-1027.
- Bollens, S.M, B.W. Frost, H. Schwaninger, C.S. Davis, K. Way, and M.C. Landsteiner. in press. Seasonal plankton cycles in a temperate fjord with comments on the match-mismatch hypothesis. *J. Plankton Res.*
- Bolz, G.R. and R.G. Lough. 1984. Retention of ichthyoplankton in the Georges Bank region during the autumn-winter seasons, 1971- 1977. *J. Northw. Atl. Fish. Sci.* 5: 33-45.

- Bolz, G. R. and R. G. Lough. 1988. Growth through the first six months of Atlantic cod Gadus morhua and haddock Melanogrammus aeglefinus based on daily growth increments. *Fish. Bull.*, U. S. 86: 223-235.
- Brink, K.H., B.A. Magnell, and M.A. Noble. 1987. Low-frequency current and bottom pressure variability. In: Georges Bank. R.H. Backus (ed.), MIT Press, pp. 140-146.
- Brooks, D. A. 1985. Vernal circulation in the Gulf of Maine. *J. Geophys. Res.*, 90: 4687-4705.
- Brown, B. E. 1987. The fisheries resources. In: R. H. Backus (ed), Georges Bank, MIT Press, Cambridge, Massachusetts, p. 480-493.
- Brown, W.S. 1984. A comparison of Georges Bank, Gulf of Maine, and New England shelf tidal dynamics. *J. Phys. Oceanogr.* 14:145-167.
- Brown, W.S. and J. Irish, 1992. The seasonal evolution of the geostrophic circulation in the Gulf of Maine, 1986-87. *J. Phys. Oceanogr.* (in press).
- Brown, W.S. and J.A. Moody. 1987. Tides. In: R.H. Backus (ed), Georges Bank, MIT Press, Cambridge, Massachusetts, p.100-107.
- Brumley, B.H., R.G. Cabrera, K.L.Deines, and E.A. Terray, 1991. Performance of a Broad-Band Acoustic Doppler Current Profiler, *IEEE Jour. Oceanic Eng.* 16(4): 402-407.
- Buckley, L. J., and R. G. Lough. 1987. Recent growth, biochemical composition, and prey field of larval haddock (Melanogrammus aeglefinus) and Atlantic cod (Gadus morhua) on Georges Bank. *Can. J. Fish. Aquat. Sci.* 44: 14-25.
- Bumpus, D.F. 1976. Review of the physical oceanography of Georges Bank. *In situ comm. Northwest Atlantic Fisheries Research Bulletin.* 12: 109-134.
- Butman, B., J.W. Loder, and R.C. Beardsley. 1987. The seasonal mean circulation: observation and theory. In: R.H. Backus (ed), Georges Bank, MIT Press, Cambridge, Massachusetts, p. 125-138.
- Butman, B. and R.C. Beardsley. 1987. Long-term observations on the southern flank of Georges Bank. Part I: A description of the seasonal cycle of currents, temperature, stratification and wind stress. *J. Phys. Oceanogr.* 17: 367-384.
- Butman, B., R.C. Beardsley, B. Magnell, D. Frye, J.A. Vermersch, R. Schlitz, R. Limeburner, W.R. Wright and M.A. Noble. 1982. Recent observations of the mean circulation on Georges Bank. *J. Phys. Oceanogr.* 12: 569-591.
- Butman, B. and R.C. Beardsley. 1991. Science in the Gulf of Maine: Directions for the 1990's. *Proceed. Gulf Maine Scientific Workshop.* Jan. 8-10, 1991 (in press).
- Caswell, H. and S. Twombly. 1989. Estimation of stage-specific demographic parameters for zooplankton populations: methods based on stage-classified matrix projection models. In "Estimation and Analysis of Insect Populations." L. McDonald, B. Manly, J. Lockwood, and J. Logan (eds). Springer-Verlag, New York. pp. 93-107.
- Catapovic, J., L. Freitag, and S. Merriam. 1991. Underwater acoustic local area network for ROV and instrument communications, *Proc. AUV-91 Conf.*, Wash. D.C.: 447-461.

- Chapman, D.C. and R.C. Beardsley. 1989. On the origin of shelf water in the Middle Atlantic Bight. *J. Phys. Oceanogr.* 19: 384-391.
- Clarke, G.L. 1933. Diurnal migration of plankton in the Gulf of Maine and its correlation in submarine irradiation.. *Biol. Bull* 65: 402-436.
- Clarke, G.L. 1934. Further observations on the diurnal migration of copepods in the Gulf of Maine. *Biol. Bull* 67: 432-455.
- Clarke, G.L., E.L. Pierce, and D.F. Bumpus. 1943. The distribution and reproduction of Sagitta elegans on Georges Bank in relation to hydrographical conditions. *Biol. Bull.* 85: 201-226.
- Cohen, E. B., D. G. Mountain, and R. G. Lough. 1986. Possible factors responsible for the variable recruitment of the 1981, 1982, and 1983 year-classes of haddock (Melanogrammus aeglefinus L.) on Georges Bank. *Northw. Atl. Fish. Org. SCR Doc.* 86/110, Ser. No. N1237. 27p.
- Cohen, E.B. and M.D. Grosslein. 1987. Production on Georges Bank compared with other shelf ecosystems. In: R.H. Backus (ed), *Georges Bank*, MIT Press, Cambridge, Massachusetts, p. 383-391.
- Cushing, D.H. 1972. The production cycle and the number of marine fish. *Symposia of the Zoological Society of London* 29: 2213-232.
- Cushing, D.H. 1975. *Marine Ecology and Fisheries*. Cambridge Univ. Press. Cambridge. 278 p.
- Daan, N. 1981. Comparison of estimates of egg production of the southern Bight cod stock from plankton surveys and market statistics. *Rapp. P.-v. Reun. Cons. int. Explor. Mer* 178: 242-243.
- Davis, C. S. 1984a. Interaction of a copepod population with the mean circulation on Georges Bank. *J. Mar. Res.* 42: 573-590.
- Davis, C. S. 1984b. Predatory control of copepod seasonal cycles on Georges Bank. *Mar. Biol.* 82: 31-40.
- Davis, C. S. 1984c. Food concentrations on Georges Bank: non_limiting effect on development and survival of laboratory reared Pseudocalanus sp. and Paracalanus parvus (Copepoda: Calanoida). *Mar. Biol.* 82: 41-46.
- Davis, C. S. 1987a. Components of the zooplankton production cycle in the temperate ocean. *J. Mar. Res.* 45: 947-983.
- Davis, C. S. 1987b. Zooplankton life cycles. In: R. H. Backus (ed.), *Georges Bank*. MIT Press, Cambridge, Massachusetts, p. 256-267.
- Davis, C.S., G.R. Flierl, P.H. Wiebe, and P. J.S. Franks. 1991. Micropatchiness, turbulence, and recruitment in plankton. *J. Mar. Res.* 49: 109-151.
- Davis, C.S. and P. Alatalo. in press. Effects of constant and intermittant food supply on life history parameters in a marine copepod. *Limnol. Oceanogr.*
- Davis, C.S., S.M. Gallagher, M.S. Berman, L.R. Haury, and J.R. Strickler. in press. The Video Plankton Recorder (VPR): Design and initial results. *Arch. Fur Hydrobiol.*

- Dickey, T.D., 1991. The Emergence of Concurrent High-Resolution Physical and Bio-Optical Measurements in the Upper Ocean and their Applications, *Rev. Physics*. 29(3): 383-412.
- Edwards, R. L., and R. E. Bowman. 1979. Food consumed by continental shelf fishes. In: H. Clepper (ed.), *Predator-prey systems in fishery management*. Sport Fishing Institute, Washington, D.C. pp. 87-406.
- Fahay, M. P. 1983. Guide to the early stages of marine fishes occurring in the western North Atlantic Ocean, Cape Hatteras to the southern Scotian Shelf. *J. Northwest. Atl. Fish. Sci.* 4: 1-423.
- Flagg, C. 1987. Hydrographic structure and variability. In: R. H. Backus (ed), *Georges Bank*, MIT Press, Cambridge, Massachusetts. pp. 108-124.
- Flagg, C.N. and S. Smith, 1989a. Zooplankton abundance measurements from Acoustic Doppler Current Profilers, *Proc. Oceans '89, IEEE & Mar. Tech. Soc.*, Seattle, WA, Sept. 18-21. 1318-1323.
- Flagg, C.N. and S.L. Smith, 1989b. On the use of the Acoustic Doppler Current Profiler to measure zooplankton abundance, *Deep-Sea Res.* 36(3): 455-474.
- Flagg, C.N., B.A. Magnell, D. Frye, J.J. Cura, S.E. McDowell and R.I. Scarlet. 1982. Interpretation of the physical oceanography of Georges Bank. EG&G Rpt No. 82-B4569, 901 pages.
- Fogarty, M. J., M. P. Sissenwine, and M. D. Grosslein. 1987. Fish population dynamics. In: R. H. Backus (ed), *Georges Bank*, MIT Press, Cambridge, Massachusetts, p. 494-507.
- Fogarty, M.J., E.B. Cohen, W.L. Michaels, and W.W. Morse. in press. Predation and regulation of sand lance populations: exploratory analysis. In: M. Dean and M.P. Sissenwine (eds.), "Multispecies models relevant to management of living resources". *Rapp. Rev. Reun. Cons. Int. Explor. Mar.*
- Frank, K., R.I. Perry and K.F. Drinkwater. 1990. Predicted response of northwest Atlantic invertebrate and fish stocks to CO₂-induced climate change. *Trans. Amer. Fish. Soc.* 119: 353-365.
- Fraser, J. H. 1962. The role of ctenophores and salps in zooplankton production and standing crop. *P.-v. Reun. Cons. perm. int. Explor. Mer* 153: 121-123.
- Frost, B.W. 1989. A taxonomy of the marine calanoid copepod genus Pseudocalanus. *Can. J. Zool.* 67: 525-551.
- Fry, B. 1988. Food web structure on Georges Bank from stable C, N, and S isotopic compositions. *Limnol. Oceanogr.* 33: 1182-1190.
- Gardner, W.D., M.J. Richardson, I.D. Walsh, B.L. Berglund. 1990. In-Situ Optical Sensing of Particulates for Determination of Ocean Processes: What Satellites Can't See, but Transmissometers Can. *Oceanography*. 3(2): 11-17.
- Garfield, N. and D.L. Evans. 1989. Shelf water entrainment by Gulf Stream warm-core rings. *J. Geophys. Res.* 92: 13003-13012.

- Garrett, C.J. 1972. Tidal resonance in the Bay of Fundy and Gulf of Maine. *Nature* 238 (5365): 441-443.
- Garrett, C.J.R., J.R. Kelley, and D.A. Greenberg. 1978. Tidal mixing versus thermal stratification in the Bay of Fundy and Gulf of Maine. *Atmos.-Ocean* 16 (4): 403-423.
- GLOBEC. 1991a. GLOBEC Theory and Modeling in Globec: A First Step. February 1991.
- GLOBEC. 1991b. GLOBEC Initial Science Plan, Report Number 1, February 1991.
- GLOBEC. 1991c. GLOBEC: Northwest Atlantic Program, GLOBEC Canada/U.S. Meeting on N.W. Atlantic Fisheries and Climate. Report Number 2, 1991.
- GLOBEC. 1991d. GLOBEC Workshop on Biotechnology Applications to Field Studies of Zooplankton. Report Number 3. February 1991.
- GLOBEC. 1991e. GLOBEC Workshop on Acoustical Technology and the Integration of Acoustical and Optical Sampling Methods. Report Number 4, September 1991.
- Gordon, A., S. Zebiak, and K. Bryan. 1992. Climate variability and the Atlantic Ocean. *EOS* 73: 161, 164, 165.
- Greenberg, D.A. 1979. A numerical model investigation of tidal phenomena in the Bay of Fundy and Gulf of Maine. *Marine Geodesy* 2 (2): 161-187.
- Greene, C.H., T.K. Stanton, P.H. Wiebe and S.McClatchie. 1991. Acoustic estimates of antarctic krill, *Nature*. 349: 110.
- Grice, G.D., R.P. Harris. M.R. Reeve, J.F. Heinbokel, and C.O. Davis. 1980. Large-scale enclosed water-column ecosystems: an overview of Foodweb I, the final CEPEX experiment. *J. Mar. Biol. Ass. U.K.* 60: 401-414.
- Haidvogel, D.B. and A.R. Robinson (eds). 1989. Data assimilation in ocean modeling. *Dynamics Atm. & Oceans*. 13: 171-517.
- Harrison, W.G., E.P. Horne, B. Irwin, and T. Platt. 1990. Biological production on Georges Bank: are tidal fronts primary sources of new production in summer? *Trans. Amer. Geophys. Union*, *EOS* 71: 96.
- Herman, Y. 1979. Plankton distribution in the past. In, "Zoogeography and Diversity of Plankton", (eds.) S. Van Der Spoel and A.C. Pierrot-Bults. Halsted Press. New York. pp: 29-49.
- Heyerdahl, E. G. and R. Livingstone, Jr. 1982. Atlantic cod, *Gadus morhua*. In: M. D. Grosslein and T. R. Azarovitz (eds), *Fish Distribution, MESA New York Bight Atlas Monograph 15*, New York Sea Grant Institute, Albany, New York. p. 70-72.
- Hill, B. T. and S.J. Jones. 1990. The Newfoundland ice extent and the solar cycle from 1860 to 1988. *J. Geophys. Res.* 95: 5385-5394.
- Holligan, P.M. and D.S. Harbour. 1977. The vertical distribution and succession of phytoplankton in the western English Channel in 1975 and 1976. *J. Mar. Biol. Ass. U.K.* 57: 1075-1093.

- Holligan, P. M., R.P. Harris, R.C. Newell, D.S. Harbour, R.N. Head, E.A.S., Linley, M.I. Lucas, P.R.G. Tranter, and C.M. Weekley. 1984a. Vertical distribution and partitioning of organic carbon in mixed, frontal and stratified waters of the English Channel. *Mar. Ecol. Prog. Ser.* 14: 111-127.
- Holligan, P.M., P.H. leB. Williams, D. Purdie, and R.P. Harris. 1984b. Photosynthesis, respiration, and N supply of plankton populations in stratified, frontal and tidally mixed shelf waters. *Nature* 17: 201-213.
- Hopkins, T.S. and N. Garfield III. 1981. Physical Origins of Georges Bank water. *J. Mar. Res.* 39: 465-500.
- Houde, E. D. 1987. Fish early life dynamics and recruitment variability. *Am. Fish. Soc. Symp.* 2: 17-29.
- Houde, E. D. 1989. Subtleties and episodes in the early life of fishes. *J. Fish. Biol.* 35: 29-38.
- Hunter, J. R. 1981. Feeding ecology and predation of marine fish larvae. In: R. Lasker (ed), *Marine Fish Larvae*. Univ. Wash. Press. p. 33-79.
- Hunter, J. R. 1984. Inferences regarding predators on the early life stages of cod and other fishes. In: E. Dahl, D. S. Danielssen, E. Moksness, and P. Solemdal (eds), *The Propagation of Cod Gadus morhua L.* Flodevigen rapportser. 1: 533-562.
- Iles, D. and M. Sinclair. 1982. Atlantic herring stock discreteness and abundance. *Science* 215: 627-633.
- Joyce, T. and P. Wiebe. 1983. Warm-core rings of the Gulf Stream. *Oceanus* 26: 34-44.
- Joyce, T.M., J.K.B. Bishop, and O.B. Brown. 1992. Observations of offshore shelf-water transport induced by a warm-core ring. *Deep-Sea Res.* 39 [Suppl. 1]: 97-114.
- Kane, J. 1984. The feeding habits of co-occurring cod and haddock larvae from Georges Bank. *Mar. Ecol. Prog. Ser.* 16: 9-20.
- Kelly, K.A. 1991. The meandering Gulf Stream as seen by the Geosat altimeter: surface transport, position, and velocity variance from 73° to 46° W. *J. Geophys. Res.* 96(9): 16721-16738.
- Kimmerer, W.J. 1987. The theory of secondary production calculations for continuously reproducing populations. *Limnol. Oceanogr.* 32: 1-13.
- Kjørboe, T., F. Møhlenberg, and P. Tiselius. 1988. Propagation of planktonic copepods: production and mortality of eggs. *Hydrobiologia* 167/168: 219-225.
- Klein, P. 1987. A simulation of some physical and biological interactions. In: R.H. Backus (ed), *Georges Bank*, MIT Press, Cambridge, Massachusetts, p. 395-405.
- Laurence, G. C., A. S. Smigielski, T. A. Halavik, and B. R. Burns. 1981. Implications of direct competition between larval cod (*Gadus morhua* L.) and haddock (*Melanogrammus aeglefinus*) in laboratory growth and survival studies at different food densities. *Rapp. P.-v. Reun. int. Explor. Mer* 178: 304-311.

- Laurence, G. C., and C. A. Rogers. 1976. Effects of temperature and salinity on comparative embryo development and mortality of Atlantic cod (Gadus morhua L.) and haddock (Melanogrammus aeglefinus (L.)). *J. Cons. int. Explor. Mer* 36: 220-228.
- Lazier, J.R.N. 1981. Oceanographic conditions at Ocean Weather Ship Bravo, 1964-1974. *Atmosphere-Ocean* 18: 227-238.
- Limeburner, R., and R.C. Beardsley. 1982. The seasonal hydrography and circulation over Nantucket Shoals. *J. Mar. Res.* 40 (supp): 371-406.
- Loder, J.W. 1980. Topographic rectification of tidal currents on the sides of Georges Bank. *J. Phys. Oceanogr.* 10: 1399-1416.
- Loder, J.W., D.G. Wright, C. Garrett, and B.A. Juszko. 1982. Horizontal exchange on central Georges Bank. *Can. J. Fish. Aquat. Sci.* 39: 1130-1137.
- Loder, J.W. and D.A. Greenberg. 1986. Predicted position of tidal fronts in the Gulf of Maine region. *Cont. Shelf Res.* 6: 397-414.
- Loder, J.W., K. Drinkwater, E.P.W. Horne, and N.S. Oakey. 1988. The Georges Bank frontal study: an overview with preliminary results. *Trans. Amer. Geophys. Union, EOS* 69:1283.
- Loder, J., D. Brickman, E. Horne. 1992. Detailed structure of currents and hydrography on the northern side of Georges Bank. *J. Geophys. Res.* (submitted)
- Lough, R. G. 1982. Observations on the impingement of warm core eddy 81-C on Georges Bank. *Trans. Amer. Geophys. Union, EOS* 63: 59.
- Lough, R. G. 1984. Larval fish trophodynamic studies on Georges Bank: sampling strategy and initial results. In: E. Dahl, D. S. Danielssen, E. Moksness, and P. Solemdal (eds), *The Propagation of Cod Gadus morhua L.* Flodevigen rapportser 1: 395-434.
- Lough, R.G. and G.R. Bolz. 1989. The movement of cod and haddock larvae onto the shoals of Georges Bank. *J. Fish. Biol.* 35 (Supplement A): 71-79.
- Lough, R.G. and R.W. Trites. 1989. Chaetognaths and oceanography on Georges Bank. *J. Mar. Res.* 47: 343-369.
- Lough, R. G., P. C. Valentine, D. C. Potter, P. J. Auditore, G. R. Bolz, J. D. Neilson, and R. I. Perry. 1989. Ecology and distribution of juvenile cod and haddock in relation to sediment type and bottom currents on eastern Georges Bank. *Mar. Ecol. Prog. Ser.* 56: 1-12.
- Lough, R. G. and D. C. Potter. in press. Vertical distribution patterns and diel migrations of larval and juvenile haddock, Melanogrammus aeglefinus, and Atlantic cod, Gadus morhua, on Georges Bank. *Fish. Bull., U. S.* (In press).
- Magnell, B., S.L. Spiegel, R.I. Scarlet and J.B. Andrews. 1980. The relationship of tidal and low-frequency currents on the north slope of Georges Bank. *J. Phys. Oceanogr.* 10: 1200-1212.
- Manabe, S., R. J. Stouffer, M. Spelman, and K. Bryan 1991. Transient responses of a coupled ocean-atmosphere model to graphical changes of atmospheric CO₂. Part I: Annual mean response. *J. Climate* 4: 785 -818.

- Marak, R. R., and R. Livingstone, Jr. 1970. Spawning dates of Georges Bank haddock. *Int. Comm. Northw. Atl. Fish. Res. Bull.* 7: 56-58.
- Michaels, W. L. 1991. The impact of mackerel predation on the survival of pelagic age-zero sandlance, cod, and haddock on Georges Bank during spring of 1986. Master of Science Thesis, Southeastern Massachusetts University. 154 p.
- Miller, T. J., L. B. Crowder, J. A. Rice, and E. A. Marschall 1988. Larval size and recruitment mechanisms in fishes: towards a conceptual framework. *Can. J. Fish. Aquat. Sci.* 45: 1657-1670.
- Miller, C.B., T.J. Cowles, P.H. Wiebe, N.J. Copley, and H. Grigg. 1991. Phenology in Calanus finmarchicus; hypotheses about control mechanisms. *Mar. Ecol. Prog. Ser.* 72: 79-91.
- Möller, H. 1984. Reduction of a larval herring population by a jellyfish predator. *Science* 224: 621-622.
- Moody, J.A., B. Butman, R.C. Beardsley, W.S. Brown, P. Daifuku, J.D. Irish, D. Mayer, H.O. Mofjeld, P. Petrie, S. Ramp, P. Smith and W.R. Wright. 1983. Atlas of tidal elevation and current observations on the northeast American continental shelf and slope. *U.S. Geol. Surv. Bull.* 1611. 122 pp.
- Mountain, D.G. and R.J. Schlitz. 1987. Some biologic implications of the circulation. In: R.H. Backus (ed), *Georges Bank*, MIT Press, Cambridge, Massachusetts, p. 392-394.
- Mullin, M.M. 1963. Comparative ecology of the genus Calanus in the Gulf of Maine. Ph.D. Thesis. Department of Biology. Harvard University, Cambridge, Massachusetts.
- National Oceanic and Atmospheric Administration, National Marine Fisheries Service. 1991. Status of the fishery resources off the northeastern United States for 1990. National Oceanic and Atmospheric Administration Technical Memorandum NMFS-F/NEC 81, p. 45-50.
- Noble, M., B. Butman, and M. Wimbush. 1985. Wind-current coupling on the southern flank of Georges Bank: variation and seasonal frequency. *J. Phys. Oceanogr.* 15: 605-620.
- O'Brien, L. 1990. Effects of fluctuations in stock abundance upon life history parameters of Atlantic cod, Gadus morhua, for the 1970-1987 year classes from Georges Bank and the Gulf of Maine. Master of Science Thesis, University of Washington. 95 p.
- O'Reilly, J.E., C.E. Evans-Zetlin and D.A. Busch. 1987. Primary production. In: R.H. Backus (ed), *Georges Bank*, MIT Press, Cambridge, Massachusetts. pp. 220-223
- O'Reilly J.E. and D. A. Busch. 1984. Phytoplankton primary production on the northwestern Atlantic shelf. Symposium on the biological productivity of north Atlantic shelf areas, Kiel, West Germany, Mar. 2-5, 1982. *Rapp P-V Reun Cons Int Explor Mer.* 183: 255-268.
- Overholtz, W. J. 1987. Factors relating to the reproductive biology of Georges Bank haddock (Melanogrammus aeglefinus) in 1977-83. *J. Northw. Atl. Fish. Sci.* 7: 145-154.
- Perry, R. I. and J. D. Neilson. 1988. Vertical distributions and trophic interactions of age-0 Atlantic cod and haddock in mixed and stratified waters of Georges Bank. *Mar. Ecol. Prog. Ser.* 49: 199-214.
- Perry, R.I., G. C. Harding, J.W. Loder, M.J. Tremblay, M.M Sinclair, and K.F. Drinkwater. in press. Zooplankton distributions at the Georges Bank frontal system: retention or dispersion? *Cont. Shelf Res.*

- Peterson, C. and T. Powell. 1991. What is Globec? GLOBEC NEWS. 1(1): 1-2.
- Peterson, W.T., P.T. Tiselius and T. Kiørboe. 1991. Copepod egg production, moulting and growth rates, and secondary production, in the Skagerrak in August 1988. *J. Plankton Res.* 13: 131-154.
- Pingree, R.D., P.M. Holligan, G.T. Mardell, and R.N. Head. 1976. The influence of physical stability on spring, summer, and autumn phytoplankton blooms in the Celtic Sea. *J. Mar. Biol. Ass. U.K.* 56: 845-873.
- Polacheck, T., D. Mountain, D. McMillan, W. Smith, and P. Berrien. 1992. Recruitment of the 1987 year class of Georges bank haddock (*Melanogrammus aeglefinus*): the influence of unusual larval transport. *Can. J. Fish. Aquat. Sci.* 49: 484-496.
- Powers, D.A. 1991. Applications of molecular techniques to large marine ecosystems. In: K. Sherman, L.M. Alexander, B.D. Gold (eds). *Stress, mitigation, and sustainability of large marine ecosystems*. AAAS. Washington, D.C.
- Powers, D.A., F.W. Allendorf, and T.T. Chen. 1990. Application of molecular techniques to the study of marine recruitment problems. In: K. Sherman, L.M. Alexander, B.D. Gold (eds); *Large marine ecosystems: patterns, process, and yields*. AAAS. Washington, D.C.
- Purcell, J. E. 1985. Predation on fish eggs and larvae by pelagic cnidarians and ctenophores. *Bull. Mar. Sci.* 37: 739-755.
- Radtko, R.L. 1979. Strontium/calcium concentration ratios in fish otolith as environmental indicators. *Comp. Biochem. Physiol.* 92A: 189-193.
- Radtko, R.L., D.W. Townsend, S.D. Folsom, and M.A. Morrison. 1990. Strontium/calcium concentration ratios in otoliths of herring larvae as indicators of environmental histories. *Environ. Biol. Fishes.* 27: 51-61.
- Ramp, S.R., R.C. Beardsley and R. Legeckis. 1983. An observation of frontal wave development on a shelf-slope/warm core ring front near the shelf break south of New England. *J. Phys. Oceanogr.* 13: 907-912.
- Ramp, S.R., R.J. Schlitz and W.R. Wright. 1985. The deep flow through the Northeast Channel, Gulf of Maine. *J. Phys. Oceanogr.* 15: 1790-1808.
- Rogers, J.C. 1984. The association between North Atlantic oscillation and the southern oscillation in the southern hemisphere. *Mon. Weather Rev.* October 1984: 1999-2015.
- Rothschild, B.J. and T.R. Osborn. 1988. Small-scale turbulence and plankton contact rates. *J. Plank. Res.* 10: 465-474.
- Runge, J.A. 1988. Should we expect a relationship between primary production and fisheries? The role of copepod dynamics as a filter of trophic variability. *Hydrobiologica.* 167/168: 61-71.
- Schlitz, R.J. and E.B. Cohen. 1984. A nitrogen budget for the Gulf of Maine and Georges Bank. *Bio. Ocean.* 3: 203-221.
- Shepherd, J. G. and D. H. Cushing. 1980. A mechanism for density-dependent survival of larval fish as a basis of a stock-recruitment relationship. *J. Cons. Int. Explor. Mer* 39: 160-167.

Sherman, K., W. Smith, W. Morse, M. Berman, J. Green, and L. Ejsymont. 1984. Spawning strategies of fishes in relation to circulation, phytoplankton production, and pulses in zooplankton off the northeastern United States. *Mar. Ecol. Prog. Ser.* 18: 1-19.

Sissenwine, M. P. 1984. Why do fish populations vary? In: R. May (ed), *Workshop on Exploration of Marine Communities*. Springer-Verlag, Berlin. p. 59-94.

Sissenwine, M.P. and E.B. Cohen. 1991. Resource productivity and fisheries management of the northeast shelf ecosystem. In: K. Sherman, L.M. Alexander, and B.D. Gold (eds.), "Food chains, yields, models, and management of large marine ecosystems". AAAS Selected Symp. 99 Westian Press, Boulder, CO, pp. 107-123.

Smith, P.C. 1983. The mean and seasonal circulation off southwest Nova Scotia. *J. Phys. Oceanogr.* 13: 1034-1054.

Smith, W. G., P. Berrien, D. G. McMillan, and A. Wells. 1981. The distribution, abundance and production of Atlantic cod and haddock off northeastern United States in 1978-79 and 1979-80. *ICES C.M.* 1981/G:52. 16 p.

Smith, W. 1983. Temporal and spatial shifts in spawning of selected fish and invertebrate species in the Georges Bank region. NOAA/NMFS Laboratory Ref. SHL Report 83-08. pp.22.

Steele, J.H. and M.M. Mullin. 1977. Zooplankton dynamics. In "The Sea" E.D. Goldberg (ed.) 6: 857-890

Stephenson, R.L. and I. Kornfield. 1990. Reappearance of spawning herring (*Clupea harengus harengus*) on Georges Bank: population resurgence not recolonization. *Can. J. fish. Aquat. Sci.* 47: 1060-1064.

Sullivan, B.K. in press. How does water column structure influence copepod populations in coastal marine systems? *Bull. Mar. Sci.*

Sundby, S. and P. Fossum. 1989. Feeding conditions of north-east Arctic (Arcto-Norwegian) cod larvae compared to the Rothschild- Osborn theory on small-scale turbulence and plankton contact rates. *ICES C.M.* 1989/G:19, 9pp.

Talley, L.D. and M. E. Raymer. 1982. Eighteen degree water variability. *J. Mar. Res.* 40: 757-775.

Taylor, P.R. 1991. Modeling Projects Initiated. *GLOBEC NEWS* 1(1): 3, 5, 6.

Thayer, G.W., J.J. Govoni, and D.W. Connaly. 1983. Stable carbon isotope ratios of the planktonic food web in the northern Gulf of Mexico. *Bull. Mar. Sci.* 33: 247-256.

Townsend, D.W., R.L. Radtke, M.A. Morrison, and S.D. Folsom. 1989. Recruitment implications of larval herring overwintering distributions in the Gulf of Maine, inferred using a new otolith technique. *Mar. Ecol. Prog. Ser.* 55: 1-13.

Walford, L. A. 1938. Effects of currents on distribution and survival of the eggs and larvae of haddock (*Melanogrammus aeglefinus*) on Georges Bank. *Fish. Bull., U. S.* 49: 1-73.

Walker, G.T. 1924. Correlations in seasonal variations in weather, IX. *Mem. Ind. Meteor. Dept.* 24: 275-332.

Walker, G.T., and E.W. Bliss. 1932. World weather. V. Mem. Roy. Meteor. Soc. 4: 53-84.

Wallace, J.M. and D.S. Gutzler. 1981. Teleconnections in the geopotential height field during the Northern Hemisphere winter. Mon. Weather Rev. 109: 784-812.

Walsh, J.J., T.E. Whitledge, J.E. O'Reilly, W.H. Phoel, and A.F. Draxler. 1987. In: R.H. Backus (ed), Georges Bank, MIT Press, Cambridge, Massachusetts, p. 234-246.

Wang, S.Y. and W.B. Stickle. 1986. Changes in nucleic acid concentration and starvation in the blue crab Callinectes sapidus Rathbun. J. Crustacean Biology 6: 49-56.

Werner, E. E., and J. F. Gilliam. 1984. The ontogenetic niche and species interactions in size structured populations. Ann. Rev. Ecol. Syst. 15: 393-425.

Wiebe, P.H., C.H. Greene, T.K. Stanton, and J. Burczynski. 1990. Sound scattering by live zooplankton and micronekton: empirical studies with a dual-beam acoustic system. Jour. Acoust. Soc. Am. 88(5): 2346-2360.

Wise, J. P. 1958. The world's southernmost cod. J. Cons. int. Explor. Mer 23: 208-212.

Wroblewski, J. and J. Cheney. 1984. Ichthyoplankton associated with a warm core ring off the Scotian Shelf. Can. J. Fish. Aquat. Sci. 41: 294-303.