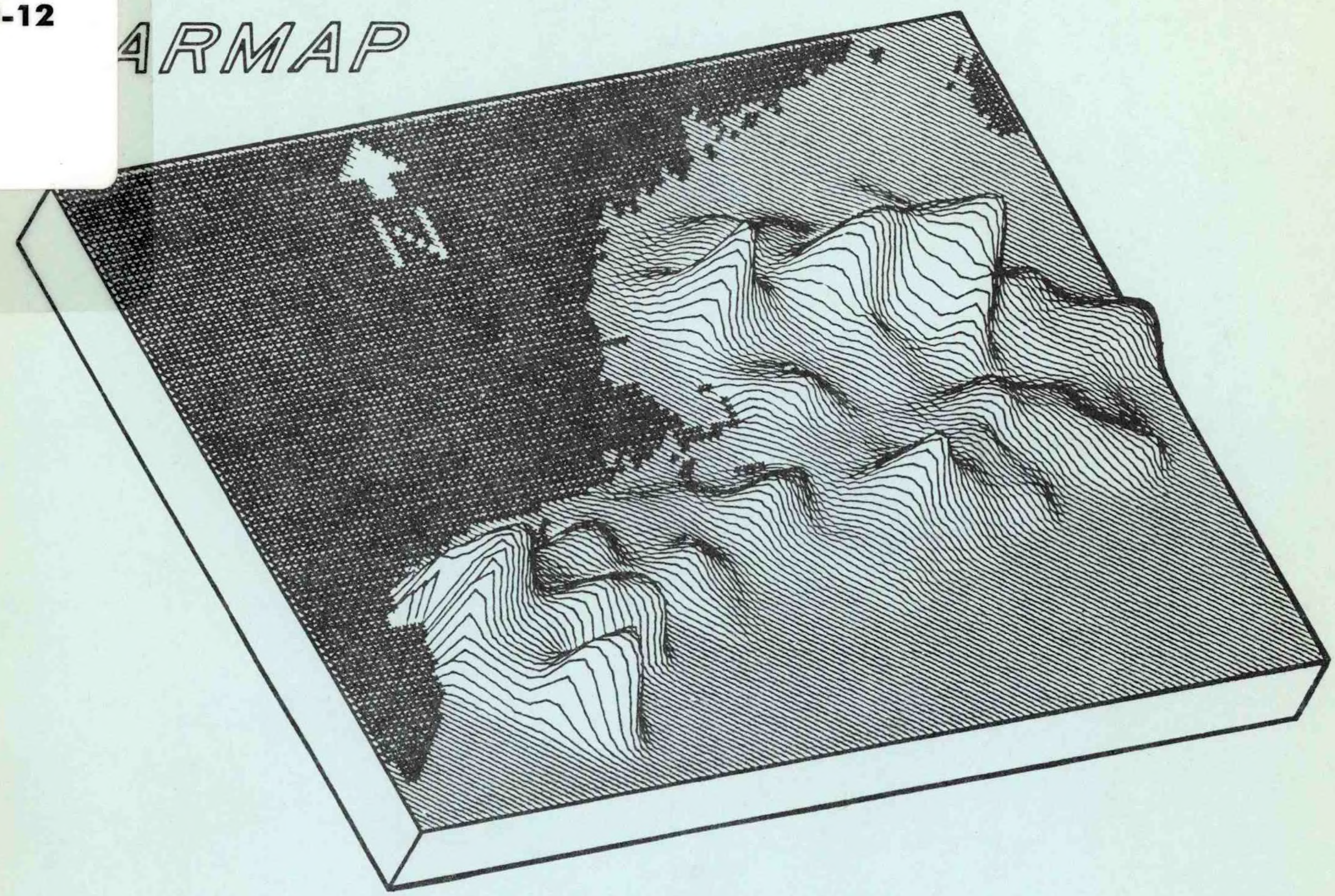
MARMAP



FISHERIES ECOSYSTEM STUDY NEWS

NATIONAL MARINE FISHERIES SERVICE
NORTHEAST FISHERIES CENTER

NARRAGANSETT LAB REF 79-12
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MARMAP

FISHERIES ECOSYSTEM STUDY

NEWS

National Marine Fisheries Service

Northeast Fisheries Center

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Cover: Relative abundance of zooplankton standing stock measured as ml/100 m^3 along the continental shelf off the U. S. east coast from the Gulf of Maine to Hudson Canyon, R/V Goerlitz 77-01 and R/V Delaware II 77-03, 3 Mar-8 April 1977.

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Northeast Fisheries Center

Kenneth Sherman

ITEM 1

OVERVIEW: MARMAP FISHERIES ECOSYSTEM STUDY

Northeast Fisheries Center

Following our initial NMFS Workshop on marine ecosystems in Seattle, it was agreed that we would maintain some level of interaction, through correspondence, within NMFS and with our colleagues in other facilities concerned with similar problems. With schedules and deadlines forever looming large on the horizon it's been difficult to look beyond the pressures of immediate crunches and provide timely summaries of our activities. We are in this report attempting to bring you up to date on our ecosystem research over the past year.

Research Philosophy

Recently the Center Directors of NMFS discussed the importance of developing an issue paper outlining the philosophy and approach of ecosystems studies in NMFS as applied to our fisheries management responsibilities. We have reviewed the initial draft and have sent our comments along to the Washington Office. From our point of view it is important that the paper focus on fisheries ecosystem studies in terms of: (1) why NMFS should be committed to long-term, broad-area, studies of the linkages among plankton, fish, benthos, and their environments to improve stock abundance forecasts; and (2) how NMFS is moving toward a better understanding of the marine ecosystem, and in particular testing specific hypotheses on how fish production is controlled by biotic and abiotic factors and influenced by man.

Fisheries Ecosystem Approach

Recognizing the broad scope of the problem at hand, much of our effort has been focused on those aspects of the problem for which we have significant data.

We are directing considerable effort to testing the long-standing hypothesis that year-class success is determined during the first year of life between the hatching of larvae and their survival to the juvenile stage. An understanding of the biological and physical system controlling larval survival will allow for significant improvements of long-term forecasts in fish-stock abundance. This is one of our most important "process-oriented" studies. It is being conducted within the broader matrix of the MARMAP Program of the Center. Several documents have been prepared describing the results of this effort including advances in the modelling of larval fish survival recently completed by J. E. Beyer and G. C. Laurence (1978), and a brief description of a recently completed multiship international "patch-study," with larval herring as a target species prepared by Greg Lough (attached).

We now have a reasonable level of ongoing MARMAP surveys (6x/yr) to provide basic plankton, fish, and environmental information for the area of the continental shelf extending from the Gulf of Maine to Cape Hatteras. Attempts are made to conduct at least four of these surveys (one each month) during spring in the Georges Bank-Southern New England areas when key species such as haddock, cod, yellowtail flounder and mackerel are spawning, to monitor egg and larval production and observe major changes in larval growth and mortality. Our research approach describing the utility of long-term monitoring surveys conducted in the MARMAP mode, and finer scale studies of important processes (e.g., recruitment, phytoplankton production, and predator-prey studies among principal fish and invertebrate species off the northeast coast) has been described in a number of key documents prepared by the staff during the past year. A listing of titles is attached. We will be happy to send copies of these papers; just call or drop us a post card listing the paper(s) of interest. Four of the papers dealing with the philosophy of our integrated "MARMAP-process-oriented matrix" are attached.

Development of Ecosystem Models

Prior to developing an ecosystem model the first task was to organize the available data on the ecosystem off the northeast coast into a systematic framework.

To get on with this job we first prepared an energy budget for Georges Bank. This was followed with critical reviews of the Laevastu-Favorite, Parrish, and Andersen-Ursin models of marine ecosystems. A summary of this effort through December 1978 has been prepared by members of the NEFC modelling group and is attached for your information.

In our view modelling is an essential tool for developing an understanding of how a marine ecosystem works, but the model itself should not become the principal goal in ecosystem studies. Further, no one model will answer all questions, nor will it be universally applicable to all ecosystems or suitable for all data bases. However there are certain basic similarities in all marine ecosystems and there are significant benefits to be derived from sharing ideas about basic processes and ways of measuring and simulating them.

During December a workshop on multispecies modelling was convened by Bill Bossert at Harvard University, sponsored by Harvard and the Northeast Regional Council. The models of Andersen-Ursin, and Laevastu-Favorite were discussed with respect to their potential as management tools. The workshop participants concluded that multispecies models could play an important role in fisheries management, but that neither of the models discussed was fully satisfactory for management purposes in their present mode. However, each model provided useful elements that will be seriously considered by the participants in the development of multispecies fishery models for use in the Northwest Atlantic.

Modelling will be one of the topics to be discussed in the upcoming ICES Symposium on the Early Life History of Fish 2-5 April 1979, Woods Hole. Dr. Ursin will be in attendance and we have taken this opportunity to invite him to spend the week following the Symposium with us expressly to discuss the philosophy of fish-ecosystem studies and to review the matrix of the ecosystems model being developed at NEFC that we call GEORGE (for Georges Bank). Following his stay in Woods Hole, Dr. Ursin will be spending about 30 days in Seattle working with Taivo and Felix on DYNUMES.

An outline of the development of our multispecies model of fish production is included as a major briefing item. Your comments on our approach are welcome.

K. Sherman
21 February 1979

Status Report on Development of a Multispecies
Model of Fish Production

M. Grosslein, W. Hahm, M. Sissenwine,

E. Henderson, and E. Cohen

ITEM 2

Status Report on Development of a Multispecies Model of Fish Production

by

M. Grosslein, W. Hahm, M. Sissenwine, E. Henderson, and E. Cohen
Northeast Fisheries Center
Woods Hole, Massachusetts 02543

Introduction

The Northeast Fisheries Center (NEFC) research program has emphasized multispecies studies since its inception. Broad scale trawl surveys of the entire nektonic community of the region have been conducted since 1963. The benthic community of the region has also been studied during this period. The research program of the center has now evolved into a comprehensive program of ecosystem study including ongoing broad scale MARMAP surveys of plankton, nekton and environmental data. The Center has collected one of the most extensive data bases on the feeding habits of adult fish that exist anywhere in the world and similar studies are now underway for larval fish. These studies are augmented by special process-oriented studies such as the experimental work on fish larvae survival conducted at our Narragansett Laboratory and the multi-ship and multi-national larval herring patch study (of the biotic and abiotic factors controlling survival) conducted in the autumn of 1979.

Our understanding of the ecosystem and the associated data base has now evolved to the stage where a multispecies model is needed to focus future laboratory and field work and efforts to formulate hypothesis on the functioning of the system. It was decided that the model should emphasize fish production because our data base is strongest here and the model results might have immediate relevance to fisheries management.

As background to the development of a multispecies model, the NEFC modeling group reviewed several models with emphasis on the Bulk-Biomass and Dynumes models by Laevastu and Favorite(1978), and the North Sea model of Anderson and Ursin (1977), which are the principal models designed to simulate dynamics of ecosystems with a focus on fish populations. The review of these models culminated in a two-day workshop at Harvard in December under the sponsorship of the New England Regional Fishery Management Council, Northeast Fisheries Center, and Harvard University. The general characteristics of the models were compared and their advantages and disadvantages were reviewed with respect to validity and predictive power, input data required, cost and ease of use, nature of assumptions and clarity of descriptions of biological processes, etc. The Bulk-Biomass model is a predator controlled (food unlimited) deterministic simulation procedure for estimating biomass changes within homogeneous geographic-depth strata; it does not allow for realistic recruitment functions nor recipient-donor interactions. The Dynumes model is a much more comprehensive model using time-dependent processes which allows for food-limited effects and presumably realistic (though not yet defined) recruitment functions, and interchange of energy among small subdivisions (1^0 squares) in relation to the velocity field of ocean currents and other environmental variables characteristic of the Gulf of Alaska region. Dynumes requires biomass data on all components and their interactions with biotic and abiotic factors within each square, and the data requirements are prodigious. The Anderson and Ursin(A-U) model is also a comprehensive model using differential equations to describe virtually all the basic biological and physical processes and their interactions which are known to exist in the marine ecosystem - the processes in general are realistic and clearly defined and documented but the data requirements are enormous. Both the Dynumes and A-U models are not suitable to be run in their entirety simply because much of the input data is not available (particularly prey-predator interactions) and because runs are so expensive. More important, the behavioral properties of these huge models have not yet been adequately evaluated.

There is a clear need to simplify and scale down the complexity and size of the models and at the same time utilize more empirical information on predator-prey interactions for more realistic simulation of multispecies interactions, and to use stochastic recruitment functions to describe the effects of variable recruitments. It was decided that the effects of circulation on organic production would not be emphasized in our model (like they are in Dynumes) because circulation dynamics of the New England shelf are not well known. The NEFC modeling group learned a great deal by reviewing these models. We will draw on the attributes of both models in the forumulation of our own. It is important to recognize that one of the major benefits from modeling is the greater awareness of functioning of a system that results from being forced to think about the system logically and quantitatively during the construction of the model. Thus, while it is important to learn from the reivew of models constructed by others, it is equally as important to learn from difficulties encountered and errors made in the construction of our own model.. The NEFC model will be tailored specifically to the available data base and designed initially for efficient simulation of effects of variations in recruitment, prey-predator interactions and fishing strategies. The model will have general applicability to the entire area covered by our MARMAP program. We have called it GEORGE because the first runs will focus on Georges Bank where we have the best data.

The initial objective of GEORGE is to investigate the influence of prey-predator interactions on the fluctuations in finfish populations under various harvest strategies assuming realistic recruitment patterns. The model is intended to aid in the synthesis and analysis of the existing biological and ecnomic data base, and to provide some guidance to the Fishery Management Councils regarding the possible long-term effects of various management strategies. In its initial form the model is not intended to simulate organic production of all the major components of the ecosystem because we do not yet have quantitative estimates of all components nor do we understand the linkages between them and the physical environment. Nevertheless we are developing GEORGE in a generalized and flexible format which can evolve and be expanded as we improve our understanding of productivity on the continental shelf.

Energy Budget for Georges Bank.

As a first step we developed a first approximation static energy budget for Georges Bank (Cohen, et al. 1978). Estimates of average annual biomass and production of phytoplankton, zooplankton, benthos, and fish were calculated and converted to Kcal/m^2/yr, and arrayed in the same manner as that for the North Sea after Crisp (1975). Production rates of all components appear higher than those reported for the North Sea and possible mechanisms for this higher productivity are postulated by Cohen and Wright (1978). This preliminary energy budget will be helpful in evaluating our general assumptions about partitioning energy among biological components and in placing reasonable limits on ranges of values used in simulations.

Energy Flow in the Nekton.

The next step was to examine patterns of energy flow through the nektonic community. The approach used was similar to that of Laevastu's bulk biomass model. Details of the method and the results are described in Grosslein, Langton, and Sissenwine 1978.

The annual rate of consumption and production of six exploited species of Georges Bank was estimated for the period 1963-1972. The six species considered included both pelagics and demersals. These are the species for which the most detailed biological information is available (including population size, age composition of the population, growth rates, fecundity). They are also the species which underwent the most significant fishery induced fluctuations in abundance.

For an individual fish, consumption was related to production by an energy balance equation: $\alpha C = G+S+Q$

where C is consumption, G is growth, S is reproductive energy, Q is metabolism, and α is the assimilation coefficient. Production equals S+G. Based on the energy balance equation, annual production and consumption rates per unit area were calculated for each species, age group, and year. The production to biomass ratios for the six species ranged from 0.29 to 0.63. Consumption to biomass ratios ranged from 3.2 to 4.9. By applying these ratios to other species for which less detailed biological information was available, estimates of production and consumption were derived for the entire nektonic community during the periods 1964-1966 and 1973-1975. The first period represents an era of developing foreign exploitation of the Georges Bank region. The second period follows nearly a decade of intense exploitation. The results are summarized in the attached table.

Both consumption and average biomass declined by about 42% from 1964-1966 to 1973-1975, but production declined only by 26%. The smaller reduction in production primarily reflects a decline in herring which have a low production to biomass ratio and an increase in the abundance of squid which are assumed to have a high production to biomass ratio. Both pelagic and demersal species declined in abundance. It is noteworthy, that during both periods, consumption by silver hake exceeds total production of the nektonic community. Extensive analysis of the gut contents of silver hake indicate that the species primarily feeds on other fish. This implies that silver hake must be feeding heavily on prerecruit fish (fish less than one year of age were not included in this analysis) which could make recruitment to finfish stocks strongly dependent on silver hake biomass.

GEORGES BANK CONSUMPTION AND PRODUCTION IN THOUSANDS OF KILOCALORIES

PER KILOMETER SQUARED.

Species Group	1964-1966			1973-1975		
	Biomass	Consumption	Production	Biomass	Consumption	Production
Cod	1890	5561	1071	920	3036	552
Haddock	4474	16117	2147	443	1418	182
Redfish	23	69	6	53	159	13
Silver hake	10052	48587	5830	7412	36318	4373
Red hake	1084	4444	499	801	3284	368
Pollock	278	1140	128	118	484	54
Yellowtail flounder	626	2874	399	481	2213	303
Other flounder	312	1279	144	239	980	110
Herring	19261	87521	5393	6201	28525	1798
Mackerel	1314	5410	446	2730	11739	928
Other finfish	1684	6904	775	2260	9266	1040
Illex	231	1617	247	1719	12033	2579
Loligo	63	441	95	273	1911	410
Total	41292	192064	17160	23650	111366	12710

Feeding Interactions

Various feeding functions are being investigated. For example, we may suppose that a fish feeds until it fulfills its daily feeding requirement. The size of this meal has been described as a power function of the predator's weight (Ration - αw^{b}, where w = weight, Andersen and Ursin, 1977) and an exponential function of temperature (Ration = R_{max} [exp(Q_{10} *temp)] Kremer and Nixon, 1978). Whether or not the predator consumes this entire meal depends on the availability of prey. The fraction of this meal that is actually consumed can be described for example by an Ivlev (1961) type function (FRAC = $1-e^{-kp}$). The species composition of this meal is complicated in a multispecies model. Feeding functions which take into account food preference (both size and food type) and digestion rates for various prey are being developed, based on the literature on feeding and digestion of fish and on extensive analysis of fish stomach contents by NEFC (Grosslein, et al. 1978; Edwards and Bowman 1978; Bowman, et al. 1976). Rich Langton and Ed Cohen will be working cooperatively with Jan Beyer in exploring the application of queuing theory in the simulation of feeding behavior, digestion, and estimation of daily rations.

Stochastic Simulation of Recruitment.

Recruitment is the dominant process determining biological productivity of Georges Bank fish stocks. Therefore, the recruitment process must be carefully considered in the development of an ecosystem simulation model of the region. Unfortunately, a clear understanding of the factors that control recruitment is lacking for Georges Bank and virtually all other ecosystems. Thus, in order to introduce a degree of realism into an evolving ecosystem simulation of Georges Bank, it has been decided that recruitment will be simulated stochastically.

An analysis of the available data describing recruitment for the Georges Bank finfish and squid community has been undertaken. Estimates of the strength of recruiting year classes and the size of their parent spawning stock have been collected for the following species: cod, haddock, silver hake, yellowtail flounder, pollock, red hake, long-finned squid, short-finned squid, herring, and mackerel. In most cases, about 10 observations of recruitment are included, but for some species as many as 30 observations are available. The frequency distribution of recruitment for each species has been compared to both a normal and a lognormal distribution. Only for haddock is the frequency distribution of recruitment significantly different from either the normal or lognormal distributions. Of course, because of the small number of observations available, the power of statistical "goodness of fit" tests was low.

The time series of recruitment observations for each species was also tested for independence (of sequential observations). Recruitment was positively autocorrelated for half of the species considered.

The relationship between spawning stock size and recruitment is now being investigated. Past experience indicates that a statistically significant relationship between these variables is unlikely for most species. In any case, subroutines are being written that will simulate recruitment stochastically based on distribution of past observations. These Monte Carlo simulations may be based on conditional probability density functions which incorporate the effects of sequential dependence between observations (autocorrelation), spawning stock size and or other factors. The subroutines will be incorporated into the Georges Bank ecosystem simulation model.

Thus, at this time, it is anticipated that recruitment of each species will be simulated without a detailed representation of its early life history. Nevertheless, prerecruit compartments will be included in the model in order to maintain accountability for all energy transfers. Energy will be transferred from the adult fish compartments of the model to the prerecruit compartment at the time of spawning. The growth rate of prerecruit fish and their pattern of mortality (a vector of relative mortality rates for each stage of the prerecruit phase) will be entered into the model exogenously as parameters. The mortality pattern will be adjusted by a variable multiplier so that the resultant frequency distribution of recruitment will correspond to the output of the stochastic recruitment simulation subroutine described above. The energy necessary to support growth of individuals of the prerecruit compartment will be transferred from likely prey compartments (primarily secondary carnivores). The energy flow from the prerecruit compartment as a result of mortality will be directed to predatory fish compartments (based on their feeding rate as determined by feeding functions), the detritus compartment and benthos compartments.

In future refined versions of the model, more detailed representation of prerecruit processes (including species interactions and negative feedback between prerecruit and recruit compartments) may be possible. Our understanding of the early life history of marine fish and the data base describing the corresponding processes is at present inadequate for the more refined simulation model.

General Description of the Model.

The general form of the model GEORGE is $\frac{dx}{dt} = A\,\underline{x} + \underline{f} + \underline{b}$, where $\underline{x}$ is the species biomass vector. This $\underline{x}$ vector includes the juvenile and adult classes of both predator and prey species. The community matrix, A, describes the transfers between predator-prey compartments (R. May, 1973). The $\underline{f}$ and $\underline{b}$ vectors represent the fish lost to fishermen, and the fish recruited to the population per time step dt, respectively. In GEORGE I, the linear version, A, $\underline{f}$, and $\underline{b}$ are constant coefficients. In GEORGE II, the deterministic nonlinear version, A, $\underline{f}$, and $\underline{b}$ are functions of the biomass vector and environmental signals such as time and temperature. In the stochastic, nonlinear models GEORGE III, a degree of random variability is placed around the estimates of A, $\underline{f}$, and $\underline{b}$. In all three models, provisions are made for variable time steps. In the later two versions, the A and $\underline{f}$ and $\underline{b}$ are re-estimated between each time step.

In the linear version, GEORGE I, the behavior of the model is determined solely by the A, $\underline{f}$ and $\underline{b}$ vectors. In the nonlinear versions, the behavior is determined by interaction of six subroutines (UPDATE, CATCH, FEED, DEMAND, GROW, COEFS) which operate in sequence to control the processes of recruitment, growth, and mortality. Various parts of these processes have been put in separate compartments (the six subroutines) to simplify program changes and to aid in the interpretation of simulation results. The six subroutines are themselves controlled by a seventh subroutine called INTERACT. For each time step INTERACT serves like a directory, sequentially calling on the other six subroutines.

The first subroutine, UPDATE, computes natural changes in the biomass vector, $\underline{x}$, that are the result of recruitment, natural mortality, and migration. The biomass vector includes age as well as species composition (i.e. the first n_1-elements of $\underline{x}$, represent the n-age classes of species-1, while the second n_2-elements represent the n_2-age classes of species-2, etc.). With every time step, UPDATE corrects $\underline{x}$ for changes due to natural mortality or migration into or out of the study area. UPDATE also "ages" the fish stocks, incrementing their passage from one age class to the next at appropriate times. The recruitment process (entry of age 1 individuals) in UPDATE will be simulated by a function based on the observed data. In short, UPDATE determines the current state of the vector $\underline{x}$ based on its state in the previous time interval and the rates of processes responsible for change during the current time step.

The second subroutine, CATCH, determines the amount of fish harvested per time step. This harvest will depend on the fishing strategies (e.g. species quotas) set by the user which take into account the availability of fish, by-catches, economic yield per unit effort, etc.

The next three subroutines, FEED, DEMAND, and GROW deal with growth. The changes in fish biomass are calculated as the difference between inputs and losses. For inputs, subroutine FEED computes prey consumption taking into account prey-predator interactions and fluctuations in abundance of prey as well as predators. Various feeding functions will be investigated as described above.

Given these inputs, the subroutine DEMAND computes the losses from the fish. This involves assimilation efficiencies and the basal and active respiratory losses. Assimilation is a function of gut efficiency and represents the fraction of the ingested material that is not defecated. Basal respiration is a physiological maintenance cost, and is a function of age and the temperature. Active respiration represents the losses incurred during swimming, feeding, and breeding activities.

The growth realized is the difference between the uptake simulated in FEED, and the digestive and respiratory losses computed in DEMAND - and is calculated in subroutine GROW. This surplus of material is then partitioned between somatic and reproductive tissue, and represents growth (There is always the possibility that negative growth, i.e. weight loss, may occur when energy requirements exceed inputs).

The sixth and last subroutine, COEFS recomputes the community matrix, A, (R. Levins, 1968) and stores it along with the $\underline{f}$ and $\underline{b}$ vectors for computation in the next time step. This community matrix is the result of the processes computed in the five previous subroutines. The utility of this subroutine will be discussed in a following section on sensitivity analysis.

Modeling options.

To run the model, the user first specifies the run parameters and program coding changes through the input/interactive portion of the program. The user then specifies the numbers of years to be simulated, as well as the desired time step within each year. To examine the results of the simulation the user can specify which populations should be included in the output tables. After glancing at these tables, the user then has the option of generating plots of populations of interest.

After examining the tables and graphs, the user has the option of stopping or continuing. Should the user decide to continue, there are the options, RESUME and BACKUP. RESUME allows the user to continue the simulation with or without changing the model's hypotheses in the interim. BACKUP allows the user to resimulate a portion of the previous run, under different hypotheses. This BACKUP option allows the user to test a series of policy scenarios, without having to resimulate the years prior to the target date.

Sensitivity Analysis or Models.

In single species models, stability and system behavior can be probed by the selective "tweaking" of coefficients. However, the relationship between input changes and output becomes increasingly clouded, with the increasing complexity of the model. This is especially difficult to assess at the multispecies level of complexity.

In the nonlinear models (using GEORGE II and GEORGE III) the user has the additional option of analyzing A, the community matrix and the f and b fishing and recruitment vectors. These components serve as "snapshots" of the dynamics of the system during a given timestep. The stability of the system and the trends of the predators and prey within the system can be studied in detail by inputting A, f and b into the linear model GEORGE I. This serves to expand and exaggerate the changes occurring in the nonlinear model, giving the user a feel of the ultimate direction of changes to be expected in the nonlinear runs.

As the coefficients are constant within a timestep and can be assumed (pretended) to be slowly changing, the traditional linear analysis methods can be applied. This would include the examination of the community matrix's eigenvalues (J. Poole, 1974). The stability and behavior of the system can be inferred from the real or imaginary eigenvalues, and the sign of these eigenvalues (Takahashi, Rabins, Auslander, 1972; E. Bender, 1978; H. Gold, 1977).

A Time Table.

The linear version, GEORGE I, was completed in August 1978, and we hope to have the deterministic, nonlinear version, GEORGE II running in 1979. From the biological standpoint the most troublesome aspect probably will be the formulation of feeding functions and prey-predator interactions, particularly those affecting juvenile stages of fishes. For the time being we will not attempt to deal with causality in the recruitment function, but simply use available time series as a statistical basis for generating realistic variability in recruitment up to the juvenile stage (age 1). Factors affecting fishing strategy will be handled by the Assessment Group. Other groups (New England Council staff, and Wm. Bossert, Harvard) are also involved in development of such models, and the council staff plans to complete their prototype model by early 1979, which will attempt to construct a stock rebuilding strategy such that the gross revenues are maximized.

In another year or so, it is anticipated that we will have sufficient new information on primary and secondary production (and also apex predators and birds) such that it will be possible to refine our energy budget calculations for the shelf. In addition, a benthic nutrient regenerative system model for the shelf is being developed by Wendell Hahm, a graduate student at URI Graduate School of Oceanography. Thus by mid-1980 we may be able to add the rest of the basic biological components to GEORGE, at least to a first approximation. It is still too early to predict how soon we may be able to link up organic production and shelf circulation in a quantitative way.

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Larval Herring Patch Study

R. G. Lough

ITEM 3

For: Coastal Oceanography and Climatology News R. G. Lough 1/8/79

Larval Herring Patch Study

An intensive international, multiship larval fish study was successfully completed this past fall in the Georges Bank-Nantucket Shoals area. Biologists and physical oceanographers from five countries (US, Canada, Federal Republic of Germany, Poland, and USSR) and eight vessels (ALBATROSS IV, ATLANTIS II, DAWSON, LADY HAMMOND, CANSO CONDOR, ANTON DOHRN, WIECZNO, and BELOGORSK) participated in the coordinated study which took place from October through mid-November. The main objective of the study was to identify and follow a mesoscale patch of recently hatched Atlantic sea herring larvae to provide short-term (hours and days) estimates of growth, mortality, and dispersal of a uniform-age larval population in relation to variation in their physical and biological environment. Such multidisciplinary, intensive patch studies are necessary to identify and measure the relative importance of the physical and biological mechanisms controlling the survival of larvae which is critical to an understanding of the recruitment process. More than two years of careful planning by scientists from the Northeast Fisheries Center (NMFS), Woods Hole, MA, and the Bedford Institute of Oceanography, Dartmouth, NS, were required to develop a strategy for focusing the multidisciplinary studies needed on all scales of sampling. Individual vessels were committed primarily to one of the following activities: (1) Mapping the patch with sufficient resolution to provide short-term population parameters and physical structure of the patch as it dispersed, (2) vertical and horizontal fine scale structure of predator-prey distributions, (3) fine scale primary and secondary productivity measurements, (4) physical processes responsible for the patch dissipation, and (5) broad scale, standard plankton-hydrography surveys of the entire region.

The initial focus for the study was on the northeast part of Georges Bank (Figure 1) which represents the principal historic spawning grounds for sea herring as well as many other valuable species. Three Canadian and three US moored current meter arrays were strategically placed in the intensive study area and a grid of 49 standard plankton stations was occupied at least once every 3-4 days. No herring larvae were found at this site, but a dense chaetognath patch was observed to reside in the southeast corner of this area for more than two weeks, just south of the Gulf of Maine-Georges Bank front, and data from the study appear adequate to explain its stability and retention on the Bank. It has long been suspected that survival of larvae and their associated zooplankton food must be related to their retention on the Bank where productivity is high. However, data on plankton dispersal in relation to water motion have largely been lacking until now. The joint experiment accomplished one of the most intensive studies to-date of the biological community in relation to the dynamics of the frontal water along the northeastern edge of Georges Bank, and it is expected we will be able to infer a good deal about the dispersal of herring larvae on eastern Georges from this patch study.

By the end of October a patch of recently hatched herring larvae was found just east of Cape Cod and mapped five times in five days between 3 and 8 November 1978 (Figure 2). Station spacing of the standard bongo hauls was between 1-2 n. mi. during patch mapping. The initial size of the patch when first surveyed was about 3x10 n. mi., as defined by concentrations of larvae greater than $15/m^2$, with the long axis of the patch oriented east-west. Larvae were mostly between 10 and 14 mm in length and believed to have hatched about 10 days earlier. The patch moved north along the 92 m depth contour at the rate of 1-2 mi. per day; however, the eastern part of the patch appeared to be pulled off into the deeper Great South Channel water, whereas the western part was retained near shore. Evidence for this shearing effect was supported by the drift of a number of drogues placed along the east-west axis of the patch. By the fourth patch mapping it was observed that another higher density patch of younger larvae had moved down from the northwest and merged with the original patch. The fifth patch mapping confirmed this notion as densities of larvae were observed to be on the order of 3 times that of the original patch and the larvae were significantly smaller in size. ALBATROSS IV returned to the patch study site again during 19-20 November and 12-14 December 1978 to conduct limited patch mapping studies. Although the densities of larvae were considerably lower, as expected, the patch could still be delimited at essentially the same location. It was oriented north-south along the near shore zone between the 18 and 92 m depth contours, and there was further evidence of larvae dispersing from the shoal waters into the Channel east of Nauset Harbor.

Undoubtedly there are many other facets to the study which will be forthcoming when all the data are analyzed, but what seems remarkable so far is the apparent cohesiveness and stability of the plankton patches observed over relatively long periods of time in coastal waters that are generally characterized by their intense variability!

R. Gregory Lough
National Marine Fisheries Service
Northeast Fisheries Center
Woods Hole, MA 02543
January 8, 1979

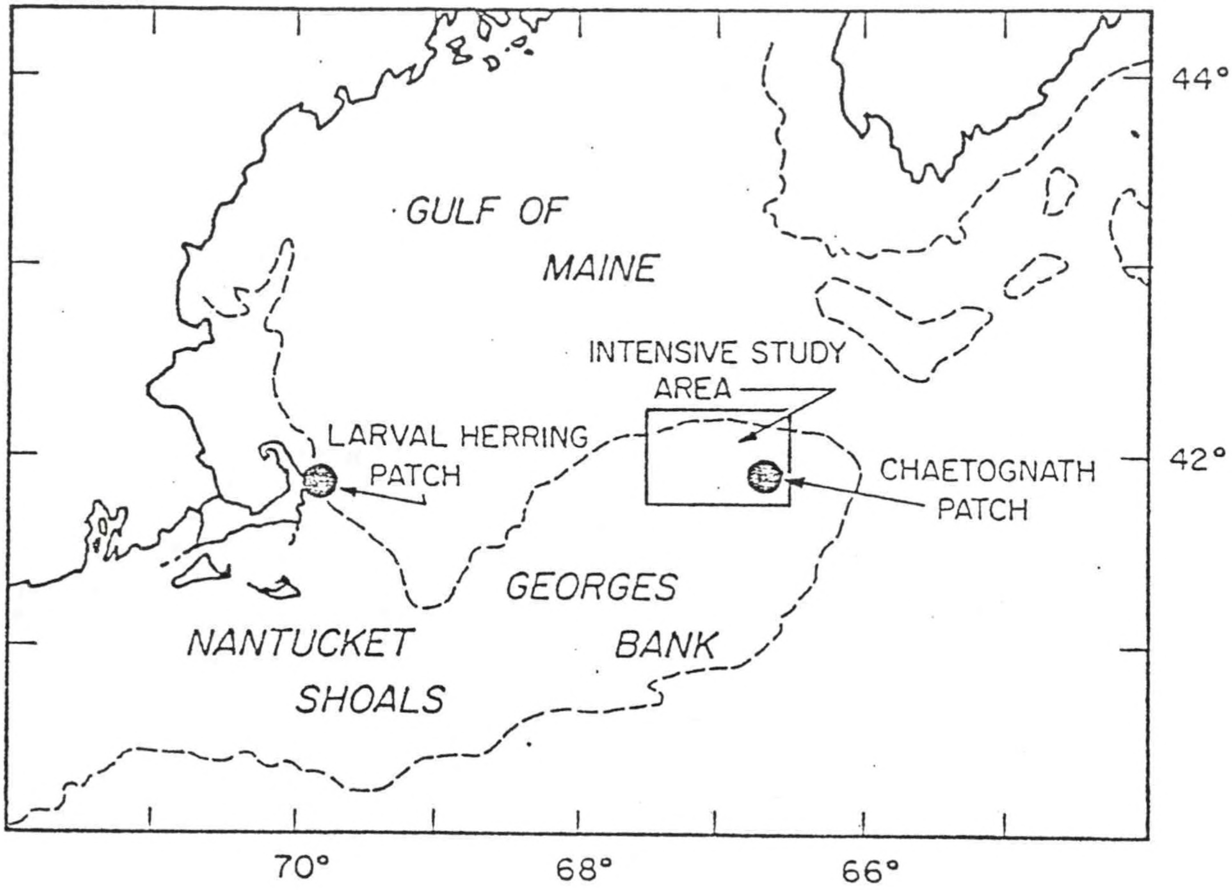

Figure 1. Chart of the Georges Bank-Nantucket Shoals area showing locations of the larval herring and chaetognath patches studied during the International Larval Herring Patch Study.

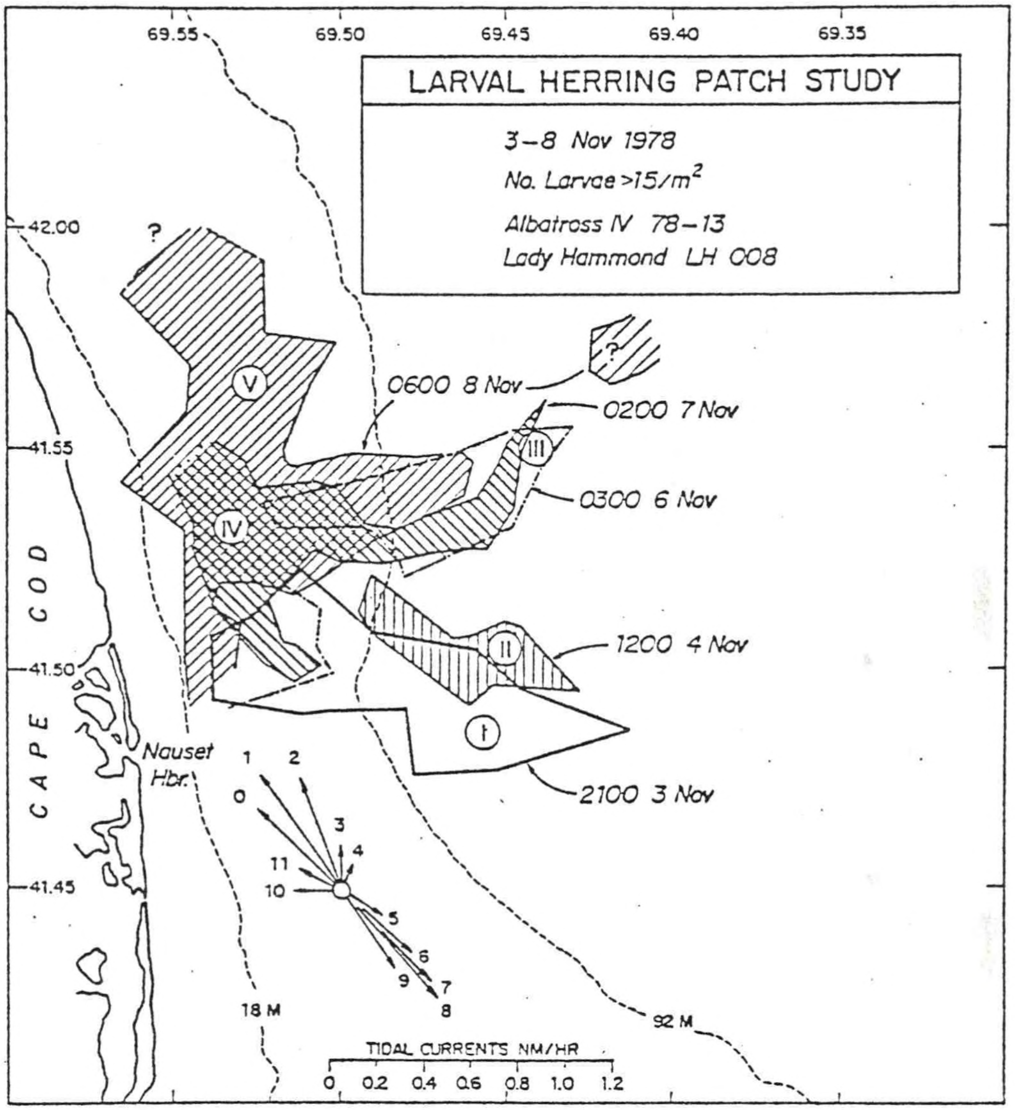

Figure 2. Delineation of the five larval herring patch mappings, 3-8 November 1978, by the vessels ALBATROSS IV and LADY HAMMOND. The patch contours represent areas where densities of larvae were greater than 15/m^2. Hourly directions and velocities of the tidal currents are shown by arrows. The figures at the arrow heads are the hours after the time of maximum flood at Pollock Rip Channel.

Listings of Recent Reports by Staff

ITEM 4

Larval Fish Physiology, Apex Predators, and Plankton Ecology Investigations
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Buckley, L. 1977. Biochemical changes during ontogenesis of the winter flounder (*Pseudopleuronectes americanus*) and the effect of starvation. ICES C.M.1977/L:29.

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List of presentations at scientific meetings and publications
during 1977 and 1978 Ichthyoplankton Investigation

In response to your recent request, I am submitting the following list of publications and scientific presentations by members of this investigation:

Papers at Scientific Meetings

Kendall, A. 1977. Annual Meeting of Ichthyologists and Herpetologists, Gainesville, Florida. Paper: "Relationships among American serranids".

Fahay, M. P. 1978. Annual Meeting of Ichthyologists and Herpetologists, Tempe. Arizona. Paper: "Distinguishing the postlarvae of two sympatric species of Merluccius in the western North Atlantic".

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Brainard, Edward C. II, and Steven R. Ramp 1979
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Trans. A.G.U. (EOS) 59(4) p. 302 (abstract only).
Paper given at AGU spring meeting, Miami, April 1978.

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The Marine Environment of the Georges Bank Region, February 1977.
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Trans., A.G.U. (EOS) 59 (4) p. 302 (abstract only).
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Current measurements in Northeast Channel
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Grosslein, M. D., R. W. Langton, and M. P. Sissenwine. 1978. Recent fluctuations in pelagic fish stocks of the Northwest Atlantic, Georges Bank Region, in relation to species interaction. ICES (International Council for the Exploration of the Sea) symposium on the biological basis of pelagic fish stock management. Contribution No. 25, 25 p. (To be published in symposium proceedings or it will be submitted elsewhere.)

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Recent Fluctuations in Pelagic Fish Stocks of the Northwest
Atlantic, Georges Bank Region, in Relationship to Species
Interactions. In: Symposium on the Biological Basis of
Pelagic Fish Stock Management. 25:ICES, Aberdeen. 47 pp.

M. D. Grosslein, R. W. Langton, and M. P. Sissenwine

ITEM 5

This paper not to be cited without prior reference to the authors.

International Council for
the Exploration of the Sea

Symposium on
the biological basis of
~~the~~ Pelagic Fish Stock Management
No. 25

Recent Fluctuations in Pelagic Fish Stocks of the Northwest Atlantic, Georges Bank Region, in Relation~~ship~~ to Species Interactions

by

M. D. Grosslein, R. W. Langton, and M. P. Sissenwine

National Marine Fisheries Service
Northeast Fisheries Center
Woods Hole Laboratory
Woods Hole, Massachusetts 02543, USA

CONTENTS

Part 1. INTRODUCTION

As a result of extremely heavy fishing during the 1960's and early 1970's the finfish and squid biomass[1] of the region from Cape Hatteras to the Gulf of Maine including Georges Bank (ICNAF Subareas 5 and 6, Figure 1) declined sharply. Trends in abundance of finfish and squid during this period, as reflected by research vessel otter trawl surveys, were reviewed by Clark and Brown (1977). They weighted the survey catch rate of each species to account for differences in catchability, and reported a steady decline in finfish and squid biomass, excluding the principal pelagic species (Atlantic herring and Atlantic mackerel)[2], from about 3.5 million tons[3] in 1964 to about 1.2 million tons in 1975. The biomass of herring and mackerel as indicated by virtual population analysis performed at the Northeast Fisheries Center (NEFC), declined from a peak abundance of 3.7 million tons in 1968 to about 1.4 million tons in 1975[4]. The total finfish and squid biomass in 1975 was substantially below the estimated level of biomass required to support the maximum sustainable yield of about 950,000 tons (Brown et al. 1976). The rate of decline was slowed by the imposition of ICNAF restrictions on total catch beginning in 1974. The total allowable catch (TAC) in 1974 was 924,000 tons followed by TACs of 850,000 and 650,000 tons in 1975 and 1976, respectively. Further reductions in total harvest occurred in 1977 (preliminary estimate of 436,000 tons) with extension of USA jurisdiction to 200 miles. Recent analyses indicate that groundfish stocks have begun to rebuild in 1976 and 1977 (Clark and Brown 1978).

A major part of the biomass decline observed during the period discussed above was due to the decline in herring stocks which began in the late 1960's. The other principal pelagic species, mackerel, increased in abundance with recruitment of the outstanding 1967 year class about the same time that the herring began its most rapid decline, but the mackerel stock also declined rapidly after 1972 (Anderson and Paciorkowski 1978). During the late 1960's, the biomass of the principal pelagics was more than double the biomass of the other finfish and squid, but by 1975 these two components of the total biomass were approximately equal in size.

Although heavy fishing clearly has been indicated as the principal cause of the general decline in fish biomass, the importance of species interactions cannot be discounted. The concept of management of whole ecosystems has only recently been generally accepted (Edwards 1976; Gulland 1977, 1978) but an awareness of the complexity of such an approach has been appreciated for some time (Borutskii 1960). If such a scheme is to be implemented it is essential to have a much

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[1] In this paper, as in Clark and Brown (1977), biomass includes all species of finfish and squid reported to ICNAF, excluding large pelagic species such as swordfish, tuna, and sharks other than dogfish. Also, inshore species such as American eel, white perch, and menhaden are excluded.

[2] In this paper herring and mackerel shall refer to Atlantic herring (Clupea harengus) and Atlantic mackerel (Scomber scombrus), which is consistent with the common names designated in American Fisheries Society, Special Pub. No. 6, 1970.

[3] Tons implies metric tons throughout this paper.

[4] The mackerel population discussed here ranges from Cape Hatteras to the Gulf of St. Lawrence. The actual biomass of herring and mackerel in ICNAF Subareas 5+6 is lower than indicated by an unknown proportion.

better understanding of species interactions in the marine ecosystem. Unfortunately studies on fish communities as integrated units are rare and the data requirements for developing predictive ecosystem models are prodigious. Nevertheless significant attempts have been made in recent years to evaluate complex biotic-abiotic systems, e.g. papers such as Anderson, et al. 1973, Lett et al. 1975, and Jones and Richards 1976. Perhaps the most complete case study of a marine ecosystem was presented at the 1975 ICES Symposium on changes in the North Sea Fish Stocks.

The purpose of this paper is to examine the available data on the Northwest Atlantic finfish community with emphasis on the Georges Bank region (ICNAF area 5Ze, Strata 13-25, Figure 1) and evaluate observed changes in biomass in relation to structure of the community and with respect to potential predator-prey interactions. Estimates of trends in production and total food consumption are made based on theoretical energy requirements of the finfish biomass. The evidence for changes in diet, species, and size composition is reviewed, and various hypotheses involving species interactions are evaluated in a qualitative sense.

Part 2. FOOD WEB

2.1 Materials and Methods.

The information on the predators and prey of the pelagic fishes discussed in this paper was compiled either from food habits studies conducted by the NEFC or from a review of the food habits literature. The data serves more as a qualitative guide to the known predators and prey of each fish species since extensive quantitative studies of the food habits of many of the pelagic fishes have not been conducted in the Northwest Atlantic.

Multispecies food habit studies have been conducted on demersal and pelagic fishes by the NEFC from 1963 to present. The collection of fish stomachs has been carried out by scientists and technicians on foreign and domestic vessels as an adjunct to the annual research vessel trawl surveys which were designed to provide quantitative inventories of fish biomass. These surveys have generally been conducted in the spring and autumn of each year and have proved invaluable in monitoring changes in the size and composition of the finfish biomass (Clark and Brown 1977). Details of the scheme of stratified random sampling used on the standardized otter trawl surveys may be found in Grosslein (1969, 1974).

The protocol for fish stomach sampling has been modified three times since 1963, resulting in three distinct food habit data bases. In the first instance, from 1963 through 1966, fish were selected at random from the catch and the stomach contents examined, and prey identified, on board ship. Data on the species of fish, predator length, and the occurrence of prey, together with the pertinent station data, were recorded for each fish. This procedure resulted in a qualitative evaluation of the type of prey consumed by 65 different species of fish. For the years 1969 through 1972 fish were again taken randomly from the catch and the stomachs excised aboard ship, but the contents were preserved in formalin for laboratory analysis. In the lab the prey was identified to the lowest possible taxon and the wet weight of each taxon determined. This procedure resulted in a quantitative estimate of the amount of a particular prey item in the stomach of the average size fish for 80 different species. Beginning in 1973 individual fish stomachs were collected from selected species of fish and the stomach contents preserved for laboratory analysis. This data was used to obtain both qualitative and quantitative food habits information for all size classes of the major groundfish and demersal-pelagic fishes in the Northwest Atlantic. The first phase of this sampling program, involving 17 species of fish, was completed in 1976 and the second phase, which will include data on 22 additional fish and squid species, will be completed in 1980. Data from all three of these data bases is used in this report and will be identified by period.

For the years 1969-1972 quantitative food habits information is available for many of the major groundfish species on Georges Bank (Bowman, Maurer, and Murphy 1976). Food habits information is also available for Atlantic mackerel and Atlantic herring for this same 1969-1972 period and/or from a study conducted in the spring of 1974 (Maurer 1976). These data were combined and the diet overlap calculated as a guide for evaluating species interaction. In order to do this the percent similarity between diets was calculated according to the formula of Whittaker and Fairbanks (1958) as follows:

$$P.S. = 100 - .5\,\Sigma\,\left|a-b\right|$$

or, more simply, by summing the smaller value, in this case the percent weight, for all prey shared by the two predators. Accordingly:

$$P.S. = \Sigma\ \min\ (a,b)$$

where:

P.S. = percent similarity
a = percent weight for a given prey group for predator A
b = percent weight for the same prey group for predator B

The values computed in this fashion may range from 0 to 100%. The closer a value is to 100 the more similar the diet of the two predators while a value of 0 implies that the food habits of the two fish are mutually exclusive.

To facilitate the comparison between predators the calculated values of percent similarity in diet were grouped into three categories (low, 0 <30; medium, 30 <60; and high 60-100) and these categories as well as the calculated values are shown in Figure 2.4.

2.2 Pelagic Fish-Food Habits.

The pelagic fish may conveniently be divided into three categories and the predator-prey interactions considered for each group individually.

Principal pelagics.

Principal pelagics, as defined by ICNAF and FAO, include the Atlantic herring, Clupea harengus, and Atlantic mackerel, Scomber scombrus. Both predators and prey of these two species have been summarized in Figures 2.1 and 2.2. The information on predators is based on food habits studies carried out by the NEFC (Maurer and Bowman 1975; unpublished data) and a review of the literature (see, for example, Bigelow and Schroeder 1953). The relative importance of the prey items for these two pelagic fishes is indicated in the figures by the boldness of the arrows and is based on food habits studies conducted by the NEFC (Maurer 1976; Bowman, Maurer, and Murphy 1976) which are summarized for Georges Bank in Table 2.1.

Herring are known to have contributed heavily to the diet of cod, spiny dogfish and silver hake in the Northwest Atlantic, at least for the years 1969-1972 (Maurer and Bowman 1975; Langton and Bowman 1978). Other known predators are pollock, red hake, haddock, white hake, squid, porbeagle, blue shark, thresher shark, shortfin mako, clearnose skate, little skate, goosefish, hickory shad, Atlantic salmon, and bluefin tuna, but for many of these predators the information is totally qualitative and the actual significance of herring as prey is not known.

Mackerel have been identified in the stomachs of a number of different fish. In the Northwest Atlantic, they are preyed on heavily by spiny dogfish, silver hake, white hake, and weakfish (Maurer and Bowman 1975). Mackerel also comprise part of the diet of Atlantic cod, red hake, white hake, squid, porbeagle, blue shark, thresher sharks, shortfin mako, sea lamprey, goosefish, striped bass, bluefin tuna, swordfish, and Atlantic bonito.

The prey of adult herring and mackerel is primarily planktonic (Table 2.1, Figures 2.1 and 2.2). The most important prey group was euphausiids, principally Meganyctiphanes norvegica, which accounted for more than 50% by weight, of the diet of the fish examined from Georges Bank for the years 1969-1972 and 1974.

Other pelagics.

Fish in the other pelagics category represent an assemblage of different taxonomic groups. They include such species as the alewife, American shad, round herring, blueback herring, redfish, black belly rosefish, butterfish, sand lance, long and shortfin squid, and a number of other species.

The food habits data on many of these Northwest Atlantic species is very sparse and little is known of the distribution of some of these pelagics. There are no commercial fisheries for a number of the species, so that detailed estimates of biomass are also unavailable. The American sand lance, longfin and shortfin squid are, however, of particular interest because they have all shown a relative increase in abundance in our otter trawl surveys in the last few years.

The sand lance is not usually considered a pelagic fish, but a recent examination of the food habits of sand lance from Stellwagen Bank in the Gulf of Maine (Meyer et al. 1978) confirmed that American sand lance is a plankton feeder, relying heavily on copepods, much like its European counterparts (see Reay 1970).

The importance of sand lance as a prey item of groundfish has also been documented (Scott 1968; Bowman and Langton 1978). Adult sand lance are restricted in their distribution by the bottom sediments, because of their burrowing behavior, but in the areas where they do occur they have been identified in the stomachs of spiny dogfish, little skate, winter skate, Atlantic cod, haddock, pollock, longhorn sculpin, and windowpane flounder. Since sand lance are plankton feeders they form a very short link in the food web between the zooplankton and groundfish.

Information on squid food habits is quite incomplete. Both longfin and shortfin squid are currently being collected by the NEFC for food habits analysis; it appears that they prey on euphausiids, fish and other squid, but no quantitative data are available yet. One detailed study on longfin squid in the Northwest Atlantic has, however, been conducted by Vovk (1972) in the years 1964 through 1969. Based both on frequency of occurrence and stomach contents volume, fish, squid, and euphausiids were, in decreasing order, the most important prey. The Atlantic herring was the fourth most important fish preyed upon. The significance of squid themselves as prey has also been summarized by Russian scientists (Zeuv and Nesis 1971). They concluded that squid is one of the most important elements of the oceanic food web being preyed on by whales, porpoises, fur seals, birds, and numerous species of fish.

Apex predators.

The impact of apex predators on pelagic fish is difficult to assess because, as with the other pelagic fishes, little is known of their distribution and there are no accurate biomass estimates for the species occurring in the Northwest Atlantic. For example, the NMFS Cooperative Shark Tagging Program has tagged a total of 16,556 sharks representing 32 species, from 1962 through 1976. As of January 1977 only 510 tags (3.08%) have been returned and, therefore, conclusions regarding biomass estimates and distribution are tentative at best.

Blue shark are rather ubiquitous and as a consequence the species composition of their diet would be expected to vary from location to location. Bigelow and Schroeder (1948) identified the blue shark's major prey as fish and cephalopods while in northern waters Bigelow and Schroeder (1953) report the presence of both Atlantic mackerel and Atlantic herring as well as spiny dogfish in the stomachs. More recently Stillwell (unpublished; see Casey and Hoenig 1977) has examined 76 blue shark stomachs from nearshore Long Island, NY. Bluefish accounted for almost 60% of the diet while an additional 20% of the diet was made up of other teleosts such as yellowtail flounder, Atlantic cod, and Atlantic herring. In contrast the diet of 17 blue sharks taken in offshore waters, in June 1976, was dominated by squid (62% of the stomach contents weight) while fish accounted for 34.5% of the diet.

Shortfin mako sharks have also been the subject of food habit studies by the NEFC (Stillwell, unpublished). Again, inshore sharks were examined and 93% of the diet was teleosts, primarily bluefish, tuna-like remains, and Atlantic cod. Bigelow and Schroeder (1948) state that this shark species preys on scombrids, clupeids, and other small fish.

Other sharks examined by Stillwell (unpublished) include 40 sandbar, eight dusky, and five smooth hammerheads. In all cases the diet was more than 75% teleost fish.

One of the other apex predators for which there is food habits information in the Northwest Atlantic is the swordfish, Xiphias gladius. Scott and Tibbo (1968) identified mackerel and herring together with several other species of fish and squid in the diet of the swordfish they examined. Rich (1947) had also found fish and squid in the diet of swordfish, and for Georges Bank he reports that the diet was comprised largely of mackerel, herring, squid, and silver hake. In the waters further north, off Cape Breton, Nova Scotia, Ovchinnikov (1970) reported that the principal food was schooled herring. In the stomach of the eight swordfish examined by scientists at the NEFC, silver hake and shortfin squid were of primary importance.

The food habits of tuna and lancetfish have also been investigated in the Northwest Atlantic (Matthews et al. 1977). As with the other apex predators fish and squid were the principal prey, with both clupeids and scombrids having been identified in the stomach contents.

2.3 Demersal Fish Food Habits

The food habits of 16 species of demersal fish collected from Georges Bank between 1969 and 1972 have been included in Table 2.1 and are further summarized in Figure 2.3. These 16 species were selected for inclusion in this report because they either form a significant part of the fish biomass and/or are known predators of herring or mackerel. The data are expressed as the percent weight of the total stomach contents for all the fish of each species examined.

An examination of the data in Table 2.1 shows that five major taxa (crustaceans, pisces, polychaetes, echinoderms, and mollusks) account for 80% of all the prey consumed. If sand and rock and unidentifiable animal remains are added to the five major taxa the total weight accounts for 94% of all the stomach contents. The other taxonomic categories may represent important prey for one or two species of fish but are not significant overall.

From Figure 2.3 it is clear that crustaceans are the most widely preyed upon category of animals which is not unexpected since they are represented by both pelagic and benthic groups.

Fish are second in importance as prey and form a major part of the diet of spiny dogfish, goosefish, silver hake, Atlantic cod, white hake, pollock, and redfish (Figure 2.3). Of the fish predators, clupeids occurred in the stomachs of Atlantic cod, spiny dogfish, red hake, and pollock but scombrids were only identified in the stomachs of goosefish and spiny dogfish (Table 2.1).

Mollusks are the last major taxa of interest because pelagic cephalopods were preyed on by six of the 16 predators: white hake, goosefish, spiny dogfish, silver hake, mackerel, and little skate. The significance of cephalopods in the nutrition of these predators is, however, difficult to accurately assess because it is common to find only the cephalopod beak in the stomach contents. If the beak is weighed as cephalopod remains it grossly underestimates the importance of cephalopods as prey.

2.4 Diet Similarity of Herring, Mackerel, and Other Species.

As a guide for evaluating the dietary interaction between the major pelagic and demersal fish species on Georges Bank the percent similarity between diets was calculated (Whittaker and Fairbanks 1958). The calculations were based on the prey listed in Table 2.1, for the years 1969-1972, and is arrayed in a trellis diagram in Figure 2.4. Calculations such as these are influenced by a number of biological and nonbiological factors so that it should be viewed only as a qualitative evaluation of potential competition or interaction. For this reason the percent similarity values were classed as low, medium, and high and this categorization was also included in the upper right half of Figure 2.4. From this array it can easily be seen that herring and mackerel have a high degree of diet overlap (71%) with each other. Herring has a medium level of diet overlap with pollock (57%), redfish (47%), and butterfish (31%). The percent similarity between herring and all other fish shown in Figure 2.4 is low, ranging from 0 to 18%. The mackerel has a diet which is quite similar to not only the herring (71%) but also to pollock (60%). Mackerel was found to have an intermediate level of diet similarity with redfish (47%), butterfish (38%), red hake (34%), and windowpane flounder (32%), while the overlap with all other species was low.

It is informative to examine the food habits data in Table 2.1 when using the similarity values as a means of singling out potential predator-prey interactions, to identify which prey are responsible for the various levels of diet overlap. For example, the relatively high degree of similarity in diet between herring and mackerel may be attributed to their reliance on euphausiids as prey. For both species of fish, euphausiids accounted for slightly more than 50% of the diet. This reliance on euphausiids is, however, unique to Georges Bank since Maurer (1976) has shown that the diet of mackerel and herring differs between geographic areas. Other prey which they also shared in common were chaetognaths, tunicates, copepods, and amphipods. Intermediate levels of diet similarity were found between Atlantic herring and three species of fish. In all cases, that is, for pollock, redfish, and butterfish, the major prey causing the similarity in diet was again euphausiids. Only for butterfish was a second prey group, chaetognaths, of any real significance. The high level of diet overlap between Atlantic mackerel and pollock may also be primarily attributed to euphausiids and secondly to prey such as caridean shrimp, mysids, pteropods, and tunicates. An intermediate degree of diet overlap was found between Atlantic mackerel, redfish, butterfish, red hake, and windowpane flounder. In the case of redfish and Atlantic mackerel, euphausiids were once again of primary importance. For the other three species of fish the overlap with the diet of Atlantic mackerel may be accounted for largely because of unidentifiable animal remains, although for red hake and windowpane flounder, caridean shrimp were of some significance. Apart from animal remains, the butterfish and Atlantic mackerel shared a number of different prey items, most all of which are pelagic invertebrates.

It is useful to expand the list of potential competitors to include other pelagic and demersal species, some of which have no directed fisheries, and to examine the relative importance of the major prey groups of herring and mackerel in the diets of these other species. In this case we have listed the major prey groups for herring and mackerel in terms of three levels on a percent wet-weight basis: trace (t) <1%, occasional (✓) 1-10%, and frequent (*) >10% (Table 2.2). Other pelagic species which have one or more "frequent" prey categories in common with herring and mackerel include the following: alewife, blueback, round herring, American shad, butterfish, sand lance, lanternfish, pearlsides, and argentine. Among these species the potential for competition with the principal pelagics might be greatest for alewife, blueback, shad, and sand lance based on seasonal and geographic distributions so far as they are known, and of these the river herring and sand lance probably would be most important from the standpoint of population size. With respect to "demersal" species in Table 2.2, all but the juvenile haddock have one "frequent" prey item in common with either herring and/or mackerel, and of these, silver hake is likely to be most important from the standpoint of both distribution and population size since it covers the entire region occupied by the principal pelagics and because it represents a much larger biomass than the other species. It might be noted that the juvenile haddock and cod probably represent fish which have taken up a demersal mode of life; the diets of younger haddock and cod which are still in midwater probably are more heavily dependent on copepods.

2.5 Larval Fish and Fish Egg Predation.

The above examination of predator-prey interactions has not particularly considered predation on fish eggs, fish larvae, and juvenile fish, and yet predation on these stages may have the primary influence on recruitment. Unfortunately, we have only limited data on the impact of predators on these earlier life stages. For example, predation on young fish has not yet been documented quantitatively. Smaller food items are digested more rapidly, because of the larger surface area to volume ratio, and as a consequence many of the fish we have identified in the fish stomachs are larger fish from the stomachs of the larger predators. In the case of both herring and mackerel, however, larval and postlarval fish were identified in the stomach contents in a limited study of food habits during spring 1974 (Maurer 1976). Larval sand lance showed the highest frequency of occurrence in herring, and red hake and sand lance larvae were most abundant in mackerel. One herring larvae observed in an adult herring was the only evidence of cannibalism, but mackerel had fish eggs in their guts which leaves open the possibility of cannabilism there. In this particular study which represented southern New England and Georges Bank for the most part, eggs and larvae of fishes represented 4.5% of the mackerel diet by weight as compared with only 0.4% for herring (Maurer 1976).

Predation of fish eggs has been adequately documented by the NEFC for only one species of fish. Analysis of haddock stomach contents, subsequent to the compilation of data summarized in Table 2.1, has revealed that haddock will prey heavily on herring eggs when available. In the autumn of 1970 on Georges Bank, haddock stomachs were found to be full of herring eggs, and when the weight of eggs was included in a summary food habits table they accounted for 28% of the diet (Langton and Bowman 1978).

In 1970 direct observations of herring egg beds on Georges Bank from a submarine, showed red hake actively feeding on eggs, and indicated that spiny dogfish, longhorn sculpins, and skates were more abundant over the egg bed than in adjacent areas, suggesting that these species probably were feeding on the eggs (Caddy et al. 1971). Fish eggs have been found in dogfish and sculpin stomachs in later studies therefore their role as a herring egg predator seems plausible. No eggs have been recorded in skate stomachs but that may be due to the manner in which skates grind up soft food items. In the 1970 study, cod stomachs were also examined and herring eggs were found in them as well (Caddy et al. 1971). Finally it should be noted that there are a number of invertebrate predators of herring eggs (e.g. moonsnails) but we have no measures of their abundance trends.

Part 3. CHANGES IN ABUNDANCE, COMPOSITION, DIET AND GROWTH PARAMETERS OF FINFISH BIOMASS

3.1 Relative Abundance and Species Composition.

Catch-per-haul data from research vessel trawl surveys conducted since 1963 have shown that, in addition to herring and mackerel, virtually all other species had also declined by the early 1970's; among commercial species only white hake and two species of squid showed significant trends of increasing abundance (Clark and Brown 1977). A comparison of average catch-per-haul of all finfish and squid on autumn trawl surveys from southern New England to the Gulf of Maine (sampling Strata 1-30 and 36-40, Figure 1) indicates a decline from 154 kg during the period 1963-1965 to 88 kg during 1972-1974 (Table 3.1). Since these are raw survey abundance indices unadjusted for catchability differences between species, they can only be used to indicate major shifts in relative composition of the biomass of species vulnerable to the survey trawl.

Obviously the raw weight index reflects mainly demersal species, and in fact about 80% of the overall decline in the survey index is represented by the reduction in indices for haddock and spiny dogfish alone. Nevertheless it is possible to get an approximate picture of the relative changes in biomass of demersal species providing that the same species are compared from one time to another. The known large changes in size of the herring and mackerel stocks appear negligible because catchability coefficients are extremely small for these species especially in autumn surveys and, except for squid, this is generally true for other pelagics as well. Major trends in abundance of most pelagics can be monitored with the survey indices in terms of numbers per haul.

The proportion of the survey catch represented by the "principal groundfish and flounder" group dropped from 50% in 1963-65 to 41% in 1972-74 with declines shown for every species, and the "other pelagics and other finfish" component decreased from 42 to 37% due to the drop in spiny dogfish and skates and rays which are the demersal species of this category. In contrast, squid increased from 0.5% to nearly 6% from 1963-1965 to 1972-1974, and "other groundfish" increased from 7% to 16% (Table 3.1). In the "other groundfish" category, goosefish and ocean pout showed significant declines, sculpins stayed about the same, and white hake and miscellaneous fishes increased.

In 1975-1977 the index for "principal groundfish and flounders" increased by more than a third with all but two of the principal groundfish species showing increases over the 1972-1974 period, with haddock showing the largest increase; slight increases were also observed for goosefish, ocean pout, and sculpins whereas white hake and miscellaneous fishes declined in the "other groundfish" category (Table 3.1). The index for skates and rays declined slightly in 1975-1977 but the index for spiny dogfish increased again while that for squid nearly doubled relative to 1972-1974 (Table 3.1).

The main point here is that there has been no drastic shift in species composition of the demersal finfish biomass, and no large buildup of other demersal finfish species to replace the principal groundfish and pelagic stocks. Instead, during the last three years the proportion of principal groundfish to other demersal species has begun to shift back toward the composition of the earlier period (1963-1965), with haddock and spiny dogfish showing the most rapid recovery on the relative scale (Table 3.1). The pollock index also increased substantially in the last period to a level more than twice that of the initial period, but this appears to be due to an anomalously high index of 13.2 in 1976. The 1975 and 1977 pollock indices were 1.4 and 6.5, respectively, which are more in line with a possible population change in one year. The increase in shortfin squid biomass in the last three years was substantial and has been documented (Clark and Brown 1978); squid is more pelagic than demersal although it is highly vulnerable to bottom trawls.

Turning now to pelagic species, in 1972-1974 the "other pelagics and other finfish" category showed apparent increases in the butterfish index and in the miscellaneous category which includes two species of river herring (alewife and blueback), round herring, shad, argentine, bluefish, and striped bass (Table 3.1). However recent assessments indicate declines in the river herring stocks (Street and Davis 1976) and in the butterfish population (Murawski and Waring, 1977). A current assessment of weakfish indicates that recruitment in recent years has been relatively strong but the survey indices show that the stock was even higher back in the middle 1960's (Murawski 1977). Also,there have been some relatively good year classes of striped bass and bluefish in recent years, particularly in the case of bluefish which expanded their range out onto the offshore banks including Georges Bank beginning about 1972, but there is some speculation this may have been partly due to a warming trend rather than population pressure to expand feeding grounds. In any case there does not appear to be a continuing trend of increasing recruitment. Finally,there is no evidence of significant change in the argentine stocks based on commercial landings or on surveys, and shad populations continue at a relatively low level based on spawning runs in the rivers of the northeastern United States.

Other pelagic species which occur in the southern part of the range of herring and mackerel are round herring and several species of anchovy which conceivably could be competitors of the principal pelagics during the winter and spring. There are no commercial fisheries for these species and therefore survey data are our only index of abundance. Their contribution to survey catches is extremely small on a weight basis, and abundance is better indicated in terms of numbers. Catch-per-haul indices for round herring increased steadily from 1968 to 1971 and then fluctuated widely from year to year up through 1977 (Table 3.2). The sampling variability of these abundance indices is quite high but there is no consistent trend throughout the decade, and if anything the average abundance of round herring was lower in the most recent years when herring and mackerel were also very scarce. There has been an increase in the anchovy abundance in the last half of the decade 1968-1977 (Table 3.2), but there is no evidence that the population has reached a size which is at all comparable to the previous level of the principal pelagics, and the populations are confined to the areas south of Cape Cod. In the same region the croaker population has increased substantially during the last half of the decade 1968-1977 (Table 3.2) but this is largely an inshore species which is present in the mid-Atlantic during warm months of the year when the herring and mackerel are mainly further to the north.

Another possible competitor is sand lance which has also shown evidence of an increase since 1968; trawl survey indices show large annual fluctuations but there is a definite indication of higher abundance at least since 1975 when the highest indices of the decade were recorded during both spring and fall surveys (Table 3.2). The low value for autumn 1976 appears to be an anomaly since abundance of sand lance larvae throughout the same survey region has been increasing substantially each year since 1974 (Smith and Sullivan 1978). However the actual size of the sand lance population is as yet unknown. Other offshore pelagics include lanternfish and pearlsides which show no evidence of major increases in population (Table 3.2).

To summarize, with respect to pelagics, it appears that there has been some increase in certain species since the decline in principal pelagics but there is no strong indication of a replacement of the herring and mackerel biomass because with the exception of sand lance and lanternfishes, the other species are largely confined to the mid-Atlantic region during warm months and/or are distributed chiefly in inshore waters.

3.2 Changes in Size Composition.

In conjunction with the declines in abundance of most species since the mid-1960's, there was a reduction in mean size of fish as would be expected under heavy exploitation. Between 1963-1965 and 1972-1974 mean lengths of most species dropped on the order of 5%-10% based on trawl survey catches over the entire survey region from Cape Hatteras to Nova Scotia (Edwards and Bowman 1978). However it is difficult to interpret mean lengths even for 3-year periods for individual species because of the large annual variability introduced by relative numbers of young fish taken on the surveys. A more general and stable index is simply the mean weight of all finfish species caught, and this includes all the miscellaneous species as well as the principal groundfish. The average weights (kg) per fish (exclusive of invertebrates, including squid) were as follows:

63	64	65	72	73	74	75	76	77
.47	.56	.50	.34	.35	.24	.30	.36	.44

The three year means were 0.51 kg, 0.31 kg, and 0.37 kg for 1963-1965, 1972-1974, and 1975-1977, respectively, which is consistent with the observed reductions in mean age by the early 1970's as a result of heavy fishing, and with the beginning increase in traditional stocks by the middle 1970's. Although some of the species which might be expected to replace the principal pelagics have low vulnerability to the survey trawl, it seems clear that there has not been a major shift to smaller size species in view of the increasing size observed in 1975-1977.

3.3 Changes in Growth and Reproduction.

One manifestation of inter- and intra-species competition for food is a change in growth rate. The Northeast Fisheries Center determines the age and length of thousands of fish of numerous species each year (46,000 individuals of 15 species in 1977, for example). The time series of data available for some of these species is adequate to detect major trends in growth. The evidence for a change in growth rate of six important species of Georges Bank fish is discussed briefly below.

It appears that the drastic decline in abundance of haddock was followed by an increase in growth rate. The mean weight of haddock ages 3-6 in the commercial catch for 1960-1976 is given in Table 3.3. The data clearly indicates that the mean weight of haddock of the ages most abundant in the commercial catch has increased, particularly since 1972 when the haddock population had declined to its lowest level and was beginning to recover. There is also some indication that growth of young haddock decreased in 1965-1967 when two very large year classes recruited to the fishery. Along with the change in growth of haddock, there is some evidence of maturation at a younger age in recent years. For 1968-1972, the percent mature at age 2 and 3 was 28% and 76%, respectively, while for 1973-1975, percent mature for these same ages was 34% and 92%, respectively (R. Livingstone, personal communication).

Anderson and Paciorkowski (1978) found no evidence of a change in growth rate of mackerel in recent years coinciding with increases or decreases in stock biomass, although there is evidence of an inverse relationship between growth rate and year-class size. MacKay (1973) found that the large 1959 and 1967 year classes had a slow growth rate relative to smaller year classes. Strong density dependent growth in the first year of life has also been reported for mackerel (P. F. Lett and W. H. Marshall, 1977. An interpretation of biological factors important in the management of the northwestern Atlantic mackerel stock. Unpublished report.).

A consistent increasing or decreasing trend in growth rate has not yet been established for Georges Bank herring. However cursory appraisal of age-length data since 1968 suggests that growth may have been somewhat greater than in earlier years, and there is evidence of increased growth rate of the strong 1970 year class (Dornheim 1975). Thus in the case of herring there may be a direct relationship between growth rate and year-class size, just the opposite of the relationship for mackerel. A younger age at first maturity was also noted for the 1970 year class of herring.

There is no noticeable difference in the mean length of Georges Bank yellowtail flounder ages 1-4 captured during autumn bottom trawl surveys from 1963-1974. There is less survey data available for older fish. Commercial length or weight at age data has not yet been adequately reviewed to conclude if the growth rate of older fish has changed over time.

Data on the mean length or weight of cod at age is only available for 1970-1976. Based on this limited time series, there does not appear to be any trend in growth rate.

The mean length at age of silver hake in the commercial catch for 1965-1976 is given in Table 3.4. It appears that the mean size of fish of a particular age has increased since the early 1970's. It is interesting that the size of the Georges Bank silver hake population was at its lowest level in the late 1960's, prior to the apparent change in growth rate. The population was substantially larger during the period when a change in growth is indicated. In the case of silver hake, the method of age determination is still evolving (ICNAF 1978) and therefore it is difficult to judge if the increase in mean size at age reflects an actual change in growth rate or differences in the method of age determinations.

In summary, only for haddock is there clear evidence of a change in growth rate (and probably age at maturity). The increase in growth rate of haddock may be related to density although it lags the decline in population size by several years. The pelagic species considered appear to have density dependent growth of outstanding year classes, although the actual relationship may be either inverse or direct.

3.4 Comparison of Diets Before and After Biomass Decline.

Methods.

Food-habit data were collected on fish from Georges Bank and the Gulf of Maine for the years 1963 through 1966 and again from 1973 through 1976. It was therefore possible to examine this time series for a shift in food habits during the 10-year interval. Bias due to size-specific diet differences was avoided because the data were selected so that the same size fish were compared in the two periods. The actual number of fish examined may differ between the two data bases, however, the length-frequency plots were very similar, within the length ranges selected, and the mean lengths of each predator species are within several centimeters for both periods.

Before a direct comparison can be made between the two time periods it is necessary to realize that there are some differences which are not necessarily biological and might have resulted simply from the methods of analysis. The older data series (1963-1966) was a qualitative evaluation of food habits based on shipboard identification of prey, while the newer series (1973-1976) was the result of a quantitative laboratory-based analytical scheme. The data are expressed as the percent occurrence of prey because of the analytical methods used in the 1963-1966 time period.

The methods of analysis are also reflected in several other aspects of the data. First, the percent of empty stomachs is consistently higher in the older series. This may have resulted from working on board ship and making a somewhat cursory examination of the stomachs, and therefore the number of empty stomachs may reflect a difference in interpretation and consequent oversimplification of the results. Secondly, in the 1973-1976 data base it would appear that there were more prey items per stomach since the frequency of occurrence values are usually higher. This is a direct result of the laboratory analysis where every identifiable prey item in a food bolus was noted. In contrast, on board ship the major prey was identified and the secondary prey might have easily been overlooked. Bearing in mind these constraints the data still serves as a useful indicator of any major shifts in diet by the various species of groundfish.

Georges Bank comparisons.

On Georges Bank the food habits of five demersal species have been documented for the 10-year interval. In general the food habits of all five species have remained reasonably stable although there are some differences that are revealed in a close examination of the food habits of each species.

The composition of the diet of little skate from Georges Bank is reasonably similar for the two time periods (Table 3.5). Overall, crustaceans were the most frequently occurring prey and within the crustacea the general pattern of predation was similar in the older and newer data series. Polychaetes were the second most important prey followed by mollusks and fish, which occurred in at least 5% of the stomachs examined. Most of the pisces prey was not identified but some pelagic fish were found in the little skate stomachs. In 1963-1966 clupeids accounted for a small part of the diet and in 1973-1976 stromateids, or butterfish, were preyed on, while sand lance were consistently found in the diet during both periods.

Silver hake are fish and crustacean predators and the changes in diet on Georges Bank over 10 years are very minor (Table 3.5). The same crustaceans were preyed on in both periods but it may be significant that euphausiids decreased in occurrence in the stomachs examined from 1973-1976 while the other pelagic crustaceans like the Crangonidae, Pandalidae, and more benthic amphipods became more prevalent. Cephalopods also occurred more frequently in the newer series which might reflect an increased availability of this prey, although they were certainly never important prey. Among the pisces prey the occurrence of scombrids in the diet in the years 1973-1976 is important but unfortunately comparative data is not available because none of the fish remains were identified in the older data base.

Atlantic cod, like silver hake on Georges Bank, prey heavily on crustaceans and fish but they are also more of a benthic predator, preying on polychaetes, mollusks, and echinoderms (Table 3.5) Virtually every taxa of crustacean listed was preyed on during both periods although there is a noticeable absence of Crangonidae from the 1963-1966 series. As with silver hake, cephalopod remains were not noted in the stomachs in the older data series although they were not very frequently occurring prey from 1973-1976. Atlantic cod are the most important clupeid predator as herring remains were consistently found in the stomach contents while in the 1969-1972 data base clupeids accounted for 30.2% of the diet by weight (Table 2.1).

Haddock have primarily benthic habits (Table 3.5) and prey on crustaceans, polychaetes, echinoderms, and mollusks. There are few obvious differences in diet between data bases. Although the actual occurrence values might differ, haddock have preyed on animals occurring in almost every one of the benthic taxa listed during both time periods. Fish rarely contributed to the diet, but in at least one instance clupeids were preyed on during the years 1963-1966.

Yellowtail flounder are also benthic predators and during both periods they relied heavily on crustaceans and polychaete worms (Table 3.5).

Gulf of Maine comparisons.

Food-habits data are available on six species of fish collected in the Gulf of Maine from 1963-1966 and 1973-1976 (Table 3.6). Of these six species, only the Atlantic cod was taken in the Gulf of Maine and on Georges Bank during both time periods. It is therefore possible to compare and contrast diets between geographic areas within data bases. Comparing the data in this manner eliminates the constraints existent when comparing the data over time and should reflect more accurately real geographical differences in the availability of specific types of prey.

For the years 1963-1966 crustaceans and mollusks were the predominant prey in both areas and occurred more frequently in the stomachs of Georges Bank cod while echinoderms and polychaetes were of secondary importance overall, but were slightly more significant as prey in the Gulf of Maine (Tables 3.5 and 3.6). From 1973-1976 crustaceans were again the predominant prey and also occurred more frequently in the stomachs of Atlantic cod on Georges Bank than in the diet of cod from the Gulf of Maine. Mollusks were, again, more significant on Georges Bank, however, the polychaete prey was also as important as the molluscan prey. Pisces were of about equal importance in both areas in both time periods but it is interesting to note that fish occurred less frequently in the cod diet from 1973-1976, regardless of the geographic area. Within these major taxa there are also some consistent differences between the two geographic areas. For example, within the Crustacea, the Cancridae and Paguridae were always more important prey on Georges Bank while euphausiids occurred more frequently in Atlantic cod stomachs from the Gulf of Maine. Within the Pisces, clupeids and redfish were only slightly, but consistently, more important as prey in the Gulf of Maine than on Georges Bank.

When comparing the diet of Atlantic cod over time within the Gulf of Maine, the pattern of predation changed little. Crustaceans and fish were the most important prey although mollusks, polychaetes, and echinoderms constituted part of the diet. Of primary importance here, is that independent of time, clupeids formed a substantial part of the identifiable pisces prey.

Two other gadids, pollock and white hake, were also collected in the Gulf of Maine and both of these species relied heavily on crustaceans and fish as prey and to a much lesser extent on polychaetes and mollusks (Table 3.6). The composition of the pollock's diet was reasonably constant over time. Euphausiids were the major crustacean prey and clupeids and gadids were the only identifiable fish remains. White hake also relied on euphausiids but were a more important predator of fish than were pollock, although the food-habits data are for the same average length fish. Gadids were the most frequently identified fish prey although clupeids were identified as prey in both time periods and scombrids occurred in the white hake diet in 1973-1976.

Gulf of Maine redfish are almost exclusively crustacean predators and euphausiids were the major prey in both 1963-1966 and 1973-1976.

The witch flounder collected in the Gulf of Maine were benthic predators relying most heavily on polychaete worms. The pattern of predation differed little between the 1963-1966 and 1973-1976 data series. The American plaice collected in the Gulf of Maine were, like the witch flounder, benthic predators. However, their most important prey was echinoderms rather than polychaetes. In both the old and new data series ophuroids were the most frequently occurring prey and the overall pattern of predation was very similar.

Part 4. PRODUCTION AND CONSUMPTION BY FINFISH AND SQUID ON GEORGES BANK

There is evidence that there is considerable diet overlap among many species on Georges Bank (Figure 2.3), and that the diet of a number of the principal groundfish species (e.g. cod, silver hake, pollock, white hake) includes a significant proportion of fish (Table 2.1). The first step toward evaluating the importance of species interactive effects (competitive or predator-prey) is to determine the amount of food consumed by each component of the nekton of Georges Bank. In order to evaluate the importance of predator-prey interactions between fish species, it is useful to know the production rate of the interacting species. Of course, man's utilization of fish populations (predation by the highest trophic level) is dependent on the production rate of the fish populations. Therefore, in this part of the paper, trends in production and consumption of the nekton of Georges Bank are considered.

Initially (Parts 4.1, 4.2) six species are considered for which the greatest amount of information is available. The results for these six species are then generalized to the entire community in Part 4.3.

4.1 Data Base and Methods.

The annual consumption and production of exploited populations of six species on Georges Bank were estimated for the period 1963-1972. During this period, population size and age composition varied widely in response to fishing pressure and unexplained variability in recruitment. The species considered were the yellowtail flounder (*Limanda ferruginea*), cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), silver hake (*Merluccius bilinearis*), mackerel (*Scomber* scombrus), and herring (*Clupea harengus*). With the exception of herring, some fishing mortality occurs at age 1. For Georges Bank herring, fishing mortality begins at age 2. This analysis applies to fish above the age of first exploitation. These species were selected primarily because estimates of stock size in numbers by age were available over a period of at least 10 years. The species considered (one flounder, two demersal roundfish, one semipelagic, and two pelagic species) are a reasonable cross section of the exploited finfish community of Georges Bank.

The haddock, yellowtail flounder, and silver hake populations considered in this paper are primarily located on Georges Bank during all seasons of the year. Most of the cod and herring stocks considered here are probably located on Georges Bank during the portion of the year when they are most productive, but they do migrate off Georges Bank during winter. The mackerel population ranges from Cape Hatteras to the Gulf of St. Lawrence with migrations across Georges Bank in spring and autumn. Thus only a minor portion of mackerel consumption and production can be attributed to Georges Bank.

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Consumption is related to production by the following energy balance equation:

$$\alpha C = G + S + Q \qquad (4.1)$$

where C is consumption, G is growth, S is reproductive material, Q is metabolism, and α is the assimilation coefficient. C, G, S, and Q are all expressed in units of energy (kilocalories, for example) per interval of time. Production (P) will be defined as G + S in this paper.

C, G, S, Q, and P were calculated for each age group of each species on a yearly basis. This was accomplished using stock size estimates in numbers at age calculated by virtual population analysis (VPA; see Ricker 1975 for a review of the method). VPAs were implemented by staff of the Woods Hole Laboratory of the Northeast Fisheries Center (NEFC), but not necessarily the authors of this paper, as part of an ongoing fishery management oriented stock assessment program. The actual VPA results used in this paper were current when the calculations discussed here were performed, but as is often the case with stock assessments, VPAs are reviewed frequently and subject to revision. The average number of fish of each age during each year was estimated by exponential interpolation:

$$\overline{N} = \frac{N_2 - N_1}{\text{Log}_e N_1 - \text{Log}_e N_2} \qquad (4.2)$$

where $\overline{N}$ is the average number of fish of a cohort during a year, N_1 is the number at the end of the year or beginning of the next year. For example, the average number of 4-year-old haddock in 1966 was estimated by applying equation 4.2 to the VPA estimate of the number of 4-year-old haddock at the beginning of 1966 (N_1) and the number of 5-year-olds at the beginning of 1967 (N_2). Thus, VPA results as recent as 1973 were required in order to estimate consumption and production through 1972. VPA results more recent than 1973 are particularly sensitive to errors in estimated terminal fishing mortality rate.

If $W_{i,j,k}$ is the size (in weight or energy units[4]) of fish of species i at age j during year k, then:

$$\Delta W_{i,j,k} = W_{i,j+1,k+1} - W_{i,j,k} \qquad (4.3)$$

$$\overline{W}_{i,j,k} = (W_{i,j+1,k+1} + W_{i,j,k})/2 \qquad (4.4)$$

where $\Delta W_{i,j,k}$ is the average growth and $\overline{W}_{i,j,k}$ is an estimate of average size corresponding to i,j,k. $G_{i,j,k}$ is estimated by $\Delta W_{i,j,k} \cdot \overline{N}_{i,j,k}$ and the total growth production of species i during year k is estimated by summing over j.

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[4] A gram wet weight is assumed equal to 1 kilocalorie unless indicated otherwise.

$\overline{W}_{i,j,k}$ is used to estimate $Q_{i,j,k}$ and $S_{i,j,k}$ as follows:

$$S_{i,j,k} = r_{i,j}\, p_{i,j}\, a_i\, \overline{W}_{i,j,k}^{\,b_i} \tag{4.5}$$

$$Q_{i,j,k} = c\, \overline{W}_{i,j,k}^{\,d} \tag{4.6}$$

where $r_{i,j}$ is the fraction of species i at age j which are females; p_{ij} is the fraction of females of species i at age j which are sexually mature; a_i and b_i are species-specific parameters relating production of reproductive material of females to body size; c and d are constants relating metabolic rate to body size. It is necessary to vary r with age (j) since males and females of some species suffer a different mortality rate, therefore their sex ratio changes with age. In fact all of the parameters probably vary by species, ages, and years, but the available information was inadequate to justify complicating the analysis further.

The size of each species at age is assumed constant over time ($W_{i,j,\cdot}$) except for haddock. Only for haddock was there clear evidence (from readily available data) of a trend in size over time. Even this trend was only obvious when data more recent than 1972 were considered. This analysis was not intended to determine if changes in growth rate have occurred, therefore the previous sentence should not be interpreted as implying that such changes do not occur. $W_{i,j,\cdot}$ for herring, cod, mackerel, silver hake, and yellowtail flounder are given in Table 4.1. For haddock, $W_{i,j,k}$ was calculated from values of length at age j during year k ($L_{i,j,k}$) using $W = .00813\, L^{3.0678}$ (S.H. Clark, NEFC, Woods Hole Laboratory, personal communication). A table of values of $L_{i,j,k}$ for haddock was constructed from the mean length of haddock in autumn bottom trawl surveys. These mean lengths were taken as the length of the cohort at the beginning of the next year. Gaps in the table (where catch of a particular age during a particular year was minimal) were filled in with calculated lengths from a von Bertalanffy length-age function fit to all of the available data from autumn bottom trawl surveys. The resulting values of $L_{i,j,k}$ for haddock are given in Table 4.2.

A sex ratio of 1:1 ($r_{i,j} = 0.5$) was assumed for all species except silver hake since the authors are not aware of any evidence to the contrary. The sex ratio of silver hake changes with age. A superficial review of bottom trawl survey data from 1973-1976 indicated the following values of $r_{i,j}$: 0.55, 0.55, 0.55, 0.55, 0.55, 0.85, and 1.0 for j = 1, 2, . . ., 6 and older. Male silver hake greater than six years old are rare.

Values of $p_{i,j}$ (a fraction of females of species i mature at age j) were estimated based on a superficial review of data on fish collected during bottom trawl surveys and from consideration of information available in the literature. Further analysis of this data is ongoing. The actual values used are reported in Table 4.3.

Inadequate data are generally available for estimating the energy content of reproductive material of mature fish as a function of weight [or for estimating a_i and b_i of Equation 4.5)]. Fecundity-length, age, or weight functions are often available, but the average size or energy value of eggs when spawned is usually not reported. The proportion of eggs reabsorbed is also unknown. Thus, for cod, herring, mackerel, and silver hake the energy value of reproductive material of females was assumed to be 20% of body size ($a_i = 0.2$, $b_i = 1.0$). Parrish (1975) reported that a value of 10% for both sexes combined was reasonable based on his review of the literature. Thus assuming a 1:1 sex ratio and most reproductive material produced by females, Parrish's review supports the assumption of 20%. Discussion in Jones and Johnston (1977) is also generally supportive of the assumption that the energy value of reproductive material is 20% of body size.

For yellowtail flounder, assumed values of a_i and b_i were based on functions relating fecundity to length, and fecundity to gonad weight (Howell and Kessler 1977). Accordingly, for yellowtail flounder, $a_i = 1.429 \times 10^{-3}$ and $b_i = 1.74$. A fecundity-weight equation calculated by R. Livingstone (NEFC, Woods Hole Laboratory, March 1977, unpublished) combined with the median size of eggs in the gonad just before spawning (based on Hodder 1963) was used to estimate $a_i = 0.5115$ and $b_i = 0.9071$ for haddock.

The parameters of Equation (4.6), which relates metabolic rate to body size, are based on a review of the literature by Geoffrey Laurence (NEFC, Narragansett Laboratory, March 1977, unpublished). Results for about 60 different marine fish species were considered. Oxygen consumption per gram wet weight per hour for each species was adjusted to 20°C (Winberg 1956). A power function was then fit to all the available data, and the parameters were adjusted to correspond to metabolism in kilocalories/hr instead of ml O_2/hr (assuming 4.77 calories per ml O_2). The result was similar to the function reported by Jones and Johnston (1977) for a resting fish at 20°C; $Q = 0.0157W^{0.8}$ based on Jones and Johnston's work, and $Q = 0.01375W^{0.79}$ based on Laurence's work. Active metabolism was assumed to be twice resting metabolism (Winberg 1956, Fry 1957). Parameter a of Equation (3.6) was further adjusted to correspond to 10°C (the approximate midpoint of the range of temperature on Georges Bank) and to correspond to annual energy utilization (kilocalories/year) resulting in $a = 10.04$ and $b = 0.79$. The assimilation coefficient, α, was assumed equal to 0.8 for all i, j, and k.

4.2 Estimates of Production and Consumption.

Using the method described above, production, consumption, the production to biomass ratio $((G_{i,j,k} + S_{i,j,k})/W_{i,j,k})$, the gross growth efficiency $((G_{i,j,k} + S_{i,j,k})/C_{i,j,k})$, and the consumption to biomass ratio were calculated for each species by age and year. Consumption and production are reported in thousands of kilocalories per kilometer squared[5]. The results summed over all

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[5] In order to calculate production and consumption per unit area, total production and consumption of each species was divided by the total area inhabited by the population considered. For mackerel, the area of the continental shelf to 200 meter depths between Cape Hatteras and the Gulf of St. Lawrence was considered (448,000 km^2). For yellowtail flounder, silver hake, and haddock, the area of Georges Bank was considered (52,479 km^2). Cod and herring production and consumption was attributed to Georges Bank and Nantucket Shoals (69,773 km^2).

ages for 1963-1972 are given in Tables 4.4-4.8. The average production and consumption by age over the period 1963-1972 is given in Tables 4.9-4.10. The calculated production to biomass ratio, gross growth efficiency (K_1), and consumption to biomass ratio by age only varies over time for haddock (since the growth rate of the other species is assumed constant over time in these calculations). These age-specific population characteristics are given in Tables 4.11-4.13 (average over 1963-1972 for haddock).

Of the six species considered, production and consumption by haddock declined most sharply (97%) during the 10-year period. Production and consumption by herring, silver hake, and cod also declined, although by 1972 all three species were showing signs of recovery. In the case of herring, the outstanding 1970 year class supported the fishery for several years in the early and mid-1970's until the autumn of 1977 when virtually no herring were found on Georges Bank by either commercial or research vessels. Mackerel production and consumption increased from 1963 to about 1970 then declined through the remainder of the period. The decline in mackerel abundance continued until at least 1977 (Anderson 1977). It may be noteworthy that periods of high productivity by herring and mackerel have not coincided during the interval for which data are available. During 1963-1972, only production and consumption of yellowtail flounder was nearly constant. Total production and consumption of the six species declined by about 60%. Calculated production to biomass ratios (P/B) ranged from 0.26 to 0.18, and calculated consumption to biomass ratios (C/B) ranged from 3.1 to 5.5. Jones and Richards'(1976) first approximation of C/B for adult fish is within the range reported in this paper. P/B, K_1 and C/B were most variable for haddock which is the only species for which annual variations in growth were considered. Annual variations in these characteristics for the other species reflect only changes in age composition. P/B, K_1 and C/B decrease with age.

4.3 A Comparison of Georges Bank Production and Consumption between 1964-1966 and 1973-1975.

Based on production to biomass ratios and consumption to biomass ratios calculated for six species (Part 4.2) and biomass estimates calculated by Clark and Brown (1977), it is possible to make a preliminary comparison of energy flow through the finfish and squid component of the Georges Bank ecosystem between 1964-1966 and 1973-1975.

The earlier period corresponds to the beginning of the buildup of fishing pressure on Georges Bank by other than North American fleets. The later period was after several years of intense fishing pressure when total biomass of the region had declined to its lowest level according to Clark and Brown (1978).

Methods.

The mean biomass of the six species considered in Part 4.2 (herring, mackerel, cod, haddock, silver hake, and yellowtail flounder) during each period was based on virtual population analysis. As already noted, biomass estimates by VPA during recent years are particularly sensitive to estimated terminal fishing mortality rates. Nevertheless, recent VPA biomass estimates are probably realistic since estimation of terminal fishing mortality rate or the strength of recruiting year classes are based on data from independent research vessel surveys or the catch rate of inshore juvenile fisheries (as is the case for herring).

The biomass of redfish (Sebastes marinus), red hake (Urophycis chuss), pollock (Pollachius virens), flounder (other than yellowtail), shortfinned squid (Illex illecebrosus), longfinned squid (Loligo pealei) and other finfish was estimated using calculations made by Clark and Brown (1977) although the specific results used here were not actually included in their published paper. All biomass estimates are expressed in kilocalories per kilometer squared. Where biomass estimates are for areas larger than (but including) Georges Bank, they were adjusted by multiplying by the ratio of the average survey catch rate on the Bank to the average survey catch rate for the larger area.

For the six species considered in Part 4.2, production and consumption as indicated in Tables 4.4-4.5 were averaged for 1964-1966. Production and consumption for 1973-1975 were calculated by applying the geometric average of P/B and C/B ratios of Tables 4.6 and 4.8. Production and consumption of redfish, pollock, other flounder, and other finfish were calculated by applying the geometric average P/B and C/B ratios for all six species and 10 years (0.46 and 4.1, respectively). P/B ratios of 0.25 and 1.5 were assumed for redfish and squid reflecting their very slow and very rapid growth, respectively. In the case of squid (with a 1 or 2 year life cycle) even a P/B ratio of 1.5 is probably conservative. C/B ratios of 3.0 and 7.0 were assumed for redfish and squid, respectively.

Results.

The calculated production and consumption by species group per unit area of Georges Bank are given in Table 4.14. Both consumption and average biomass declined by about 42% between 1964-1966 and 1973-1975, but production declined by only 26%. The small reduction in production reflects primarily a decline in herring which have a low P/B ratio and the increase in squid which are assumed to have a high P/B ratio. Both pelagic and demersal species declined unlike the situation in the North Sea where pelagic production was replaced by demersals.

Part 5. SUMMARY AND DISCUSSION

5.1 Biological Interactions Affecting Pelagic Stocks.

There have been several recent papers suggesting that predation and/or competition by mackerel are major factors controlling recruitment and biomass of herring where the populations coexist in the same region (Lett and Kohler 1976; Winters 1976). In our study we sought to determine the possible mode and extent of such interactions between these two species through food habits analysis. Unfortunately, the data are too sparse to provide a definitive measure of feeding interaction, particularly for possible predation on larval stages. So far, analysis of gut contents of adult herring and mackerel in the Georges Bank area provides no evidence that either species preys on the larvae of the other. This does not, of course, prove that such predation does not occur, since larvae of other species (mainly sand lance larvae) have been found in both herring and mackerel stomachs. Consideration of the distribution of larvae of both species through space and time in relation to seasonal migrations of adults, and size differentials of the young, leaves open the possibility of prey-predator interactions involving larval stages. For example, herring larvae occur inside the 100 m contour from Georges Bank to southern New England all during autumn, winter, and spring, and could be preyed upon by either adult mackerel (presumably in autumn before migration south toward the mid-Atlantic) or by young-of-the-year mackerel which generally move offshore in late autumn and would be large enough to prey on all sizes of herring larvae throughout the autumn and winter. The actual distribution of 0-group mackerel in their first winter is not well known in the Georges Bank area, and therefore the potential for predation on young mackerel is simply unknown. Mackerel spawn in the same areas in May and June as adult herring and the newly metamorphosed herring larvae or "0-group" herring could conceivably prey on mackerel eggs or larvae at that time; but here again distribution of 0-group herring on Georges Bank is not known. However, in view of the much slower growth and longer larval period of herring as compared with mackerel, the potential for mackerel predation on herring larvae is probably greater than the reverse.

The rapid decline in herring on Georges Bank in the late 1960's was coincident with the strong recruitment to the mackerel stocks but the relatively strong 1970 year class of herring occurred at about the peak mackerel biomass. Right now, both species are at a low level indicating that there are other factors than mackerel-herring predation that are influencing the biomass of these two species, most likely fishing pressure perhaps in combination with environmental factors.

The likelihood that predation or competition by other species has contributed to the decline in herring and mackerel does not seem very high. Most of the demersal finfish predators were declining at the same time, and other pelagic species which could be either predators or competitors were also declining, or if they increased did so only after the major decline in herring and mackerel had already occurred. Thus what changes in composition of the pelagic components may have occurred in the most recent years would seem more likely to have been a result, rather than a cause, of the herring-mackerel decline. And in general the evidence suggests that with the exception of significant increases in sand lance and squid, and the low level of herring and mackerel, the overall composition of the finfish community changed relatively little and the demersal components show signs of rapidly returning to a pattern similar to that observed before the decline.

Evidence has been presented that there has been a significant reduction in food consumption coincident with the decline in finfish biomass. Assuming that there had been no change in basic productivity during the period of the study this would imply that there was a substantial food surplus at the low point of the finfish biomass. There is some evidence for higher growth rates for some demersal and pelagic species and for earlier maturation (particularly haddock). However, in examining the data on the fish food habits after the 10-year time interval (Tables 3.5 and 3.6) it was obvious that there were no drastic shifts in diet. Possibly the most noticeable,and consistent, difference was the relatively small decrease in the importance of fish as prey for Atlantic cod and a corresponding upward shift in the occurrence of crustaceans in the diet. Daan (1973), in comparing the northern and southern North Sea cod, observed a similar shift in diet between crustaceans and fish and tentatively concluded that the preponderance of crustaceans in the diet of the southern area cod reflected suboptimal feeding conditions for the larger, normally piscivorous, fish. Since the finfish biomass had declined in the Northwest Atlantic in the latter, 1973-1976, period the situation may be parallel to the North Sea with resulting suboptimal feeding conditions. However, the shift in frequency of occurrence of prey was probably not significant enough and apparently was not reflected in a decreased growth rate which could be related to a change in the nutritional value of the diet. Of course, if the change was significant, a lower caloric value in the diet might simply be counteracted by larger meals, and if there was less predation on the benthos due to a reduced finfish biomass then this argument seems plausible but somewhat circular without data on gut contents weight.

Since the diets of similar size fish did not change drastically over time, despite a reduced finfish biomass and a potential surplus of energy, it's interesting to speculate on the usefulness of a food habits time series data when it's restricted to adult fishes. It may be that by the time fish reach their adult size the food habits are so restrictive that there is little likelihood of a change in diet without the complete removal of the normally recognized prey. It is possible that a food habit time series on the small, juvenile or even larval fish, might reveal more changes in diet or the potential for species interaction. Of course, as for the adults, food habits data needs to be considered in relation to other biological factors which might segregate juveniles and larvae through space and time. In any case it should be emphasized that, as yet there has been no consistent trend of increased recruitment of a number of species (e.g. gadoids whose larvae or juveniles depend upon primary carnivores which make up a significant part of herring and mackerel diet) comparable to that which has been observed in the North Sea (See Part 5.3). It is perhaps conceivable that sand lance have taken up the surplus since their larvae occur in the late winter and spring when cod and haddock larvae are produced. However, it is too early to tell whether such a shift has occurred and whether it will persist.

5.2 Environmental Factors.

The role of the physical environment in controlling fish production has largely been beyond the scope of this study. However, it may be noted that a number of authors have correlated fish catches with temperature in the Northwest Atlantic (Sissenwine 1974, Sutcliffe et al. 1977, Dow 1969, Loucks and Sutcliffe 1978). The actual mechanisms associated with temperature which presumably control recruitment have not actually been identified. Nevertheless the correlations are intriguing and warrant further evaluation.

Of particular interest here is the fact that, based on bottom temperatures, there has been a general warming trend in the Gulf of Maine and Georges Bank area since about 1967 (Davis 1977). Coincident with this trend, there has been a gradual shift toward a later spawning time for herring on Georges Bank (Lough 1976). It is not known how such a trend might affect survival of herring and mackerel eggs and larvae but clearly it is a factor which needs more study.

5.3 Comparison of Georges Bank to the North Sea.

In the North Sea, the decline in biomass of herring and mackerel during the 1960's was accompanied by an increase in biomass of certain other species, particularly the gadoids. Jones and Richards (1976) indicate that the decline in herring and mackerel biomass could have released enough food energy to support the increased biomass of gadoids. In the case of Georges Bank (1964-1966 vs. 1973-1975), the decline in herring and mackerel biomass was accompanied by a decline in almost all demersal species including cod, silver hake, and most notably haddock. Even so, the relative change in surplus food available (assume the rate of production by fish prey is unchanged) before and after the decline in biomass of both areas is similar. The total consumption of exploitable size fish of nine species considered by Jones and Richards for the North Sea decline by 33% between the early and late 1960's. Total exploitable size finfish and squid consumption on Georges Bank declined by 42% between 1964-1966 and 1973-1975.

The consumption per m^2 of Georges Bank appears higher than the North Sea: 192 vs 55 Kcalories/m^2 for the high biomass period and 111 vs 36 Kcalories/m^2 for the low biomass period. The difference in consumption between the two areas is actually smaller than these values indicate since the North Sea values only apply to nine species generally at an older age than for Georges Bank. Other finfish and squid account for 5% and 20% of the total Georges Bank consumption during the two periods, respectively. The North Sea values typically apply to fish age 2 and older whereas the Georges Bank values apply to age 1+ (except for herring). Nevertheless, it is likely that total consumption per unit area is higher on Georges Bank than in the North Sea. Of course, the area of the North Sea is greater than Georges Bank (570,000 km^2 vs 52,579 km^2).

Crisp (1975) estimated the production of North Sea pelagic and demersal fish species as 8.0 and 2.5 Kcalories/m^2 year, respectively. These estimates are based on fisheries production (by assuming exploitation rates). Georges Bank production of pelagics (herring, mackerel, and squid) was 6.2 and 5.7 Kcalories/m^2 year during periods of high and low biomass, respectively. The corresponding values for demersals were 11.0 and 7.0 Kcalories/m^2 year. Thus, the pelagic production of the two areas is similar, but the demersal production of Georges Bank is substantially higher than the North Sea.

Actually, the production estimates considered here are not strictly comparable. Crisp's (1975) estimates are based on fishery yield, therefore they represent growth and recruitment. The energy of recruits is actually a minimum estimate of growth production of prerecruits. It is not production of exploitable size fish. On the other hand, Crisp's estimates do not include production of reproductive material.

Based on the calculations in Part 4, the average recruitment to production (growth and reproduction) ratio (R/P) for 1963-1972 was 0.54, 0.08, 0.42, 0.17, 0.09, and 0.08 for herring, cod, mackerel, silver hake, yellowtail flounder, and haddock, respectively. Therefore, for species like herring and mackerel with high R/P ratios, recruitment is a significant force acting to increase the size of the population. It is interesting that the species with the highest R/P ratios are both pelagics and also have the two lowest P/B ratios of the six species considered. Of course, R/P depends on the designated age at recruitment for each species.

The average recruitment to biomass ratio (R/B) of the six species for 1963-1972 was 0.16, 0.05, 0.14, 0.10, 0.06, and 0.03, respectively (same order as above). Assuming that annual reproductive energy is 10% of the biomass for sexually mature fish (as was done for several species in this paper) R/B would have to be somewhat less than 10% for recruitment energy to balance reproductive energy (since not all individuals are mature). Thus, it is probably reasonable to compare Crisp's estimates of production to those calculated in this paper since recruitment and reproductive energy are similar in magnitude and approximately balance. The fact that recruitment and reproductive energy are similar in magnitude implies that the early life stages of fish consume much more energy than is contributed in the form of eggs.

In summary, the biomass and consumption of both pelagic and demersal species declined on Georges Bank (1964-1966 vs 1973-1975) while only the former declined in the North Sea (early and late 1960's). Production and consumption per unit area of Georges Bank appears to be higher than for the North Sea. This probably reflects higher production per unit area at all trophic levels.

5.4 Future Research

Throughout this paper we have summarized the available data on finfish biomass, food habits, and potential species interaction for many of the Northwest Atlantic fish. The result has been a discussion of the state of the art, to date, and it is now appropriate to include a brief outline of future research requirements that would in some cases quantify and in others simply refine our understanding of the marine ecosystem.

1) Food habits studies need to be expanded to consider all life stages of the fish under consideration. This includes not only an evaluation of predator and prey size but also the relation between food habits and the temporal and spatial distribution of the fish.

2) Extensive behavioral studies on selected "key predators" are needed to better understand the interrelationships that have developed between predator and

prey. This would include both field and laboratory observations in selected, representative areas that would be accessible on a year-round basis.

3) As a parallel to studies on key predators, key prey should also be studied. There are relatively few groups of animals that constitute the major components of the fishery forage base. These important benthic and planktonic prey may be identified from food habit studies and the distribution, abundance, and life history of these selected prey must be investigated over time.

4) Accurate field data is urgently needed on the rate of digestion and caloric value of prey if we are to obtain precise estimates of the daily ration that a given species and size of fish requires in nature. Studies on feeding chronology should be complemented by <u>in situ</u> behavioral observations and laboratory digestion rate and growth studies which are based on a specific predator's natural diet.

5) Estimates of population size and production and consumption rate of almost all species need to be improved. The need is particularly keen for species not traditionally the target of fisheries. Some of these species (squid, sand lance, and large pelagic sharks) potentially play an important role in energy flow of the ecosystem. Even for the traditionally exploited species, better information is needed on reproduction and metabolism.

5.5 Conclusions Regarding Pelagic Fish Stock Management.

In keeping with the purpose of this symposium, it is appropriate to comment on the relationship of this paper to the biological basis of pelagic fish stock management. For the Georges Bank area, a greater proportion of the total production of pelagic species (herring and mackerel) occurs as prerecruits (less than 1 or 2 years old) than occurs for prerecruits of demersal stocks. The recruitment to biomass ratio is higher for the pelagics than for the demersals. On the other hand, the production to biomass ratio and gross growth efficiency is lower for the pelagics than for the demersals.

Intuitively these differences might imply that pelagic stocks will react more quickly to environmental fluctuations, and possibly make them more susceptible to recruitment overfishing. Furthermore since the principal pelagics depend solely upon planktonic forms for food during adult as well as early life stages, their distribution might be expected to be more variable and over the long run they may be more sensitive to variations in primary and secondary production trends.

While there may be some basic difference in the energetics of pelagics relative to demersals, production by both components are related by feeding interations (either competition or predator-prey). However, it is still not possible to draw firm conclusions about direct or indirect relationships between pelagic and demersal productivity. Therefore, at our present level of understanding of marine ecosystems, there does not yet appear to be any unique biological basis for pelagic fish stock management.

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Table

2.1. Stomach contents of demersal fish that were collected on Georges Bank from 1969 through 1972. The data is expressed as a percent of the total stomach contents weight for each species.* The number of fish examined, the percent of empty stomachs, mean weight of prey per stomach and the mean predator length are included at the bottom of the table for each species of fish. Subtotals for the major taxa are offset to the left. (Data from Bowman, Maurer, and Murphy 1976).

Prey groups \ Predators	Spiny dogfish		Goosefish		Silver hake		Atlantic cod		White hake		Red hake		Atlantic mackerel[2]		Little skate		Atlantic herring[1]		Pollock		Redfish		Butterfish		Windowpane		Yellowtail		Haddock		Winter flounder	
CRUSTACEA	1.3		0.1		20.5		16.8		45.5		52.6		67.8		66.2		54.4		70.7		77.8		37.8		28.6		12.2		23.7		8.3	
Caridean shrimp		-		0.1		4.6		3.8		37.4		17.7		11.5		8.0		-		3.3		-		-		26.7		2.5		0.7		-
Penaeid shrimp		-		-		-		-		-		-		-		-		-		-		0.2		-		-		-		-		-
Anomuran crabs		0.4		-		-		3.1		1.0		14.0		0.1		25.1		-		-		-		0.1		-		0.7		0.9		0.2
Brachyuran crabs		0.4		-		-		5.8		0.4		4.6		-		6.4		-		-		-		-		-		-		0.3		0.3
Astacidean		-		-		-		0.1		-		-		-		-		-		-		-		-		-		-		-		-
Euphausiids		-		-		13.2		0.4		4.8		2.3		51.8		-		51.2		65.2		44.4		7.5		-		-		5.5		-
Mysids		0.1		-		-		0.7		-		-		2.2		-		-		0.1		-		-		-		-		0.3		-
Caprellid amphipods		-		-		-		-		-		0.1		-		-		-		-		-		-		-		0.1		-		-
Gammaridean amphipods		-		-		0.3		0.5		0.1		3.7		0.1		10.0		0.1		-		0.1		0.3		-		0.1		9.9		2.7
Hyperiid amphipods		-		-		-		-		-		-		-		0.1		-		-		0.1		0.6		-		-		-		-
Isopods		-		-		-		-		-		1.7		-		2.2		-		-		-		-		-		0.5		0.2		-
Copepods		-		-		-		-		-		-		1.9		-		1.9		-		-		0.1		-		-		-		-
Cumaceans		-		-		-		-		-		-		-		-		-		-		-		-		-		0.1		-		-
Cirripeds		-		-		-		-		-		-		-		-		-		-		-		-		-		-		-		-
Unidentified		0.4		-		2.6		2.2		1.8		0.5		0.2		12.5		1.2		2.1		33.1		29.2		1.9		10.2		6.1		5.1
PISCES	88.9		97.2		78.2		60.7		43.0		6.2		0.8		4.9		-		23.6		20.6		-		-		0.1		-		0.1	
Clupeidae		6.8		-		-		38.2		-		4.1		-		-		-		0.8		-		-		-		-		-		-
Scombridae		16.9		20.0		-		-		-		-		-		-		-		-		-		-		-		-		-		-
Pleuronectiformes		12.2		-		-		5.1		-		-		-		0.7		-		-		-		-		-		-		-		-
Gadidae		-		24.2		-		2.5		11.5		-		-		-		-		0.5		-		-		-		-		-		-
Cottidae		-		6.2		-		2.7		-		0.3		-		1.3		-		-		-		-		-		-		-		-
Ammodytidae		-		-		-		0.1		-		-		-		-		-		-		-		-		-		-		-		-
Fish eggs		2.0		-		-		0.6		-		0.3		-		-		-		-		-		-		-		-		-		-
Unidentified		51.0		46.9		78.2		11.5		31.5		1.6		0.8		2.9		-		22.3		20.6		-		-		0.1		-		0.1
POLYCHAETA	0.2	0.2	-	-	-	-	1.1	1.1	0.1	0.1	2.4	2.4	-	-	15.6	15.6	-	-	0.1	0.1	-	-	-	-	-	-	46.4	46.4	23.9	23.9	33.0	33.0
ECHINODERMATA	-		-		-		0.4	0.4	-		0.2	0.2	-		-		-		-		-		-		50.3		2.2		12.8		0.3	
Asteroids		-		-		-		-		-		-		-		-		-		-		-		-		-		-		0.2		0.1
Ophiuroids		-		-		-		-		-		-		-		-		-		-		-		-		-		-		9.3		0.1
Echinoids		-		-		-		-		-		-		-		-		-		-		-		-		50.3		-		2.5		0.1
Holothuroids		-		-		-		-		-		-		-		-		-		-		-		-		-		-		0.8		-
Unidentified		-		-		-		-		-		-		-		-		-		-		-		-		-		2.2		-		-
MOLLUSCA	1.6		2.4		0.6		15.2		7.5		20.0		1.0		0.2		2.5		1.7		-		-		-		1.3		6.2		1.0	
Gastropoda		0.1		-		-		4.4		0.1		20.0		-		-		-		0.1		-		-		-		0.1		0.4		0.3
Pelecypoda		-		-		-		9.2		-		-		-		-		-		-		-		-		-		1.1		5.2		0.7
Cephalopoda		1.5		2.4		0.6		-		7.4		-		0.6		0.2		-		-		-		-		-		-		-		-
Pteropoda		-		-		-		-		-		-		0.4		-		2.5		1.6		-		-		-		-		-		-
Unidentified		-		-		-		1.6		-		-		-		-		-		-		-		-		-		0.1		0.6		-
CHAETOGNATHA	-	-	-	-	-	-	-	-	-	-	-	-	2.3	2.3	-	-	28.6	28.6	-	-	-	-	7.5	7.5	-	-	-	-	-	-	-	-
TUNICATA	-	-	-	-	-	-	-	-	-	-	-	-	7.9	7.9	-	-	0.1	0.1	0.1	0.1	-	-	21.4	21.4	-	-	0.3	0.3	-	-	2.6	2.6
CNIDARIA	-				-		0.7	0.7	-		-		-		-		0.1		1.0	1.0	-		-		-		10.6		0.1	0.1	13.0	
Hydrozoans		-		-		-		-		-		-		-		-		0.1		-		-		-		-		-		-		3.0
Anthozoans		-		-		-		-		-		-		-		-		-		-		-		-		-		10.6		-		10.0
SIPUNCULIDA	6.2	6.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
NEMERTEA	0.2	0.2	-	-	-	-	-	-	-	-	-	-	-	-	0.2	0.2	-	-	-	-	-	-	-	-	-	-	0.1	0.1	-	-	-	-
ANIMAL REMAINS	1.6	1.6	0.3	0.3	0.7	0.7	2.9	2.9	3.9	3.9	18.5	18.5	20.2	20.2	12.0	12.0	14.3	14.3	2.8	2.8	1.5	1.5	33.3	33.3	21.1	21.1	3.0	3.0	10.0	10.0	22.1	22.1
SAND AND ROCK	-	-	-	-	-	-	2.4	2.4	-	-	0.1	0.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3.8	3.8	23.6	23.6	18.7	18.7
Number of stomachs		152		25		236		817		128		195		56		174		90		197		54		67		30		709		408		71
% empty		22.4		44.0		26.3		6.6		20.9		23.1		37.5		10.3		21.4		3.6		31.5		40.3		60.0		20.5		6.6		25.4
$\bar{x}$ wt per stomach(g)		10.3		132.1		4.5		29.9		6.3		1.7		0.6		2.2		0.4		12.8		1.0		0.2		0.6		0.4		5.8		1.8
$\bar{x}$ length (cm)		67		65		30		50		45		33		27		44		26		54		20		17		22		31		47		40

[1] Includes some data from 1974.

[2] All mackerel data are from 1974

Table 2.2. Relative abundance of the major prey of adult herring and mackerel found in the stomachs of other selected species. Abundance coded in percent by weight in three categories: <1% (t), 1-10% (✓), and >10% (*). Prey not recorded (-).

Predator (Fish species)	Prey									
	Crustacea					Mollusca				
	Amphipods	Decapods	Euphausiids	Mysids	Copepods	Pteropods	Chaetognaths	Tunicates	Pisces	Unidentified animal remains
Herring	t	✓	*	-	*	✓	*	t	t	t
Mackerel	t	✓	*	-	*	*	t	*	✓	t
Alewife[1]	✓	t	*	*	t	✓	✓	✓	✓	✓
Red hake	✓	t	✓	*	✓	-	-	-	✓	t
American shad	t	-	*	-	t	-	-	-	*	✓
Butterfish	t	✓	✓	-	t	-	✓	*	-	✓
Longfin hake	-	*	*	-	-	-	-	-	✓	✓
Silver hake	t	*	*	t	t	-	t	-	*	-
Sand lance	✓	-	✓	✓	*	-	✓	-	-	✓
Pollock	t	*	*	-	-	-	-	-	*	✓
Redfish	✓	*	*	-	t	-	-	-	✓	✓
Longnose Grenadier	t	✓	*	✓	t	-	-	-	-	*
Lanternfish	*	-	*	-	*	-	-	-	-	-
Pearlsides	-	-	-	-	*	-	-	-	-	-
Juvenile haddock[2]	*	*	✓	t	t	-	-	-	-	✓
Juvenile cod[2]	*	t	✓	*	*	-	t	-	t	*
Argentine	-	✓	*	-	t	-	-	-	-	*

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[1] Blueback, a closely related species of river herring, has a diet similar to alewife.
[2] After taking up demersal mode of life (personal communication from R. Bowman).

Table 3.1. Stratified mean catch per tow (kg) for finfish and squid in autumn trawl surveys for three periods, 1963-65, 1972-74, and 1975-77, in the combined area of southern New England, Georges Bank, and the Gulf of Maine (Strata 1-30 and 36-40, Figure 1). Catch per tow subtotals of major groups in kg and percent (in parentheses) shown at the top of each group.

Species	1963-65	1972-74	1975-77
Principal groundfish and flounders	77.0 (50.0)	35.8 (40.9)	48.9 (43.8)
Atlantic cod	7.2	6.6	6.0
Haddock	28.6	2.9	9.3
Redfish	13.1	9.2	10.2
Silver hake	8.0	3.3	5.6
Red hake	3.9	2.0	3.3
Pollock	3.2	2.8	7.0
Yellowtail flounder	5.8	4.4	1.0
Other flounder	7.2	4.6	6.5
Other groundfish	10.8 (7.0)	14.0 (16.0)	13.2 (11.8)
Goosefish	3.7	2.9	3.0
Ocean pout	0.5	0.1	0.2
Sculpins	0.8	0.9	1.1
White hake	3.0	6.6	5.5
Miscellaneous[4]	2.8	3.5	3.4
Principal pelagics	0.6 (0.4)	0.2 (0.2)	0.0 (0.0)
Atlantic herring	0.5	0.1	0.0[1]
Atlantic mackerel	0.0[1]	0.1	0.0[1]
Other pelagics and other finfish[2]	64.8 (42.1)	32.6 (37.2)	40.3 (36.1)
Butterfish	1.5	1.8	3.0
Spiny dogfish	47.4	19.1	27.1
Skates and rays	15.1	10.3	9.0
Miscellaneous[3]	0.8	1.4	1.2
Squid	0.7 (0.4)	5.0 (5.7)	9.1 (8.2)
Short-fin	0.0[1]	0.4	5.2
Long-fin	0.6	4.6	3.9
TOTAL finfish and squid	153.9	87.6	111.5

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[1] Less than 0.05.

[2] Excludes data for tunas, sharks, swordfish, American eel, menhaden, and white perch.

[3] Includes round herring, alewife, blueback, shad, argentine, bluefish, and striped bass.

[4] Index represents all other groundfish but reflects mainly catches of cusk, scup, sea raven, wolffish, sea robins, and smooth dogfish.

Table 3. 2. Stratified mean catch per tow (no.) for selected species in bottom trawl surveys from 1968-1977 in the combined area from Cape Hatteras to the Gulf of Maine (Strata 1-30, 36-40, 61-76, see Figure 1). Data for autumn surveys shown for all species; spring survey data also presented for some species (in parentheses).[1]

Species	1968	1969	1970	1971	1972	1973	1974	1975	1976	1977
Round herring	10.7	22.1	62.6	75.3	0.7	66.2	2.9	23.0	6.4	24.0
Alewife	0.9 (11.4)	0.5 (11.8)	1.0 (10.8)	0.7 (5.1)	1.5 (3.9)	0.4 (19.8)	0.2 (14.0)	0.3 (4.1)	0.9 (9.8)	0.6 (5.7)
Blueback	0.5 (4.7)	0.0 (0.3)	0.1 (0.9)	0.4 (1.5)	0.0 (2.7)	0.1 (0.8)	0.0 (1.1)	0.0 (0.2)	0.0 (1.7)	0.6 (0.5)
Shad	0.0 (0.2)	0.2 (0.0)	0.1 (0.0)	0.1 (0.0)	0.2 (0.0)	0.0 (0.5)	0.0 (0.7)	0.0 (0.1)	0.1 (0.1)	0.0 (0.0)
Anchovy	0.0	0.0	0.0	1.1	0.0	2.3	4.1	0.0	77.4	0.4
Argentine	0.1 (0.1)	0.1 (0.3)	0.1 (3.4)	0.0 (1.2)	0.3 (0.2)	0.1 (0.7)	0.0 (2.6)	0.3 (1.4)	0.1 (1.1)	0.4 (0.4)
Sand lance	0.3 (3.9)	0.1 (1.3)	0.0 (2.1)	0.0 (10.9)	0.8 (0.1)	0.0 (15.8)	0.2 (1.0)	17.4 (0.1)	0.1 (107.0)	16.5 (37.1)
Bluefish	0.0	0.5	0.0	0.1	0.2	0.9	0.5	0.2	1.0	0.4
Croaker	0.0	0.2	0.2	0.0	0.4	1.3	0.4	6.1	2.0	20.4
Lanternfish	0.3	88.3	0.1	0.8	0.8	0.3	0.2	0.9	0.0	0.1
Pearlsides	0.1	0.0	0.1	0.0	0.3	0.0	0.6	0.0	0.0	0.0

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[1] Values of 0.0 indicate positive catches <0.05.

Table 3.3. Mean weight (in kg) of haddock in commercial catch from Georges Bank, 1960-1976 and ages 3-6.

Year	Age			
	3	4	5	6
1976	1.73	2.52	3.30	-
1975	1.69	2.42	1.37*	3.44
1974	1.71	3.48*	3.07	3.64
1973	1.54*	2.25	2.66	2.72
1972	1.69	1.85	2.23	3.05
1971	1.20	1.61	2.33	2.72
1970	1.14	1.87	2.04	2.23
1969	1.41	1.70	2.00	2.05
1968	1.13	1.38	1.61	2.12
1967	0.95	1.22	1.56	2.27
1966	0.88	1.33	1.91	2.35
1965	1.02	1.45	1.81	2.25
1964	1.12	1.48	1.79	2.22
1963	1.14	1.47	1.75	2.28
1962	1.03	1.38	1.76	2.20
1961	1.06	1.49	1.80	2.29
1960	1.16	1.59	1.88	2.46

*extremely small year class with the number of age determinations probably inadequate for these values to be meaningful.

Table 3.4. Mean length at age of silver hake in the commercial catch, Georges Bank.

Year	Age			
	3	4	5	6
1976	29.8	31.1	31.6	44.5
1975	31.2	34.6	36.7	39.0
1974	32.1	34.5	38.1	34.9
1973	30.9	35.8	39.3	40.0
1972	33.3	35.7	38.6	37.6
1971	28.9	31.2	34.1	36.6
1970	29.5	31.4	34.3	37.0
1969	28.8	31.8	35.0	38.1
1968	27.6	31.1	35.3	39.4
1967	28.9	31.4	35.0	39.3
1966	27.8	31.0	35.3	41.0
1965	27.8	30.2	34.9	39.2

Table 3. 5. Stomach-contents data, expressed as percent frequency of occurrence of all the stomachs of each species examined, for demersal fishes collected on Georges Bank for the years 1963 through 1966 and 1973 through 1976.

	Predators/Year									
	Atlantic cod		Silver hake		Haddock		Little skate		Yellowtail	
	1963-1966	1973-1976	1963-1966	1973-1976	1963-1966	1973-1976	1963-1966	1973-1976	1963-1976	1973-1976
POLYCHAETA	4.9	21.7	0.0	0.0	31.2	50.6	38.0	47.2	32.5	40.9
Terebelliformia	0.0	0.0	0.0	0.0	0.0	1.1	0.0	0.0	0.7	4.1
Sabelliformia	0.0	0.0	0.0	0.0	0.6	2.4	0.0	0.0	0.0	0.7
Nereidiformia	1.6	8.7	0.0	0.0	0.9	14.9	7.6	10.9	0.0	10.7
Other Polychaeta	3.3	15.0	0.0	0.0	30.3	44.0	30.7	41.9	32.1	37.1
CRUSTACEA	57.4	72.0	42.6	50.7	34.6	79.5	59.4	85.3	19.3	58.4
Amphipoda	0.8	26.8	3.0	22.2	20.5	66.8	24.1	62.3	15.7	53.3
Axiidae	0.0	0.8	0.0	0.3	0.0	1.3	0.0	0.4	0.0	0.0
Cancridae	7.4	32.3	0.0	0.3	0.2	14.0	1.0	23.8	0.0	2.7
Crangonidae	0.0	23.6	5.9	17.6	2.8	10.6	12.9	45.3	0.7	10.0
Majidae	1.6	8.3	0.0	0.0	0.0	5.6	0.3	3.0	0.0	0.0
Paguridae	10.7	24.8	0.0	0.3	1.1	9.7	21.5	31.7	0.0	5.8
Pandalidae	3.3	31.5	3.0	14.7	0.9	6.7	0.3	8.7	0.0	0.3
Pasiphaeidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Other Decapoda	36.1	23.6	3.0	7.8	6.4	19.2	11.9	17.0	0.4	2.7
Isopoda	0.0	9.4	0.0	0.0	3.0	12.7	4.6	19.6	0.7	7.9
Euphausiacea	4.9	3.1	30.7	0.8	2.4	2.4	3.0	0.0	0.0	0.3
Mysidacea	0.0	0.8	0.0	2.3	0.0	2.4	0.0	2.6	0.0	0.3
Copepoda	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.3
Other Crustacea	0.8	15.0	0.0	13.7	3.4	18.1	2.6	21.9	2.6	7.2
MOLLUSCA	16.4	19.7	0.0	0.7	11.1	17.2	5.0	5.7	1.1	5.5
Pelecypoda	4.9	10.2	0.0	0.0	3.0	15.1	1.7	4.9	0.0	4.8
Gastropoda	6.6	10.6	0.0	0.0	2.8	3.9	1.7	0.0	0.7	0.3
Cephalopoda	0.0	0.8	0.0	0.7	0.4	0.2	0.7	0.4	0.0	0.0
Other Mollusca	5.7	4.3	0.0	0.0	4.9	2.4	1.0	0.4	0.4	0.3
ECHINODERMATA	3.3	5.5	0.0	0.0	31.0	32.8	0.3	0.4	2.6	1.0
Echinoidea	1.6	0.4	0.0	0.0	6.0	7.8	0.0	0.4	0.0	0.7
Ophiuroidea	1.6	4.3	0.0	0.0	23.1	26.1	0.0	0.0	1.8	0.0
Other Echinoderms	0.8	2.0	0.0	0.0	3.0	3.4	0.3	0.0	1.1	0.3
LARVACEA	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.4	0.0	0.0
ASCIDIACEA	0.0	0.0	0.0	0.0	0.0	2.2	0.0	0.0	0.4	2.4
THALIACEA	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
CHAETOGNATHA	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0
PISCES	36.9	29.1	7.9	15.7	1.9	4.5	5.6	11.3	0.0	1.0
Clupeidae	2.5	2.8	0.0	0.0	0.2	0.0	0.3	0.0	0.0	0.0
Gadidae	5.7	0.8	0.0	0.7	0.4	0.0	0.3	0.0	0.0	0.0
Ammodytidae	0.0	0.0	0.0	0.3	0.0	0.0	0.7	1.1	0.0	0.0
Scombridae	0.0	0.0	0.0	2.3	0.0	0.0	0.0	0.0	0.0	0.0
Scorpaenidae	1.6	0.4	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0
Stromateidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0
Bothidae	0.0	0.8	0.0	0.3	0.0	0.0	0.3	0.4	0.0	0.0
Pleuronectidae	0.0	0.4	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0
Rajidae	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Other Pisces	28.7	28.3	7.9	12.1	1.5	4.5	4.0	10.6	0.0	1.0
No. Examined	122	254	101	306	468	464	303	265	274	291
No. Empty (% Empty)	15 (12%)	6 (2%)	49 (49%)	103 (34%)	91 (18%)	24 (5%)	62 (20%)	26 (10%)	133 (49%)	108 (37%)
x length (cm)	61	59	31	29	47	46	46	45	35	34
[redacted]	[redacted]	[redacted]	[redacted]	[redacted]	[redacted]	[redacted]	[redacted]	[redacted]	[redacted]	[redacted]

Table 3.6. Stomach contents data, expressed as percent frequency of occurrence of all the stomachs of each species examined, for demersal fishes collected in the Gulf of Maine for the years 1963 through 1966 and 1973 through 1976.

	Predators/Year											
	Atlantic cod		Pollock		White hake		Redfish		Witch flounder		American plaice	
Prey	1963-1966	1973-1976	1963-1966	1973-1976	1963-1966	1973-1976	1963-1966	1973-1976	1963-1966	1973-1976	1963-1966	1973-1976
POLYCHAETA	2.1	10.3	1.7	4.0	1.4	0.8	0.3	0.0	46.3	87.9	5.5	10.6
Terebelliformia	0.0	1.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	18.2	0.0	4.8
Sabelliformia	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.6	7.6	0.0	2.3
Nereidiformia	1.3	8.2	0.6	0.6	0.0	0.0	0.0	0.0	8.0	51.9	0.8	3.4
Other Polychaeta	0.9	5.5	1.2	3.4	1.4	0.8	0.3	0.0	37.7	73.1	4.8	16.1
CRUSTACEA	39.9	50.7	39.0	61.5	26.9	42.8	31.0	48.9	7.3	28.4	2.7	9.0
Amphipoda	2.2	9.6	0.0	14.4	0.0	3.5	0.0	3.4	4.2	22.3	0.0	5.6
Axiidae	0.0	0.0	0.0	0.0	0.0	2.3	0.0	0.0	0.0	0.0	0.0	0.0
Cancridae	3.9	0.7	0.0	0.0	1.0	0.4	0.0	0.0	0.0	0.0	0.2	0.0
Crangonidae	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.4	0.0	0.0	0.0	0.0
Majidae	1.3	2.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Paguridae	3.0	1.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0
Pandalidae	7.7	17.1	0.6	6.3	4.4	13.2	0.8	1.1	0.3	0.0	0.0	2.0
Pasiphaeidae	0.0	2.7	0.0	3.4	0.0	5.4	0.0	4.9	0.0	0.0	0.0	0.0
Other Decapoda	20.2	11.6	20.0	4.0	8.2	10.5	2.3	4.5	0.3	1.5	1.1	0.6
Isopoda	0.4	2.1	0.0	0.6	0.0	2.7	0.3	0.0	1.0	1.9	0.2	0.3
Euphausiacea	7.3	16.4	26.7	25.9	13.9	13.2	27.5	34.6	0.3	0.8	1.1	0.8
Mysidacea	0.0	0.0	0.0	0.6	0.0	0.4	0.3	0.8	0.3	0.0	0.0	0.3
Copepoda	0.0	1.4	0.0	0.0	0.0	0.0	0.0	3.0	0.0	0.0	0.0	0.0
Other Crustacea	0.0	13.7	0.0	17.2	0.0	7.0	0.1	6.8	1.0	3.0	0.0	0.8
MOLLUSCA	4.7	6.8	2.9	3.4	1.0	1.6	0.3	0.0	2.6	15.2	2.1	7.9
Pelecypoda	0.9	0.7	0.0	0.0	0.0	0.0	0.0	0.0	1.9	14.0	1.3	6.8
Gastropoda	0.9	1.4	0.0	1.1	0.0	0.0	0.0	0.0	0.3	0.0	0.2	0.8
Cephalopoda	1.3	2.7	2.9	2.9	1.0	1.6	0.3	0.0	0.0	0.0	0.0	0.0
Other Mollusca	1.7	2.1	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.8	0.6	0.3
ECHINODERMATA	6.0	9.6	0.0	0.0	0.3	0.0	0.0	0.0	1.9	11.4	35.9	45.2
Echinoidea	0.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.6
Ophiuroidea	5.2	9.6	0.0	0.0	0.0	0.0	0.0	0.0	1.0	2.7	35.5	41.8
Other Echinoderms	0.0	2.1	0.0	0.0	0.3	0.0	0.0	0.0	1.0	10.2	0.0	3.1
LARVACEA	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
ASCIDIACEA	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.0	0.0	0.3
THALIACEA	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
CHAETOGNATHA	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
PISCES	33.9	26.0	11.0	16.7	21.8	29.6	0.8	3.0	0.3	2.3	0.2	0.8
Clupeidae	4.3	4.8	2.9	0.6	0.7	1.6	0.0	0.0	0.0	0.0	0.0	0.0
Gadidae	9.4	0.7	1.2	0.0	5.1	7.4	0.5	0.0	0.0	0.0	0.0	0.0
Ammodytidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Scombridae	0.0	0.0	0.0	0.0	0.0	0.8	0.0	0.0	0.0	0.0	0.0	0.0
Scorpaenidae	3.0	1.4	0.0	0.0	1.0	0.8	0.0	0.4	0.0	0.0	0.0	0.0
Stromateidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Bothidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pleuronectidae	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0
Rajidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Other Pisces	19.3	19.2	7.6	16.7	16.7	19.8	0.3	2.6	0.3	2.3	0.2	0.8
No. Examined	233	146	172	174	294	257	400	266	313	264	524	354
No. Empty (% Empty)	60 (26%)	21 (14%)	88 (51%)	21 (12%)	164 (56%)	90 (35%)	268 (67%)	123 (46%)	127 (41%)	19 (7%)	269 (51%)	147 (42%)
x Length (cm)	62	59	57	57	57	59	31	33	46	48	38	36
Length Range (cm)	40-79	40-79	20-79	20-79	40-89	40-89	20-39	20-39	30-59	30-59	20-59	20-59

Table 4.1. Weight at age in grams ($W_{i,j,\cdot}$)[1] for herring, cod, mackerel, silver hake, and yellowtail flounder.

Age	Herring	Cod	Mackerel	Silver hake	Yellowtail flounder
1	-	170	95	32	39
2	87	620	175	97	160
3	140	1,410	266	188	331
4	180	2,510	350	291	510
5	220	3,880	432	390	674
6	240	5,450	506	485	811
7	275	7,150	564	569	920
8	300	8,930	615	639	1,005
9	320	10,750	659	699	1,068
10	340	12,550	693	746	1,115
11	360	14,310	693	786	1,149
12	360	15,100	693	821	1,174

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[1] Weight at age for herring are the values used in the most recent ICNAF and Northeast Fisheries Center assessments of the Georges Bank stock. Cod weight at age values are based on a length-age function reported by Penttila and Gifford (1976) and a weight-length function reported by Serchuk, Wood, Clark, and Brown (1977, Analysis of the Georges Bank and Gulf of Maine Cod Stocks, NEFC Lab. Ref. No. 77-24, unpublished). Mackerel weight at age values are from Anderson (1977). Silver hake weight at age values are based on Almeida (1978, Determination of the von Bertalanffy Growth Equation for three stocks of silver hake, *Merluccius bilinearis*, in the Northwest Atlantic Ocean, NEFC Lab. Ref. No. 78-13, unpublished). Yellowtail flounder weight at age values are from Lux and Nichy (1969) and Lux (1969).

Table 4.2. Haddock length at age for 1963-1973. See the text for explanation of the source of these values.

Year	Age										
	1	2	3	4	5	6	7	8	9	10	11
1963	21.10	33.60	40.17	50.49	55.00	59.38	64.54	64.83	69.01	69.82	72.50
1964	21.10	33.57	40.17	50.49	55.00	59.38	64.54	64.83	69.01	69.82	72.50
1965	21.10	28.90	35.46	47.08	55.27	56.42	62.78	65.67	68.07	72.80	72.50
1966	21.10	30.58	38.02	43.89	52.29	56.40	63.02	65.99	71.92	69.81	72.50
1967	21.10	27.56	37.92	43.33	49.64	53.14	61.23	68.90	70.34	71.24	70.50
1968	21.10	37.15	42.92	50.71	51.77	55.90	65.07	69.34	72.00	71.09	72.50
1969	21.10	33.60	46.37	49.64	53.03	57.81	61.93	67.27	67.61	71.82	72.50
1970	21.10	33.60	40.17	54.92	56.35	59.49	60.68	62.75	69.60	70.10	72.50
1971	21.10	37.86	47.82	52.50	58.21	57.33	61.02	62.51	67.60	71.89	72.50
1972	21.10	33.60	50.83	53.43	55.94	62.00	58.50	65.90	66.88	70.31	72.50
1973	21.10	33.37	40.17	57.12	61.19	59.38	59.78	68.84	64.23	68.13	72.61

Table 4.3. Fraction of females mature at age ($p_{i,j}$).

Species	Age				
	1	2	3	4	5
Herring	0.00	0.00	0.20	0.91	1.00
Cod	0.00	0.25	0.75	1.00	1.00
Mackerel	0.00	0.50	1.00	1.00	1.00
Silver hake	0.00	0.00	1.00	1.00	1.00
Yellowtail flounder	0.00	0.52	0.67	1.00	1.00
Haddock					

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[1] Estimates for herring are based primarily on the geometric mean of the fraction mature at age for 1960-1965 (Boyar 1968). Estimates for cod, silver hake, and haddock are assumed values which are compatible with the estimated age at 50% maturity indicated by bottom trawl survey data (Robert Livingstone, NEFC, Woods Hole Laboratory, March 1977, unpublished). Estimates for mackerel correspond to the values used in stock assessments to calculate spawning stock size (Emory Anderson, NEFC, Woods Hole Laboratory, personal communication). These estimates are compatible to a minimal amount of data available from bottom trawl surveys. Estimates for yellowtail flounder are from Royce et al. (1959).

Table 4.4. Total calculated production (summed over all ages) in thousands (10^3) of kilocalories per kilometer squared.

Year	Herring	Cod	Mackerel	Silver hake	YT	Haddock	Total
1963	5273	1003	491	8742	456	2683	18648
1964	5345	1032	439	7957	402	1989	17164
1965	5445	1032	408	5347	347	2738	15317
1966	5302	960	491	3249	383	1369	11754
1967	5116	989	870	2373	456	1369	11173
1968	4471	960	1904	2044	529	657	10565
1969	3439	802	2061	1989	511	292	9094
1970	2579	688	2043	1862	493	201	7866
1971	1777	616	1652	1606	438	146	6235
1972	3382	688	1309	1953	385	91	7806

Table 4.5. Total calculated consumption (summed over all ages) in thousands (10^3) of kilocalories per kilometer squared.

Year	Herring	Cod	Mackerel	Silver hake	Yellowtail	Haddock	Total
1963	76422	5503	5660	70080	3340	17630	178635
1964	82455	5660	5301	65317	3030	18086	179849
1965	89090	5703	5082	44822	2519	17046	164252
1966	89921	5230	5831	27795	2610	10622	142009
1967	85765	5202	9223	20367	3121	7829	131507
1968	74659	5030	18750	17484	3559	5092	124574
1969	57119	4299	21627	16954	3687	2975	106661
1970	42947	3683	22197	16243	3395	1916	90381
1971	29190	3353	18993	13031	3176	1241	68984
1972	43004	3540	15521	14509	2884	821	80279

Table 4.6. Calculated production to biomass ratio (summed over all ages) for 1963-1972.

Year	Herring	Cod	Mackerel	Silver hake	Yellowtail flounder	Haddock
1963	0.33	0.57	0.37	0.64	0.52	0.53
1964	0.30	0.56	0.34	0.61	0.59	0.39
1965	0.28	0.55	0.33	0.58	0.61	0.61
1966	0.26	0.59	0.35	0.56	0.71	0.44
1967	0.25	0.64	0.42	0.55	0.71	0.61
1968	0.27	0.64	0.48	0.56	0.66	0.39
1969	0.27	0.61	0.43	0.56	0.64	0.29
1970	0.27	0.59	0.40	0.53	0.62	0.29
1971	0.27	0.61	0.37	0.62	0.51	0.35
1972	0.39	0168	0.35	0.74	0.58	0.33
Geometric average	0.29	0.60	0.34	0.59	0.63	0.41

Table 4.7. Gross growth efficiency (summed over all ages) for 1963-1972.

Year	Herring	Cod	Mackerel	Silver hake	Yellowtail flounder	Haddock
1963	0.07	0.18	0.09	0.13	0.14	0.15
1964	0.07	0.18	0.08	0.12	0.13	0.11
1965	0.06	0.18	0.08	0.12	0.14	0.16
1966	0.06	0.19	0.08	0.12	0.15	0.13
1967	0.06	0.19	0.09	0.12	0.15	0.18
1968	0.06	0.19	0.10	0.12	0.14	0.13
1969	0.06	0.19	0.10	0.12	0.14	0.10
1970	0.06	0.19	0.09	0.11	0.14	0.10
1971	0.06	0.19	0.09	0.12	0.14	0.12
1972	0.06	0.19	0.09	0.12	0.14	0.12

Table 4.8. Consumption to biomass ratio (summed over all years) for 1963-1972.

Year	Herring	Cod	Mackerel	Silver hake	Yellowtail flounder	Haddock
1963	4.8	3.1	4.2	5.1	4.5	3.5
1964	4.6	3.1	4.1	5.0	4.4	3.5
1965	4.5	3.1	4.1	4.9	4.5	3.3
1966	4.4	3.2	4.2	4.8	4.8	3.5
1967	4.4	3.4	4.5	4.8	4.8	3.5
1968	4.5	3.4	4.7	4.8	4.6	3.0
1969	4.5	3.3	4.5	4.8	4.6	2.8
1970	4.5	3.2	4.4	4.7	4.5	2.8
1971	4.5	3.2	4.2	5.0	4.5	2.8
1972	4.9	3.5	4.2	5.5	4.4	2.9
Geometric average	4.6	3.3	4.3	4.9	4.6	3.2

Table 4.9. Average calculated production in thousands (10^3) kilocalories per kilometer squared, 1963-1972.

Age	Herring	Cod	Mackerel	Silver hake	Yellowtail	Haddock	Total
1	NC	172.0	354.1	1065.8	136.9	191.6	1920.4
2	1334.1	210.7	308.6	1106.0	146.0	193.5	3298.9
3	889.9	176.3	227.5	908.9	96.7	213.5	2512.8
4	897.1	118.9	145.8	381.4	38.3	195.3	1776.8
5	454.3	80.2	72.3	131.4	12.8	125.9	876.9
6	386.9	54.5	28.1	65.7	3.7	107.7	646.6
7	169.1	33.0	15.4	32.9	1.8	56.6	308.8
8	60.2	18.6	9.6	12.8	-	52.9	154.1
9	21.5	8.6	4.9	3.7	-	11.0	49.7
10	1.4	4.3	-	-	-	3.7	9.4
11	-	-	-	-	-	1.8	1.8

NC = not considered.

Table 4.10. Average calculated consumption in thousands (10^3) of kilocalories per kilometer squared, 1963-1972.

Age	Herring	Cod	Mackerel	Silver hake	YT	Haddock	Total
1	NC	756.6	3121.6	6531.7	663.0	985.5	12063.4
2	14934.7	1028.9	3081.0	9059.3	981.9	1361.8	28919.6
3	15367.5	927.2	2583.7	7827.4	845.0	1368.8	28919.6
4	13880.0	670.6	1871.2	3989.5	408.8	1346.9	22167.0
5	10294.7	494.4	1057.0	1587.8	149.7	1115.1	13698.7
6	6907.1	356.8	486.1	755.6	51.1	846.8	9403.5
7	3659.9	1096.2	290.8	372.3	18.3	605.9	6043.4
8	1457.4	144.7	196.2	147.8	7.3	465.4	2418.8
9	524.5	71.7	102.3	43.8	1.8	146.0	890.5
10	31.5	27.2		16.4		51.1	126.2
11		4.3		1.8		31.0	37.1

NC = not considered.

Table 4.11. Calculate production to biomass ratio by age.

Age	Herring	Cod	Mackerel	Silver hake	Yellowtail flounder	Haddock[1]
1	NC	1.14	0.59	1.01	1.33	1.06
2	0.47	0.80	0.46	0.64	0.72	0.61
3	0.27	0.64	0.37	0.54	0.47	0.50
4	0.29	0.53	0.31	0.40	0.36	0.49
5	0.19	0.44	0.25	0.33	0.28	0.34
6	0.24	0.37	0.21	0.33	0.23	0.38
7	0.19	0.32	0.19	0.32	0.20	0.25
8	0.17	0.29	0.17	0.29	0.18	0.30
9	0.16	0.26	0.15	0.27	0.17	0.19
10	0.16	0.23	-	0.25	0.16	0.17
11	-	0.21	-	0.24	-	0.15

NC - not considered

[1] Average value for 1963-1972.

Table 4.12. Calculated gross growth efficiency by age.

Age	Herring	Cod	Mackerel	Silver hake	Yellowtail flounder	Haddock[1]
1	NC	0.23	0.11	0.15	0.21	0.20
2	0.09	0.20	0.10	0.12	0.15	0.14
3	0.06	0.19	0.09	0.12	0.11	0.16
4	0.06	0.18	0.08	0.10	0.10	0.15
5	0.04	0.16	0.07	0.08	0.08	0.11
6	0.06	0.15	0.06	0.09	0.07	0.13
7	0.05	0.14	0.05	0.09	0.06	0.09
8	0.04	0.13	0.05	0.08	0.06	0.11
9	0.04	0.12	0.04	0.08	0.06	0.08
10	-	0.12	-	0.07	0.05	0.07
11	-	0.11	-	0.07	-	0.06

NC - not considered

[1] Average value for 1963-1972

Table 4.13. Calculated consumption to biomass ratio by age.

Age	Herring	Cod	Mackerel	Silver hake	Yellowtail flounder	Haddock[1]
1	NC	5.0	5.2	6.5	6.5	5.4
2	5.2	3.9	4.6	5.2	4.8	4.2
3	4.7	3.3	4.2	4.7	4.1	3.8
4	4.5	3.0	4.0	4.2	3.7	3.4
5	4.2	2.7	3.8	3.9	3.5	3.0
6	4.2	2.5	3.6	3.8	3.3	2.9
7	4.1	2.3	3.5	3.7	3.2	2.7
8	4.0	2.2	3.4	3.6	3.1	2.7
9	3.9	2.1	3.4	3.5	3.1	2.5
10	-	2.0	-	3.4	3.0	2.4
11	-	1.9	-	3.4	-	2.4

NC - not considered

[1] Average value for 1963-1972.

Table 4.14. Georges Bank consumption and production in thousands of kilocalories per kilometer squared.

Species Group	1964-1966			1973-1975		
	Biomass	Consumption	Production	Biomass	Consumption	Production
Cod	1890	5561	1071	920	3036	552
Haddock	4474	16117	2147	443	1418	182
Redfish	23	69	6	53	159	13
Silver hake	10052	48587	5830	7412	36318	4373
Red hake	1084	4444	499	801	3234	368
Pollock	273	1140	128	118	484	54
Yellowtail flounder	625	2874	399	481	2213	303
Other flounder	312	1279	144	239	980	110
Herring	19251	87521	5393	6201	28525	1798
Mackerel	1314	5410	446	2730	11739	928
Other finfish	1684	6904	775	2260	9266	1040
Illex	231	1617	247	1719	12033	2579
Loligo	63	441	95	273	1911	410
Total	41292	192064	17180	23650	111366	12710

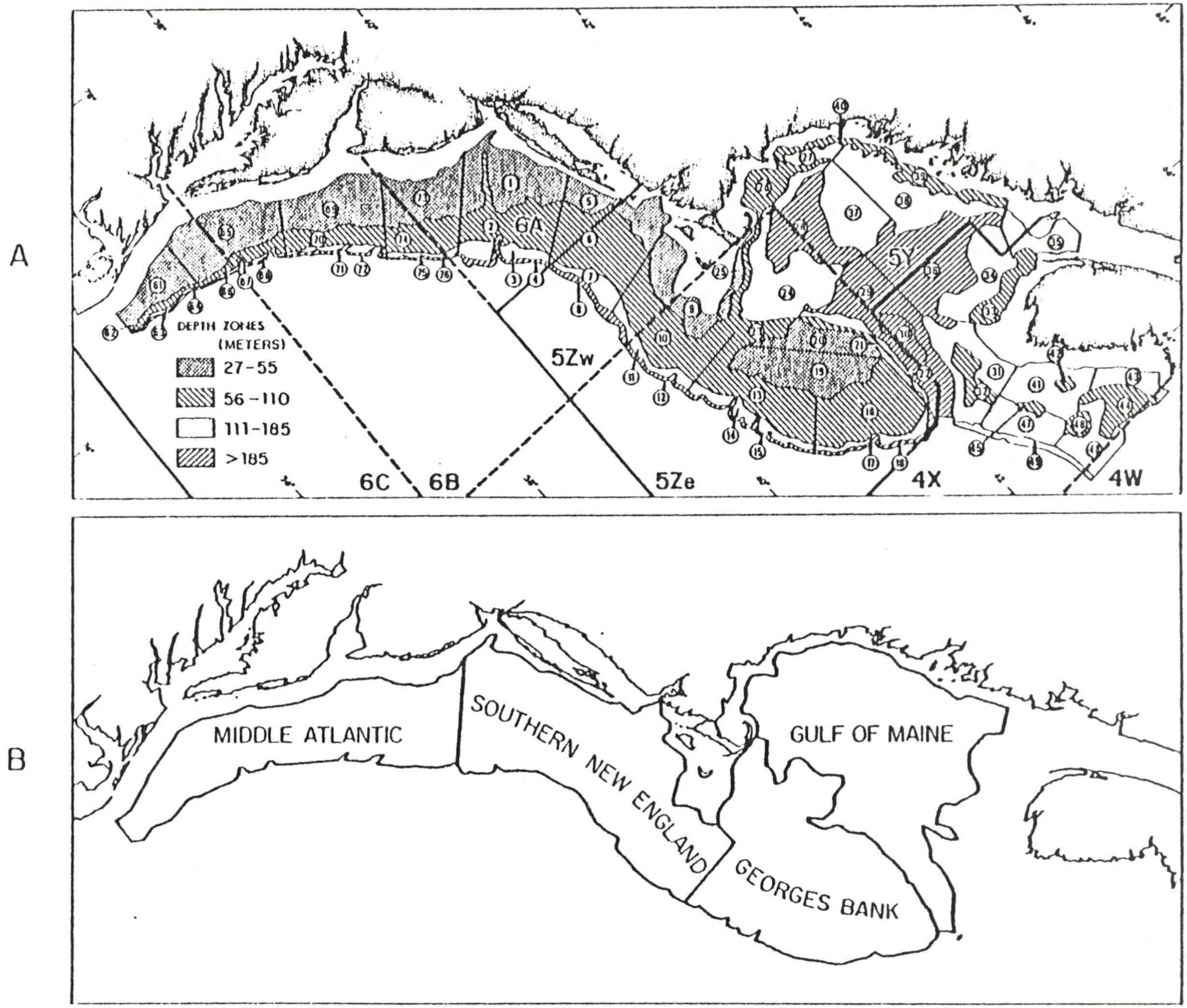

Figure 1. Area of study from Cape Hatteras to Nova Scotia. A. Survey sampling strata with ICNAF statistical division boundaries superimposed. B. General ecological areas used in analysis of biomass, species composition, and food habits.

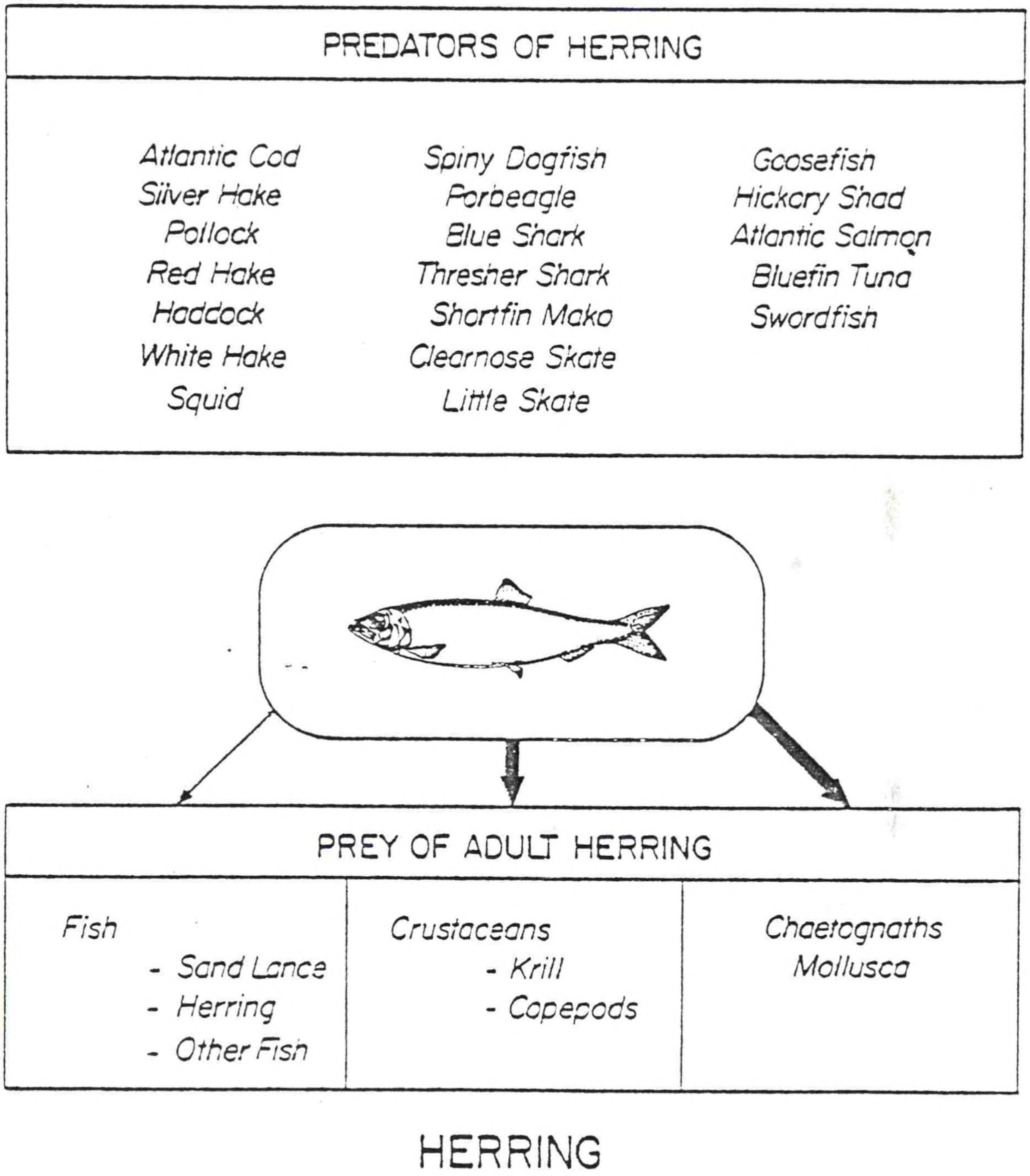

Figure 2.1. Predators and prey of herring.

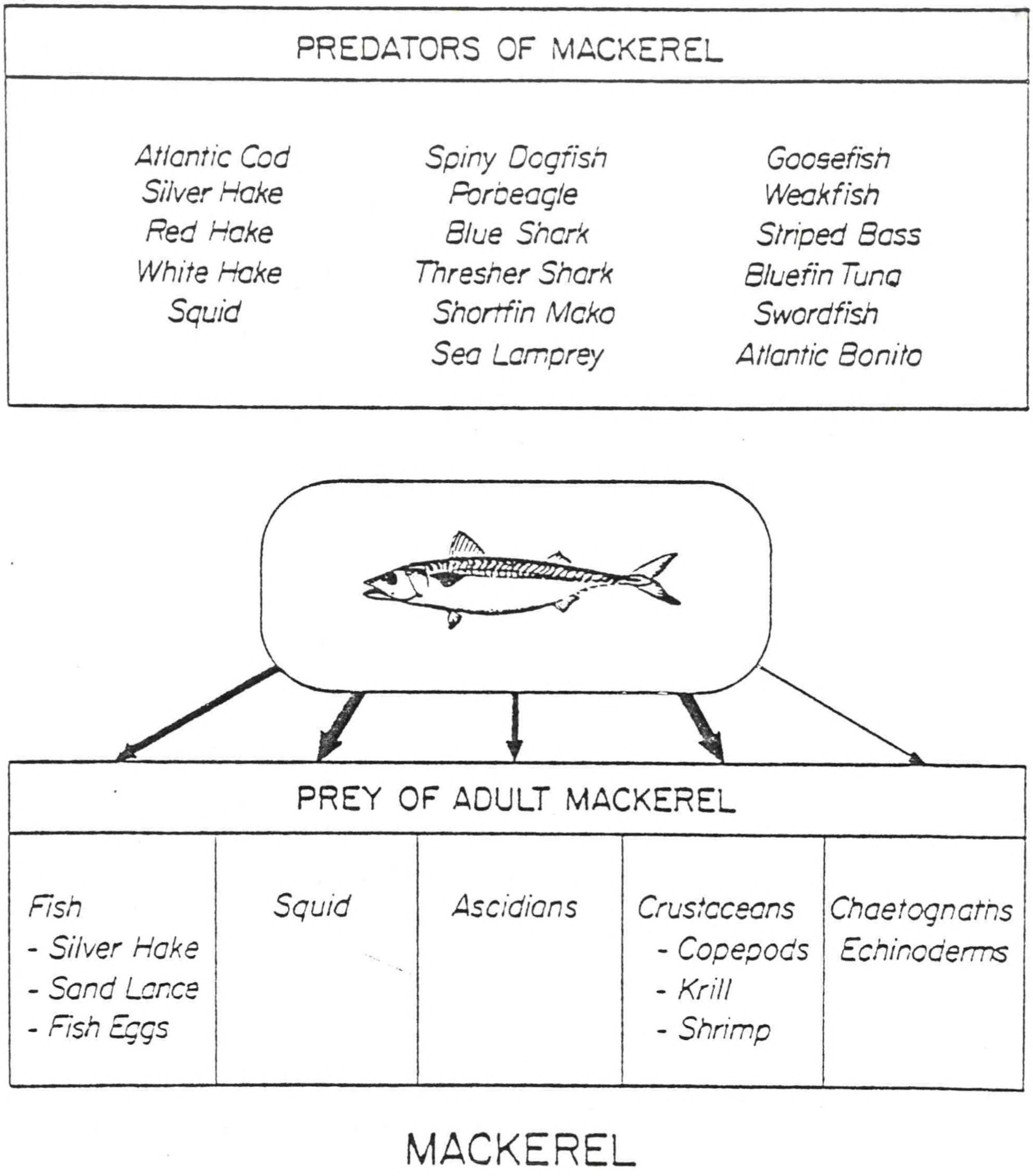

Figure 2.2. Predators and prey of mackerel.

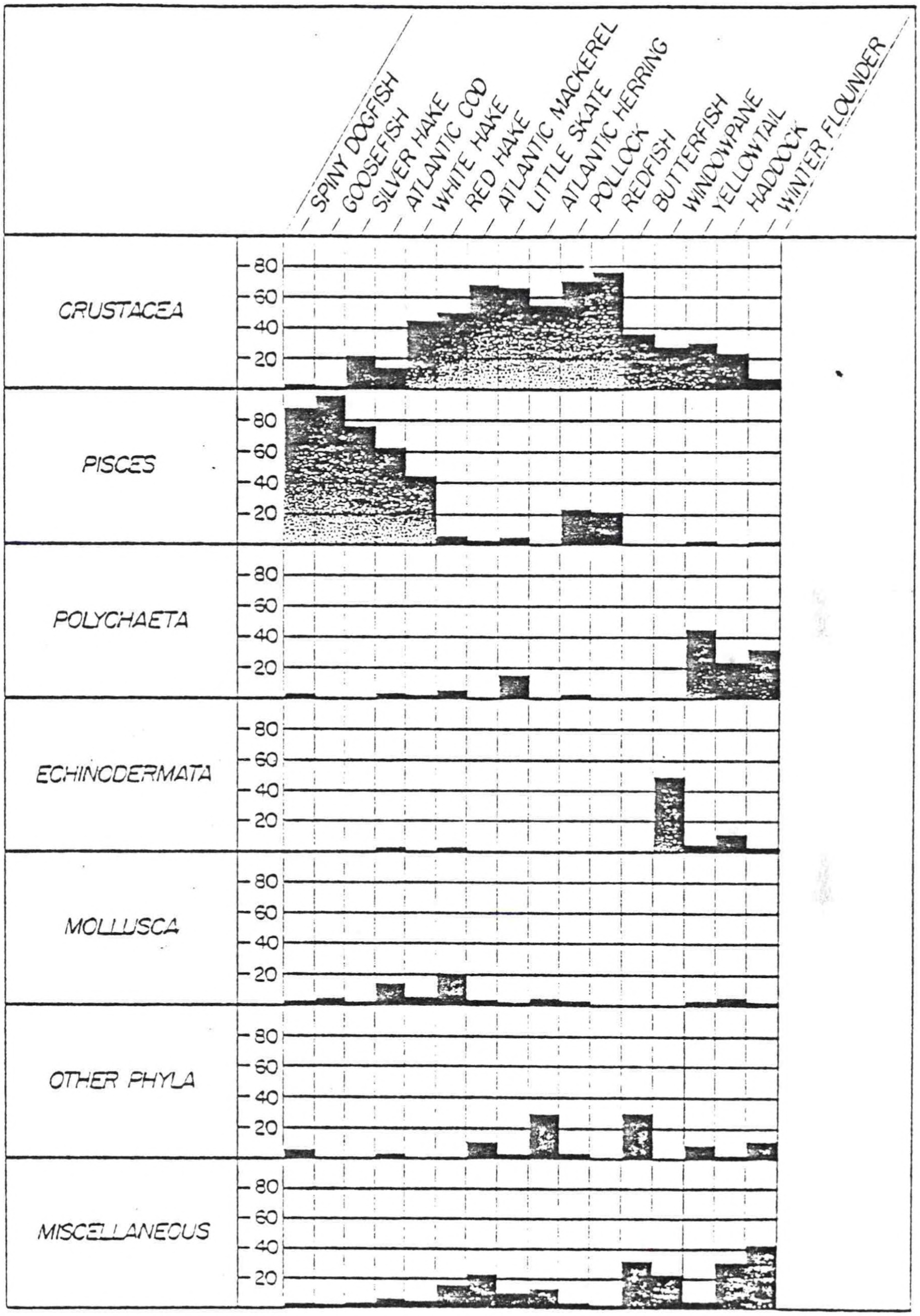

Figure 2.3. A diagrammatic representation of the prey of 16 species of fish collected on Georges Bank between the years 1969 through 1972. The data are expressed as percent weight.

	Spiny Dogfish	Goosefish	Silver Hake	Atlantic Cod	White Hake	Red Hake	Atlantic Mackerel	Little Skate	Atlantic Herring	Pollock	Redfish	Butterfish	Windowpane	Yellowtail	Haddock	Winter Flounder
Spiny Dogfish	╲	■	▥		▥											
Goosefish	66	╲	▥		▥											
Silver Hake	53	48	╲		▥					▥	▥					
Atlantic Cod	29	17	19	╲		▥										
White Hake	36	46	44	25	╲					▥			▥			
Red Hake	9	2	12	30	29	╲	▥	■				▥	▥			▥
Atlantic Mackerel	3	2	20	9	22	34	╲		■	■	▥	▥	▥			
Little Skate	7	5	11	24	20	60	24	╲						▥	▥	▥
Atlantic Herring	2	0	15	5	10	18	71	14	╲	▥	▥	▥				
Pollock	25	23	42	23	36	13	60	11	57	╲	■					
Redfish	23	21	37	16	29	14	47	17	47	69	╲	▥				
Butterfish	2	0	11	6	11	30	38	26	31	13	38	╲				▥
Windowpane	2	0	7	9	32	38	32	25	16	8	3	23	╲			
Yellowtail	3	1	6	14	8	22	6	44	4	8	21	23	7	╲	▥	▥
Haddock	3	0	10	18	13	27	17	44	17	12	13	22	15	49	╲	■
Winter Flounder	3	0	4	11	7	30	23	37	16	5	7	30	23	59	62	╲

0 >30 □   30 >60 ▥   60 >100 ■

Figure 2.4. Percent similarity between the diets of 16 species of fish collected on Georges Bank between the years 1969 through 1972. The calculated values are based on the food habits data presented in Table 2.3.

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M. D. Grosslein, B. E. Brown, and R. C. Hennemuth

ITEM 6

INTERNATIONAL STATISTICAL ECOLOGY PROGRAM

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S11: ENVIRONMENTAL BIOMONITORING OF ASSESSMENT, PREDICTION, AND MANAGEMENT - CERTAIN CASE STUDIES AND RELATED QUANTITATIVE ISSUES

Co-ordinators and/or Co-editors:

M. I. Artuz, J. Cairns, G. P. Patil and W. E. Waters

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A Draft: Comments and suggestions are invited. Plans are made for the revised final versions to appear in a series of volumes in the near future. For further information, contact the program office, co-ordinators or the authors.

Research, Assessment, and Management of a Marine Ecosystem in the Northwest Atlantic--A Case Study

by

M. D. Grosslein, B. E. Brown, and R. C. Hennemuth

National Marine Fisheries Service
Northeast Fisheries Center
Woods Hole, Massachusetts 02543, USA

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1. INTRODUCTION

The continental shelf off the northeastern United States is a highly productive region supporting large recreational and commercial fisheries for many species of fish and shellfish. In recent years, extremely heavy commercial fishing has reduced finfish biomass levels drastically and there has been a clear need to evaluate the production potential of these resources, and to separate natural causes of population fluctuations from man's impacts in the form of fishing and environmental degradation. Both the nature of the fisheries and the ecosystem clearly pointed to the necessity of treating the fisheries management from a multispecies point of view; and understanding man's impact clearly required a much improved knowledge of the dynamics of the marine ecosystem.

This paper outlines the approach for the research and management of offshore marine resources on the shelf from Cape Hatteras to the Gulf of Maine. It represents a case study of an attempt to develop a management approach within the framework of a marine ecosystem model. Emphasis is on a multispecies approach to the management of exploited fish populations, begun more than a decade ago by the Northeast Fisheries Center (NEFC) of the US National Marine Fisheries Service (NMFS). More recent efforts at a total ecosystem approach are briefly described and include research by other agencies

The final section of this paper outlines some statistical problems in the analysis and interpretation of fish and zooplankton sampling data.

2. DEVELOPMENT OF MULTISPECIES FISHERIES MANAGEMENT

2.1 Catch and Effort Statistics

The basis for the development of a multispecies approach to fisheries management began with the initiation of a well developed system for recording catch and effort statistics. Although both the United States and Canada began statistical collections before 1900 (Sette and Needler 1930) the modern era of statistical collections of catch and fishing effort can be considered to begin after World War II. This involved comprehensive collection of commercial catch-effort data through sales records, port interviews, and in some cases logbooks. Sampling programs were also initiated to collect length measurements and age samples of key species. Both the United States and Canada have field staff engaged in this work at major ports. The data are used to estimate the locations of catches from designated statistical areas (Figure 2.1.1; in some cases even smaller breakdowns, e.g., 10-minute square data is available), the size and age composition of the catch, and the fishin effort by gear trips and vessel size. Part of the catches are discarded at sea; these have been poorly estimated and what data are available has come sometimes by fishermen reports and sometimes from sampling at sea. The latte efforts have been few. It is important to note that where sales categories contain several species, such as landings sold for industrial purposes, port agents take samples to estimate species composition. Concomitant with collection of catch-effort statistics is the need to have them in usable form for analyses. Extensive computer data banks have been established by both the US and Canada.

The International Commission for the Northwest Atlantic Fisheries (ICNAF) was established in 1949 with the goal of conserving the fishery resources of the Northwest Atlantic Ocean, and promoting the maintenance of a maximum sustained catch (ICNAF Handbook 1974a).

ICNAF immediately began collecting and publishing fishing catch-effort statistics by standard Statistical Division (see Figure 2.1.1) As the fisheries distant-water fleet expanded so did the details required by ICNAF. Prior to 1960 the area southwest of the Fundian Channel was exclusively a US sea with only minor Canadian fisheries. The following two decades witnessed a rapid buildup of distant-water fleets and the southward expansion by Canada. Fortunately, more detailed requirements for statistical reporting to ICNAF closely followed this expansion. Since the extension of coastal state jurisdiction by the US and Canada in 1977, distant-water fleet statistics have been reported in small area detail and coastal state observers have sampled catches at sea on the foreign vessels. Commercial statistics are published in ICNAF Statistical yearbooks but for more detailed data one needs to access US and Canadian computer files.

In the United States recreational fisheries are also very important. Mail surveys of recreational fisheries were made in 1960, 1965, and 1970 (ref. Clark 1962; Deuel and Clark 1968) and a phone survey was conducted in 1974 (personal communication D. Deuel, Northeast Fisheries Center, Narragansett, RI, USA). Occasionally special surveys have been made of selected segments of the recreational fishery. Beginning in fall 1978, an extensive intercept and phone survey of recreational catch was initiated by NMFS.

2.2 Research Vessel Trawl Surveys

Data from the fisheries are critical to establishing a management program but data independent of the biases inherent in commercial statistics are also essential. In particular pre-recruit estimates were needed as well as more complete estimates of the finfish biomass as a whole. To achieve this a long-range program of bottom trawl surveys on research vessels was begun by the United States in 1963. This approach was a major departure from earlier research which had concentrated on a variety of unconnected cruises focusing on a few species. The design of the survey was stratified random using depth, latitude, and traditional fishing areas (often related to bottom type) as factors in stratification. Initially (1963 to 1966) the survey covered the area from Hudson Canyon to western Nova Scotia (Figure 2.2.1), In 1967 the coverage was extended south to Cape Hatteras. An autumn series exists since 1963, a spring series since 1968. Vessel, gear, time of tow (½ hour), speed of tow, and other operational procedures have been standardized as well as the processing of fish on deck and the data in the laboratory. The basic minimum routine data recorded for each catch include the weight and length frequency of each species of finfish, and selected invertebrates such as squid, lobster, crab, and shrimp. In addition scales, otoliths, gonads, and stomachs are collected for assessment and ecological studies including growth, mortality, reproduction, and food habits. Details on the sampling procedures are given by Grosslein (1969 a, b, c), Grosslein (1974), and Clark (1978).

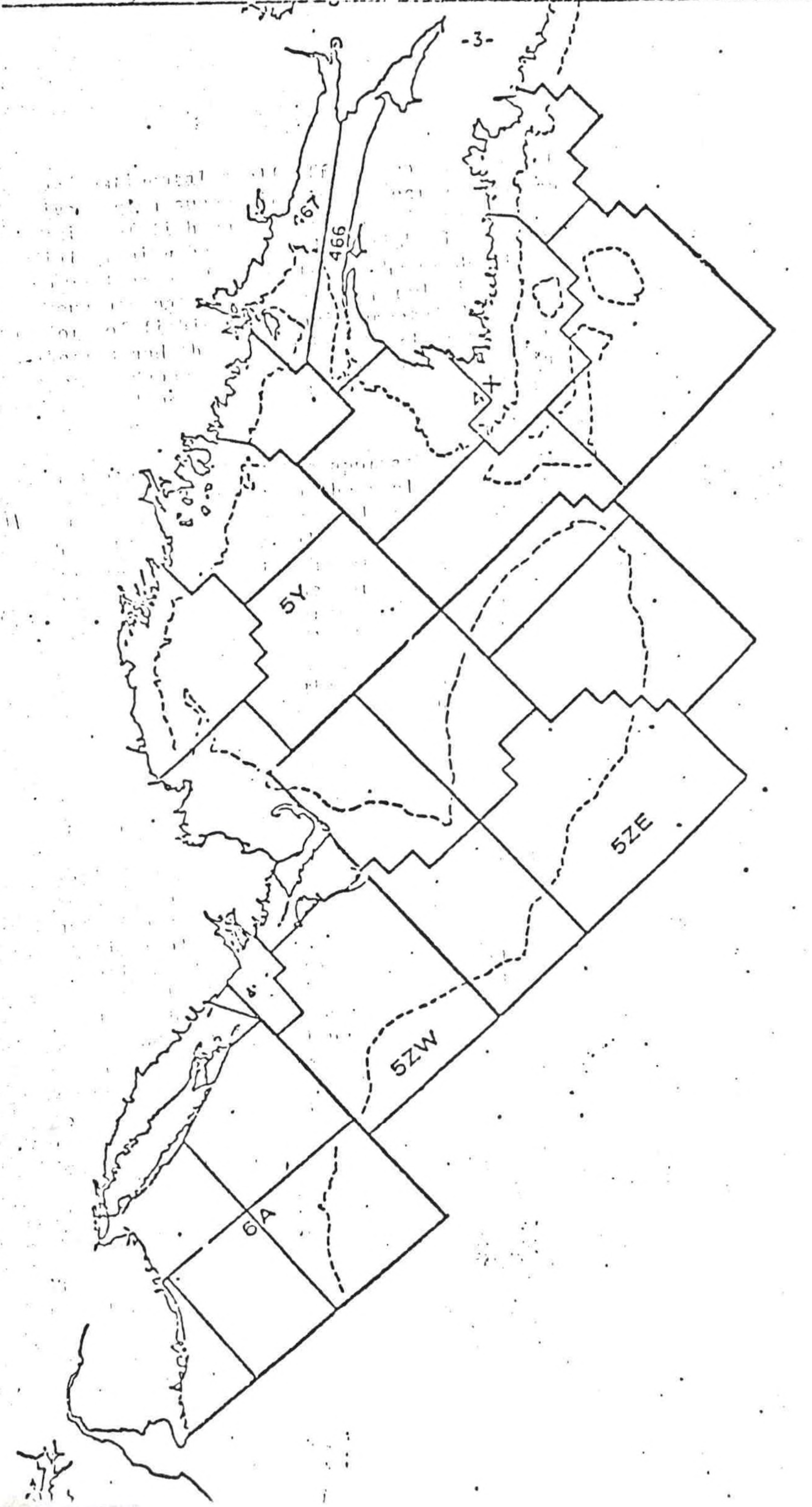


Figure 2.1.1 U.S. Statistical Areas and ICNAF Divisions (bold lines, 5ZE, 5ZW, etc.) for catch and

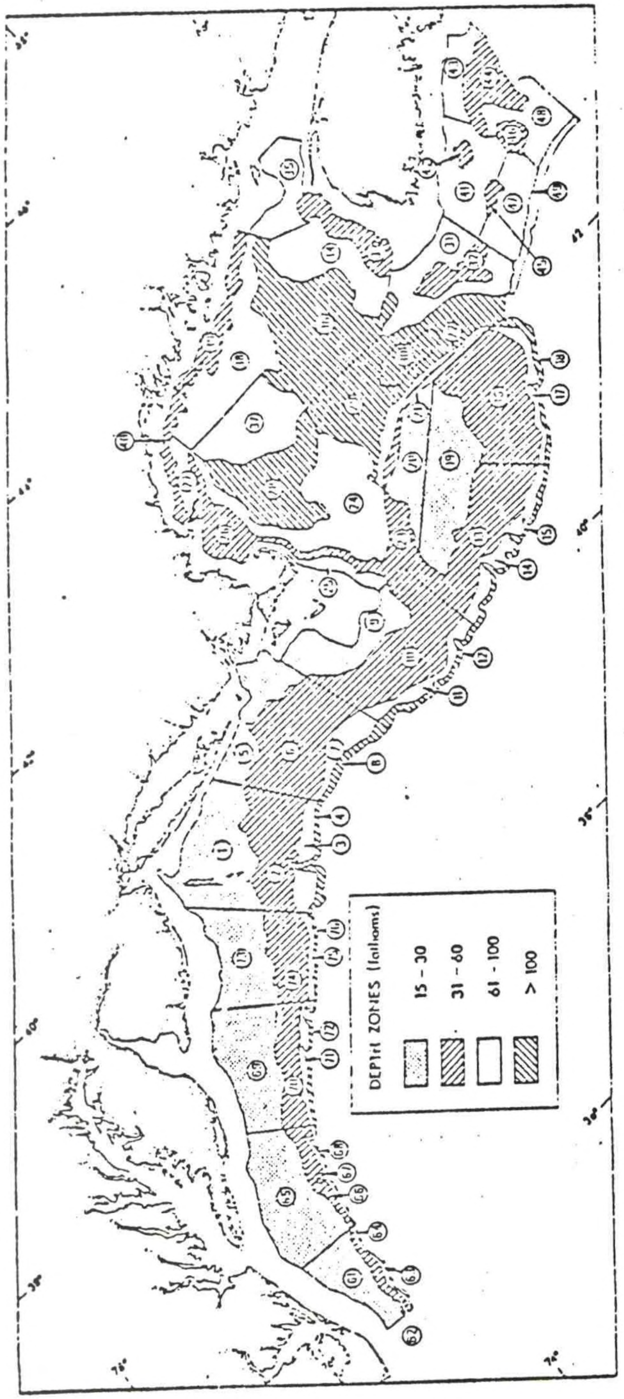


Figure 2.2.1 Offshore (> 15 fathoms) sampling strata used for U.S. bottom trawl surveys by Northeast Fisheries Center.

Since 1972 inshore strata have been surveyed in the Middle Atlantic area and the sampling scheme extended to Florida (Figure 2.2.2). Since 1977 a summer survey has been carried out in the shallower areas (less than 110 m) with inshore stations in the Gulf of Maine and Southern New England as well as in the Middle Atlantic. Numerous additional surveys by both the US and other nationals have taken place both in other seasons and concurrent with the US autumn surveys. The greatest number of such cruises have been conducted by the USSR, but France, Federal Republic of Germany, the German Democratic Republic, and Poland have also used this design. Although other countries used different vessels and gear the common random stratified design has facilitated analyses. Canada has conducted similar surveys on the Scotian Shelf since 1970 (Figure 2.2.3), and a few years later the program was extended to include the Grand Bank and Labrador.

This large time-series data bank collected with standardized procedures capable of being analyzed statistically in a comparable way from survey to survey has provided the key in the ability to develop multispecies approaches to fisheries management.

2.3 Events Demonstrating Need for Multispecies Approach

Brown (1976) briefly described the history of fishery management and the expansion of the fisheries in the area off the northeastern US. From the early 1930's to the early 1960's, fisheries resource assessment science and fishery management focused on single species--essentially an autecological approach to fisheries. The newly developed population dynamics models used by the scientists focused on unit stock populations, although as ecologists, fishery scientists were well aware that each species was affected in some way by all other components of the ecosystem. For example, McHugh (1959) stressed the need to consider "management en masse" in the Middle Atlantic marine fisheries. Interactive effects were assumed to be accounted for in the responses of a single species monitored over fairly long periods of time. This was not an unreasonable approach prior to 1960 for the region off the US coast because of the relatively low fishing effort directed at a few species. Events from 1961-1973, however, completely destroyed the validity of the single-species approach to fisheries management. During that time the entrance of distant-water fleets resulted in a large and very rapid expansion of the fisheries. Total catch increased approximately three times, while effort is estimated to have increased sixfold (Brown et al. 1976). Most of this fishery was conducted by relatively unselective otter trawl gear harvesting virtually every species of a size large enough to be retained in the net. Some nets had mesh sizes as small as 40 mm. Some species were taken as by-catch (i.e., catch other than the object of the fisheries) but many stocks such as Georges Bank herring and squid, which previously had been little exploited, became the focus of major directed fisheries. The entrance into specific fisheries often took place sequentially as intensive fishing reduced stocks which had temporarily increased in abundance due to a few strong year classes, classical examples being haddock and yellowtail flounder. Such a fishing strategy has been called pulse fishing.

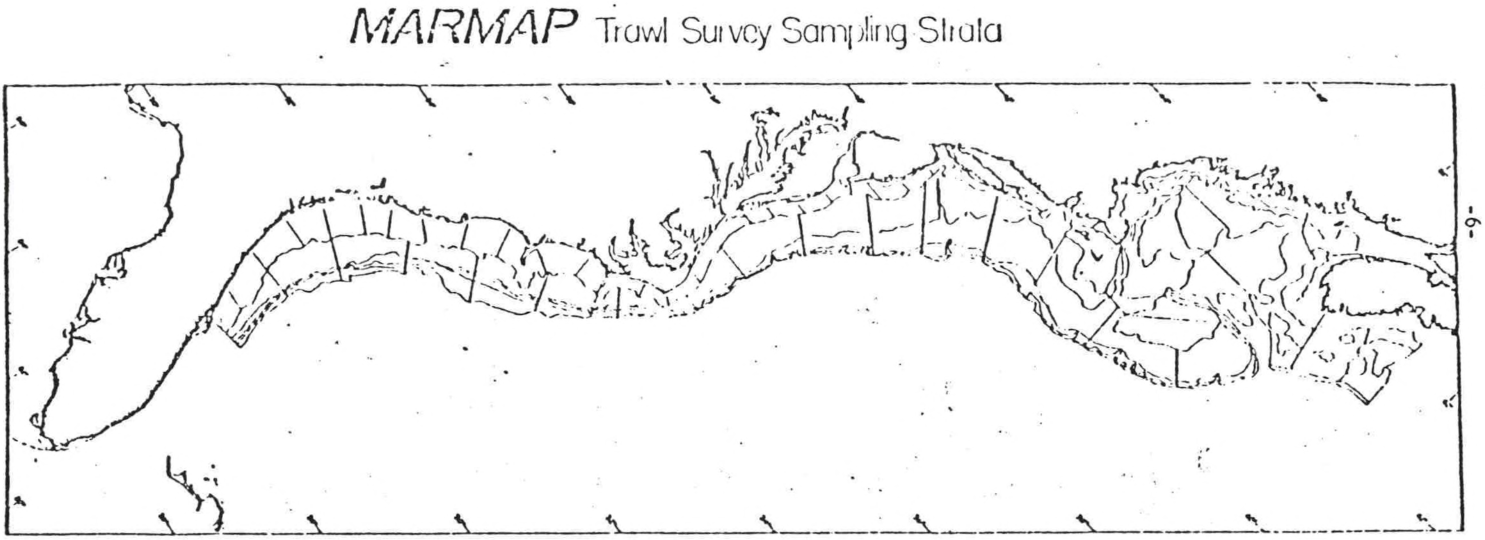


Figure 2.2.2 Trawl survey sampling strata for U.S. Marine Monitoring, Assessment, and Prediction Program (MARMAP) since 1972.

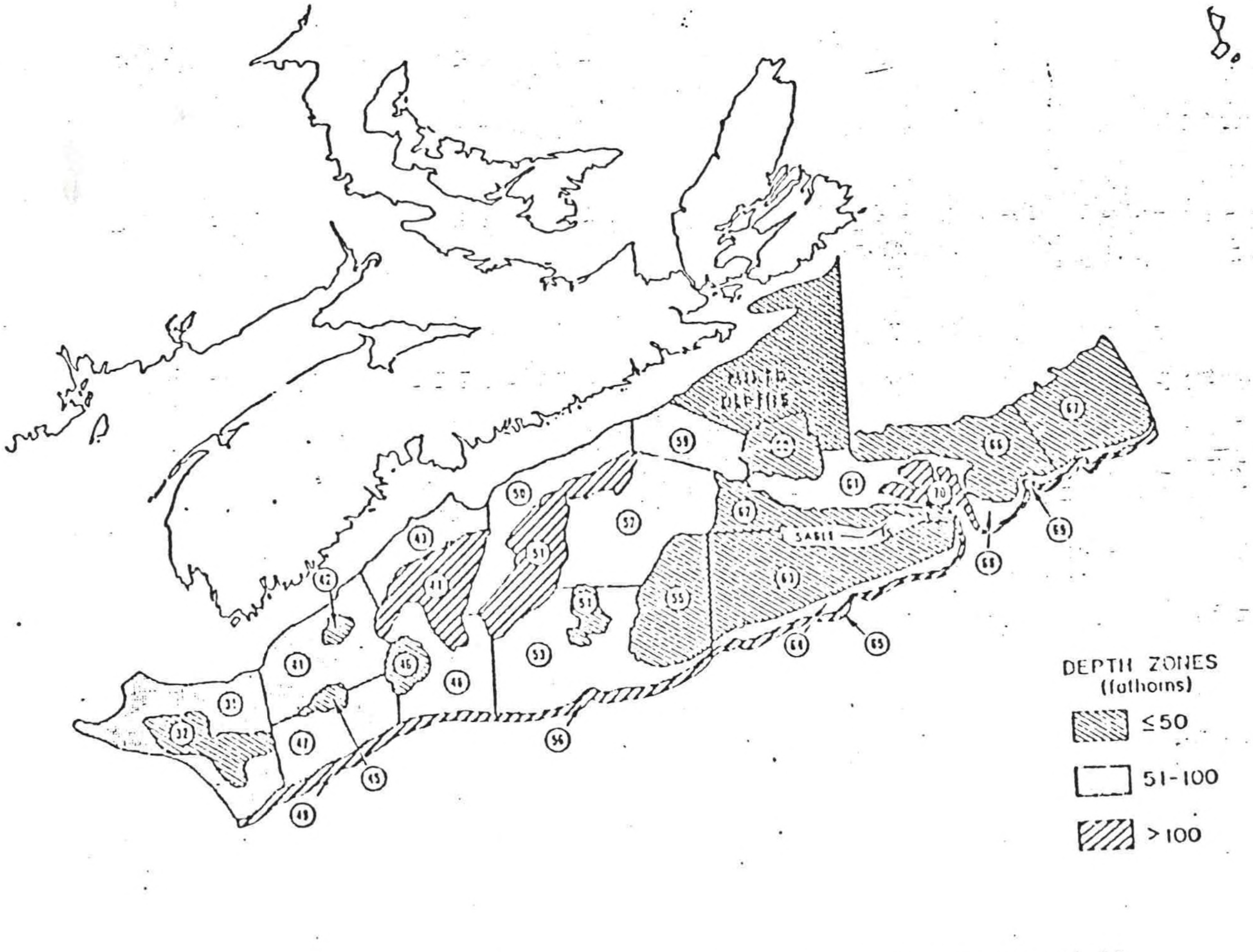


Figure 2.2.3 Sampling strata used in Canadian bottom trawl surveys on the Nova Scotian Shelf.

Single-species management began with catch limitations on haddock in 1970 (ICNAF 1969) followed by yellowtail flounder in 1971 (ICNAF 1970) and herring in 1972 (ICNAF 1972). By the 1972 June annual meeting of ICNAF the evidence was mounting that a total system of multispecies management was needed and ICNAF greatly expanded its management system for 1973. The wide mix of species available to the relatively unselective trawl gear (Grosslein and Bowman 1973) made the move to multispecies inevitable. (Figure 2.3.1).

Brown et al. (1976), Clark and Brown (1977), and Clark and Brown (in press) describe the mounting evidence of the effect of the expansion of the fisheries on the total finfish biomass. By 1972 declines had not only been noted in several species but Brown and Brennan (1972) and Grosslein (1972) presented evidence from survey cruise and commercial catch/effort analysis that the total finfish resource had declined to below half of what the virgin stock might have been and that fishing effort was exceeding that which would produce MSY (Figure 2.3.2, Brown et al. 1976; and Figure 2.3.3, Clark and Brown, in press). The responsibility of the Assessment Subcommittee of ICNAF to provide advice on all of the resources in the ICNAF area provided the proper forum for scientific acceptance of an approach for multispecies management. Any species for which assessment research was done by a member scientist was discussed by the subcommittee. The basic procedure used in these yearly assessments was to review all the available knowledge about the biology and current status of the stock and to try to predict the relative effects of potential catches. These assessments were subject to interactive peer review in the Assessment Subcommittee and written summaries were presented in the ICNAF Redbook Series.

As these discussions expanded to more and more species, they drove home very clearly that the effect of the Northwest Atlantic fishing fleet in this area was to depress productivity across the board. The most easily demonstrated effect was that of "by-catch." "By-catch" was defined as species taken on a fishery other than the species primarily caught. This meant that a regulation designed to control fishing mortality on one stock would also result in mortality on other stocks. Linear programming models (Brown et al. 1973, and Brown et al. in press) were used to simulate this situation and provide guidance for commissioners in setting regulations.

At the 1972 ICNAF Annual Meeting the quota system for 1973 was expanded to almost all of the major species being fished (ICNAF 1972). At the January 1973 Special Meeting (ICNAF 1973) the quota system for 1973 was further extended to cover all species either singly or in species groups. Discussion was begun on an overall regulation and at a Special Meeting in October 1973, an overall allowable catch was set for 1974 for finfish plus squid resources in ICNAF Subarea 5 and Statistical Area 6 (ICNAF 1974b). The long-range plan was designed to halt the decline in biomass in 1974 and 1975 and then begin recovery in 1976.

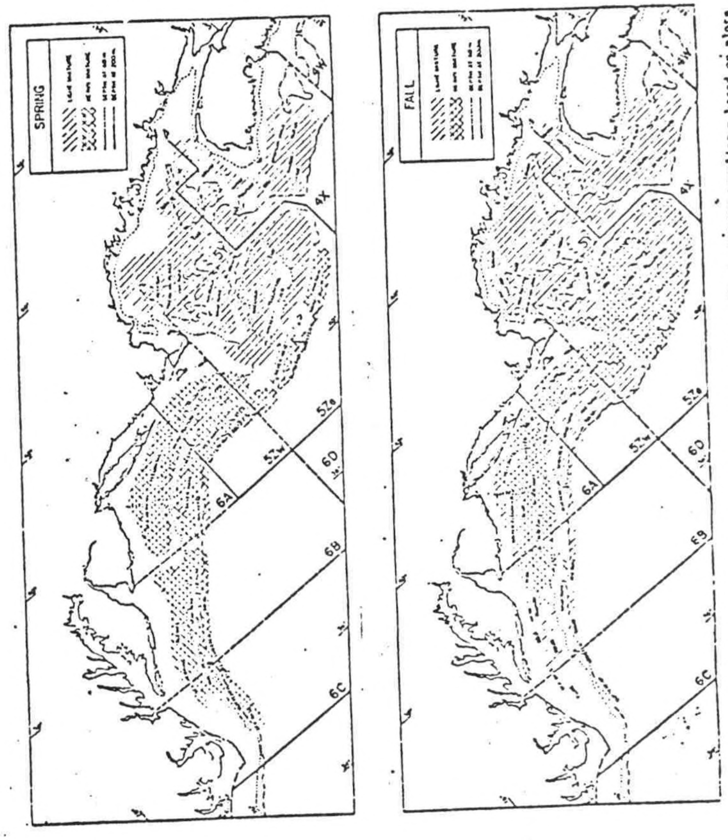


Figure 2.3.1 Generalized picture of mixture of important species vulnerable to bottom trawling - based on plots of individual catches of groundfish surveys.

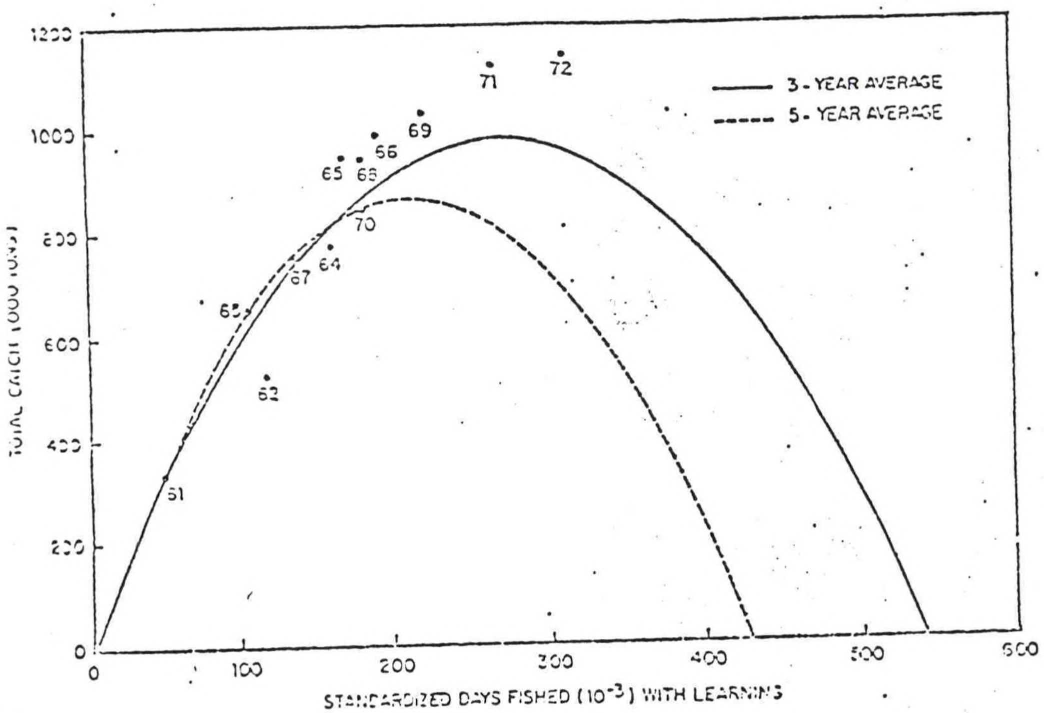


Figure 2.3.2 Total catch (finfish plus squid) vs. standardized effort (with learning) for SA 5 + 6, 1961-72, using a 3-year average over standardized effort (days fished) and a 5-year average over standardized effort. Original data points (catch vs. standardized days fished) are plotted.

This policy of overall multispecies management was in effect for 1974, 1975, and 1976. In 1977 the United States and Canada extended their jurisdiction to cover the area previously under ICNAF management. However, for various reasons 1977 can be considered a continuation of the ICNAF management decisions. As the survey estimates of biomass (Figure 2.3.3, Clark and Brown, in press) indicate this management approach was achieving its objective of recovery of the finfish plus squid biomass.

Estimates of the total productivity of the fishery resources of SA 5 and 6 in terms of maximum sustained yield (MSY) assuming that the present relative mix of species is desired, was estimated to be between 850,000 and 1,000,000 metric tons by Brown et al. (1976). They used a Schaefer yield curve (Schaefer 1954) with several major components of the fishing effort adjusted for learning during the first years of the fishery utilizing survey data as a standard. If no such adjustment is made, estimates from catch-effort data range from 940,000 to 1,300,000 MT. Another approach to estimating MSY is that of Gulland (1971) for predicting yield from virgin populations. Taking Clark and Brown's (1977) estimate of virgin biomass (B) of 8,000,000 MT and natural mortality rates (M) of 0.2 and 0.25 then $u_{max} = 0.5\ MB_0$,—i.e., 800,000 to 1,000,000 MT.

2.4 Estimation of Critical Population Parameters

In fish population dynamics there are several critical parameters that are needed as inputs. These are instantaneous natural mortality rate M, instantaneous fishing mortality rate F, growth, maturation, and fecundity. Mortality rates are generally estimated first as total mortality rate Z and this is separated into fishing and natural components. Total mortality rates are most commonly estimated from relative abundance of fish of the same cohort in successive years using the following model:

$$N_{i,t+1} = N_{i,t}e^{-Z_t} .$$

where i = cohort on year class
t = time (one year is the usual time period for fish population models past the larval stages)
Z = instantaneous natural mortality rate.

Estimates of N_{t+1} and N_t can be made using virtual population estimation procedures. More frequently ratios of indices of $N_{i,t+1}$ from commercial or survey vessels are used and occasionally ratios of marked individuals.

The fishing mortality rate is usually obtained by subtracting M from Z. Although F can be estimated directly from mark and recapture studies (see Ricker 1975, p. 83) but the difficulty of successfully conducting such studies to estimate mortality rates in the large-scale ocean environment usually precludes their use in marine fisheries. It should be noted that F is generally age specific as can be seen in catch-at-age data.

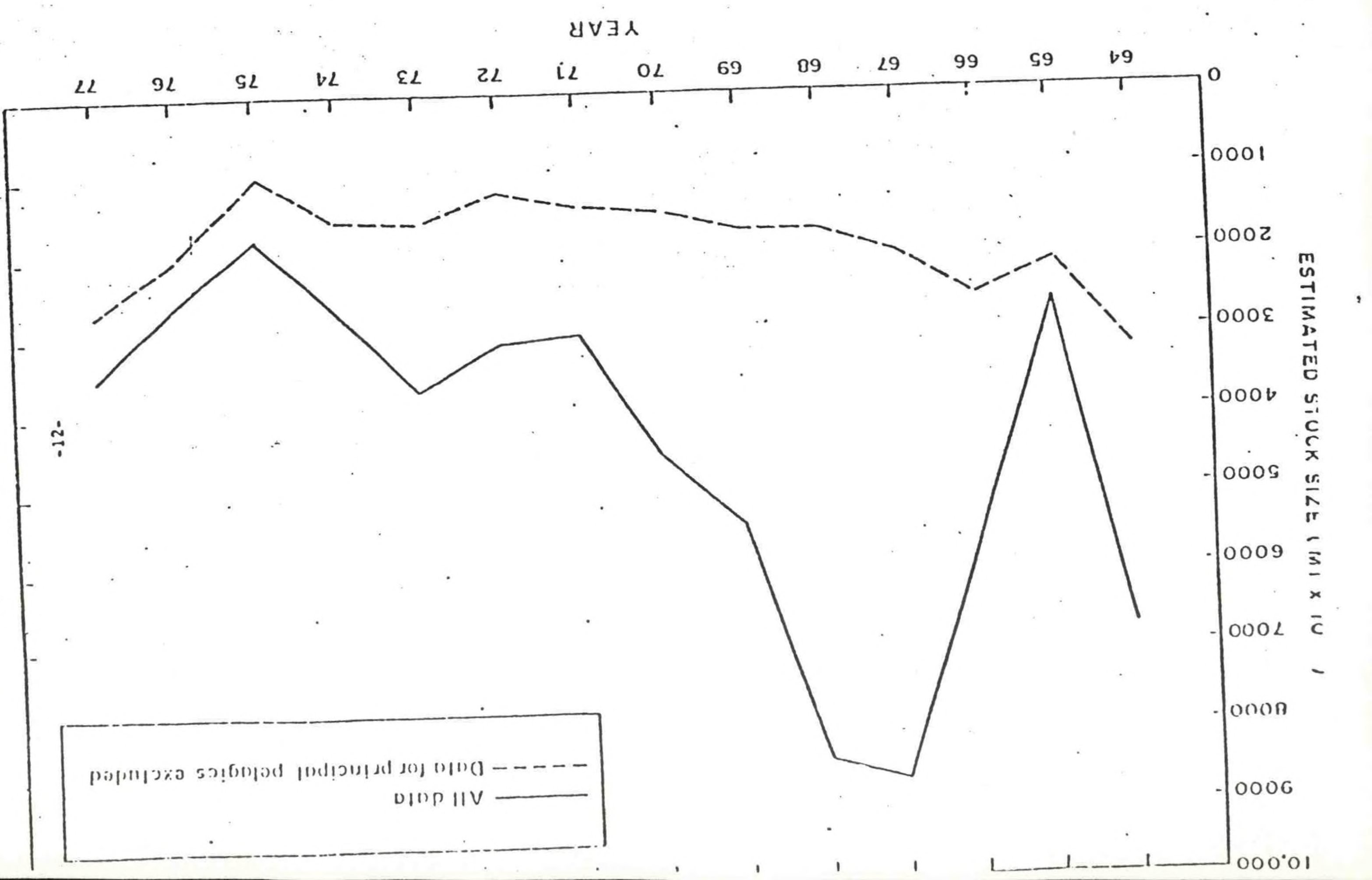


Figure 2.3.3 Estimates of fishable biomass by year for ICNAF Subarea 5 and Statistical Area 6, 1964-75, calculated with retransformed survey data (from Clark and Brown [1977], Figure 13).

Natural mortality is the most difficult parameter to estimate, and the value used in the assessment of a particular stock is determined by inference from other stocks with similar biology and from general biological considerations, i.e., few predators can swallow large cod while many can swallow sand lances (Ammodytes sp.). When age data are available at the beginning of a fishery when there is little effort, ratios of N_t and N_{t+1} may provide estimates of Z which are close to M. If a measure of fishing effort proportional to F is available then that effort can be plotted against Z and the intercept (when effort equals zero) interpreted as M (Ricker 1975, p. 11). An understanding of the causative sources of natural mortality obviously is needed to move ahead in the modeling of natural mortality.

A large amount of fishery research effort has been devoted to aging. In 1977 the Northeast Fisheries Center aged 46,000 individual fish of 15 different species. Aging, of course, is necessary to define year-class composition of commercial catch and also research samples, for use in estimating mortality rates and relative strength of year classes. Aging is also critical to define age at maturity, and relationships of fecundity to age. These parameters are related to age and size and can change with time (see Lett in press, for example) and these may well serve as a buffer against exploitation. Knowledge of the parameters are critical for examining the potential of the spawning stock and thus require monitoring.

There are still numerous stocks for which the size, age-maturity, fecundity relationships are not yet elaborated. Production of gonadal products is an important component of the energy requirements of fish and is critical to the dynamics of fish production. Size at maturity for 20 species was monitored by the Northeast Fisheries Center by examining 8,000 individuals in the first half of 1978.

In addition to the above uses, aging is needed to determine size at age and the changes in average size at age. With appropriate analyses (for example adjusting for differential harvest rates) these data can be used to estimate growth rates. These rates are necessary for the estimates of the basic yield-per-recruit models discussed earlier and for yearly assessments to examine biomass trends. Finally growth is needed for estimation of productivity in ecosystem models.

2.5 Status of Fish Production Modeling

Sissenwine et al. (in press) discussed this subject in detail and the following is taken mainly from that paper.

Net production by a given year class (cohort of fish spawned during the same year) is the difference between the sum of the weight gained by individuals in the population and the sum of the weight of fish lost due to death. Figure 2.5.1 gives an example of the time history of the number of surviving individuals of a year class (N), the average weight of an individual of the year class ($\overline{w}$) and the total biomass of the year class ($N \cdot \overline{w}$). The maximum possible yield from a particular year class is the peak of the total biomass curve. To obtain this yield, the entire biomass must be harvested instantaneously which is usually impossible and economically unacceptable. A central problem of fishery science has been to model yield for combination of fishing mortality rate (F) and age at which a year class is first exploited (t_c). The basic procedures used are given by Beverton and Holt (1957) and Ricker (1975).

Surplus-production models

There is often inadequate information available to distinguish between components of production of a fish population resulting from growth and recruitment. Therefore, surplus production (SP) is sometimes related to stock biomass (B) empirically and the empirical relationship is used to model the effect of fishing on the population. Under stable environmental conditions, recruitment and growth are balanced by natural mortality for an unexploited population, thus, there is no surplus production. When fishing begins, biomass is reduced and the available food is used more efficiently by the remaining population. Thus surplus production is generated so that the population would recover to B_{max} if fishing were stopped. Ricker (1975) attributes these hypotheses concerning the relationship between production and population biomass to Peterson (1922) and Baranov (1926, 1927).

Graham (1935) incorporated these ideas into a model of surplus production. He assumed that the instantaneous rate of surplus production per unit of biomass ($\frac{1}{B}\frac{dB}{dt}$) is directly proportional to the difference between the actual biomass and the carrying capacity the area will support. The specific model is:

$$\frac{1}{B}\frac{dB}{dt} = r\,(B_{max} - B)$$

r = instantaneous rate of increase of stock at a density approaching zero. Application of the above equation to fisheries was popularized by Schaefer (1954, 1957).

Pella and Tomlinson (1969) argue that the functional relationship between dB/dt and B is not always symmetric and, therefore, they considered a more general model where the surplus production rate equals a linear combination of B and B^m for any value of m. A family of generalized surplus production curves is plotted in Figure 2.5.2. The quadratic function (m=2) is still most widely used because it is more easily fit to data (particularly under the assumption of equilibrium). Furthermore, the available data to which surplus production models are fit is often inadequate to indicate the degree of asymmetry in the functional relationship between dB/dt and B.

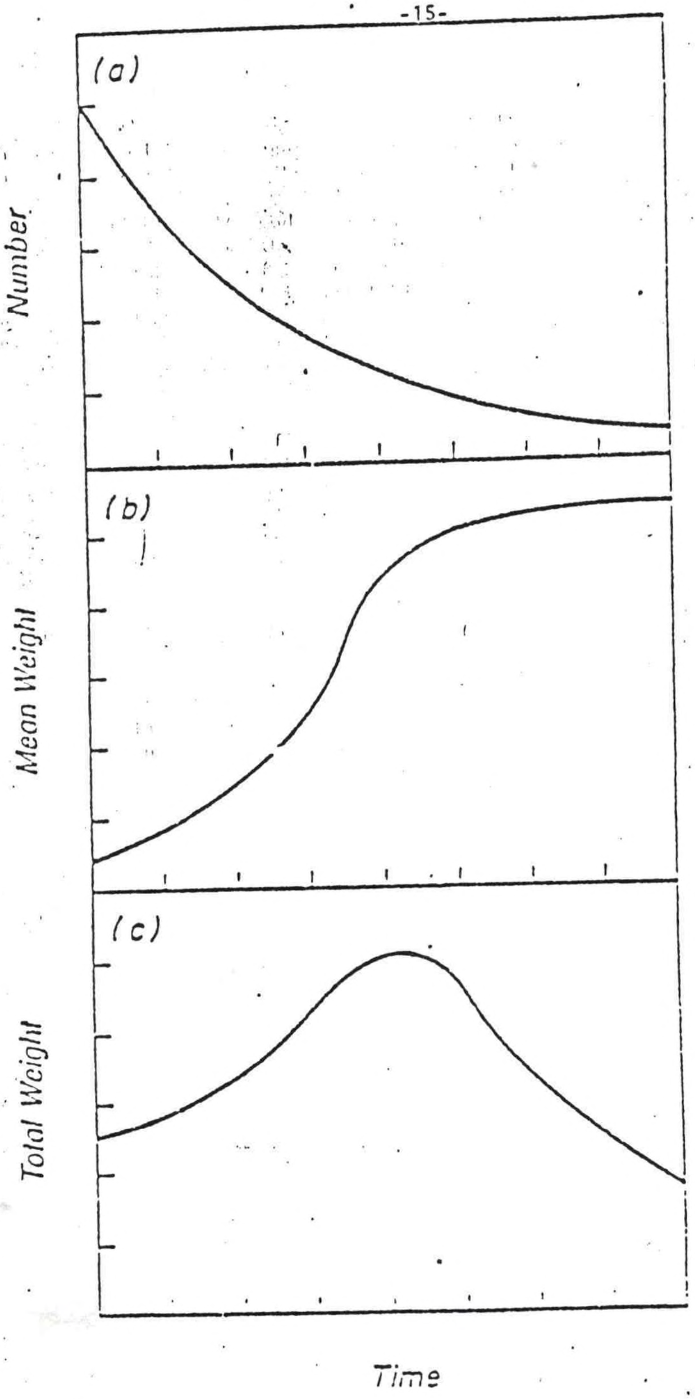


Figure 2.5.1 Example of a time history of the changes in a year class in terms of the number, mean weight, and biomass.

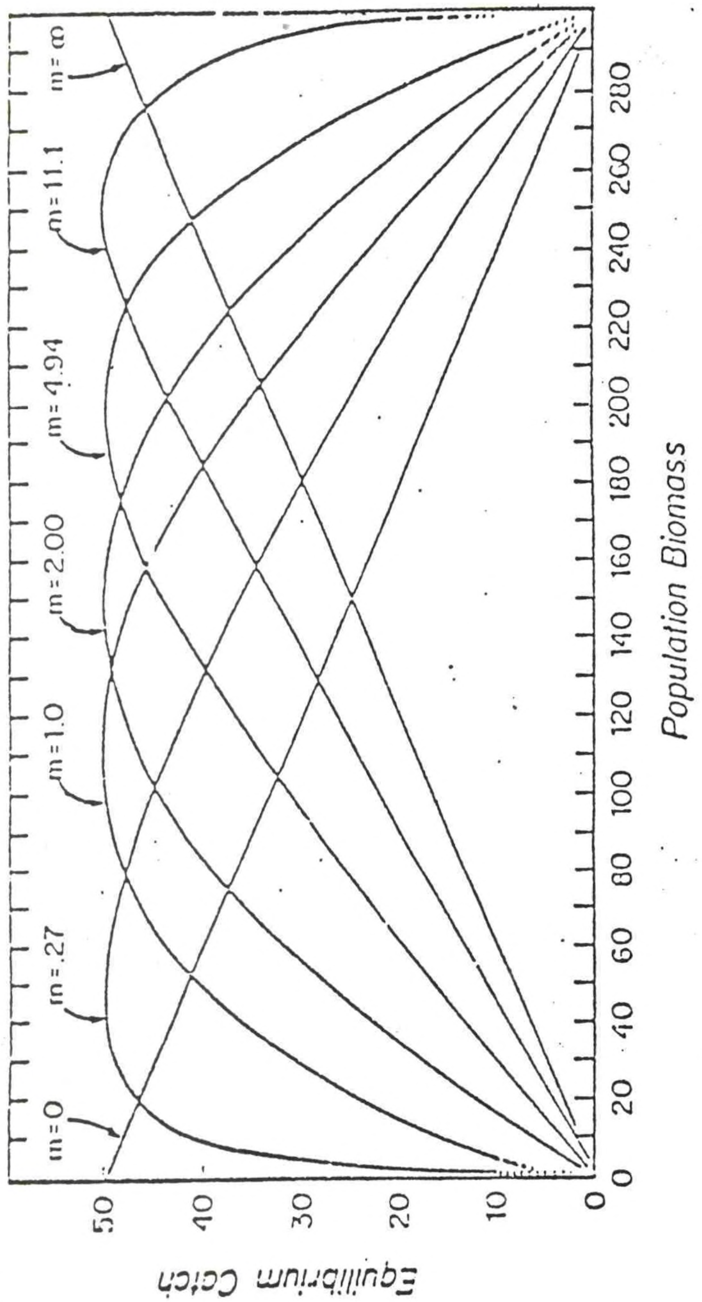


Figure 2.5.2 Family of generalized surplus-production curves after Pella and Tomlinson (1969).

Two glaring deficiencies limit the usefulness of the preceding models: (1) there is no time lag between the change in population size and the change in the rate of population increase, and (2) the rate of population increase is assumed independent of the age composition of the population. Walter (1973) proposed two surplus-production models (to be fit to catch and effort data) to account for time lags. The models assume that density dependent growth and mortality are proportional to the biomass at some previous time. Marchesseault, Saila, and Palm (1976) also proposed a surplus-production model incorporating a time lag.

Recently Walter (1978) proposed a model which offered a modification to the basic Schaefer formation by taking into account changes in recruitment. Recruitment is treated as an impulse (added to B) once a year, and the dynamics of population biomass are described by Equation (25) between impulses of recruitment. Walter provided expressions for long-term equilibrium yield under assumptions of a linear and density-dependent stock-recruitment relationship.

Other variations of the Schaefer model have been considered in recent years. Schnute (1977) allowed for stochastic variation in the fishery and provided a method for predicting yield in future years. Pope (1975 a, b) modified the Schaefer model in order to determine optimum yield in a mixed fisheries situation by attempting to account for biological interactions between species. Pope concluded that interactions cause the combined MSY to be less than the sum of the individual MSY's of the species. Brown et al. (1976) came to the same conclusion when applying the Schaefer model to total catch (all species combined) per unit effort and total fishing effort for the fisheries of the US continental shelf north of Cape Hatteras.

The surplus-production models described above ignore the year-to-year effect of environmental fluctuations on populations. They also ignore (with a few exceptions) the direct effect of species interactions. Thus, considerable unexplained variation in surplus production is likely. Fishery scientists often assume that when a surplus-production model is fit to a time series of data that extends over periods of both favorable and unfavorable environmental conditions, the model will provide a useful representation of the stock-production relationship for average conditions. Furthermore, it is often assumed that management based on the model will produce the predicted results on the average. For example, it is often assumed that a fishing mortality of F_{msy} will produce a long-term average yield of MSY from a population fluctuating about an average size of B_{msy}. Doubleday (1976) and Sissenwine (1977 a, b) demonstrated that, in fact, for a fluctuating environment, the long-term average yield and population size will probably be lower than predicted by the Schaefer model. Beddington and May (1977) conclude that as F increases toward F_{msy}, variability in population biomass increases. Thus, it is unrealistic to ignore environmental fluctuations when applying deterministic surplus-production models.

Stock-recruitment models

Most of the variability in production by exploitable marine fish populations results from variability in recruitment. Cushing and Horwood (1977) noted that recruitment may vary by up to a factor of 100. Variability in recruitment is certainly related to abiotic factors (such as climate conditions). While attempts to relate recruitment to the size of the spawning stock have not been particularly successful, such attempts have been made.

The two most commonly considered stock-recruitment (S-R) models are attributed to Beverton and Holt (1957) and Ricker (1954). Cushing (1971) also proposed an exponential relationship between stock and recruitment. Cushing's exponential model is similar in shape to the Beverton and Holt S-R model.

Ricker distinguished two types of mortality during the pre-recruit stage of the life cycle: density independent and density dependent mortality. Ricker hypothesized that density dependent mortality is caused by cannibalism and, therefore, the density dependent mortality rate is proportional to the density of the spawning stock. The biological mechanism of cannibalism leads to:

$$R = A\,S\,e^{-DS}$$

where A is the coefficient of density independent mortality and D is the coefficient of density dependent mortality. For multi-age spawning species, S (the size of the spawning stock) is measured in eggs spawned and R as lifetime egg production of recruits suffering only natural mortality (Ricker 1975). The above equation can also be explained biologically if larval growth is density dependent (as might occur when larvae compete for food) and mortality decreases when the larvae reach and exceed a critical size (Beverton and Holt 1957).

The family of Ricker curves is plotted in Figure 2.5.3. The diagonal straight line at 45° angle to the horizontal axis is the equilibrium line. For points above the 45° line, recruits more than replace their parents and the stock grows when there is no fishing. For points below the 45° line, the size of the population declines. The equilibrium yield expressed in recruit eggs is equal to the vertical distance between the curve and the 45° line for each value of S.

Beverton and Holt (1957) also considered both density dependent and density independent mortality, but they assumed that density dependent mortality is linearly related to larval density during a limited time period. For A and D still representing the coefficient of density independent and dependent mortality, respectively,

$$R = \frac{1}{A + D/s}$$

A family of Beverton and Holt curves is plotted in Figure 2.5.4 with a 45° line. The equilibrium yield for each curve is again represented by the distance between the curve and the 45° line for a particular value of S. Ricker (1975) tabulated critical characteristics of these stock-recruitment relationships such as (1) size of the spawning stock needed to maximize recruitment, (2) maximum equilibrium exploitation rate, and (3) size of spawning stock needed to support the maximum equilibrium catch.

The Ricker S-R function has been more widely applied to fish populations than the Beverton and Holt function. Dome-shaped functions are apparently more effective in fitting data for two weakly related variables regardless of the biological justification for the function. Also, because of confounding of the dependent and independent variables when the function is linearized the fit of the Ricker model to a pair of randomly generated series of numbers often appears statistically significant. Thus, a nonlinear fitting procedure (such as Marquardt 1963) should be used when applying the Ricker S-R function.

A stock-recruitment function can be combined with a yield-per-recruit analysis. Beverton and Holt (1957) and Walters (1969) developed combined S-R and YPR models. These self generating models (with respect to recruitment) can be used to simulate populations and examine sustainable yield. Unfortunat these are deterministic models and it is unrealistic to ignore the stochastic nature of the system. This point was clearly demonstrated for surplus production models (which are discussed below) by several recent papers.

Examples of the Ricker S-R function along with the data to which the functions were fit are given in Figure 2.5.5. Substantial unexplained variability remains, but this situation is not unusual. In fact, the traditional stock-recruitment functions probably fail to explain a statistically significa portion of the observed variability in recruitment for most fish populations. This failure may partially result from the inadequate data bases (both quantit and quality) available to describe stock and recruitment.

Because of the observed variability in recruitment, some authors (Thompson and Bell 1934; Graham 1935) have concluded that recruitment is independent of spawning stock size. Actually, the underlying relationship between recruitment and spawning stock size may be obscured by environmentally related noise, but a S-R relationship must exist particularly at low levels of spawning stock size. Recruitment of the Georges Bank haddock stock is quite variable and a S-R relationship has not been resolved empirically, but recruitment has been generally lower and more variable when the spawning stock size is small (Grosslein and Hennemuth 1973). During the period of 1964-1977, only the 1975 year class was exceptionally strong and all others were below average size. During this same period the spawning stock size was extremely low as a result of overfishing. During 1935-1960, when spawning stock size was much higher, year classes as large as the 1975 year class occurred about every third year. Thus, environmental conditions may have to be particularly favorable when spawning stock size is low for a strong year class to be produced.

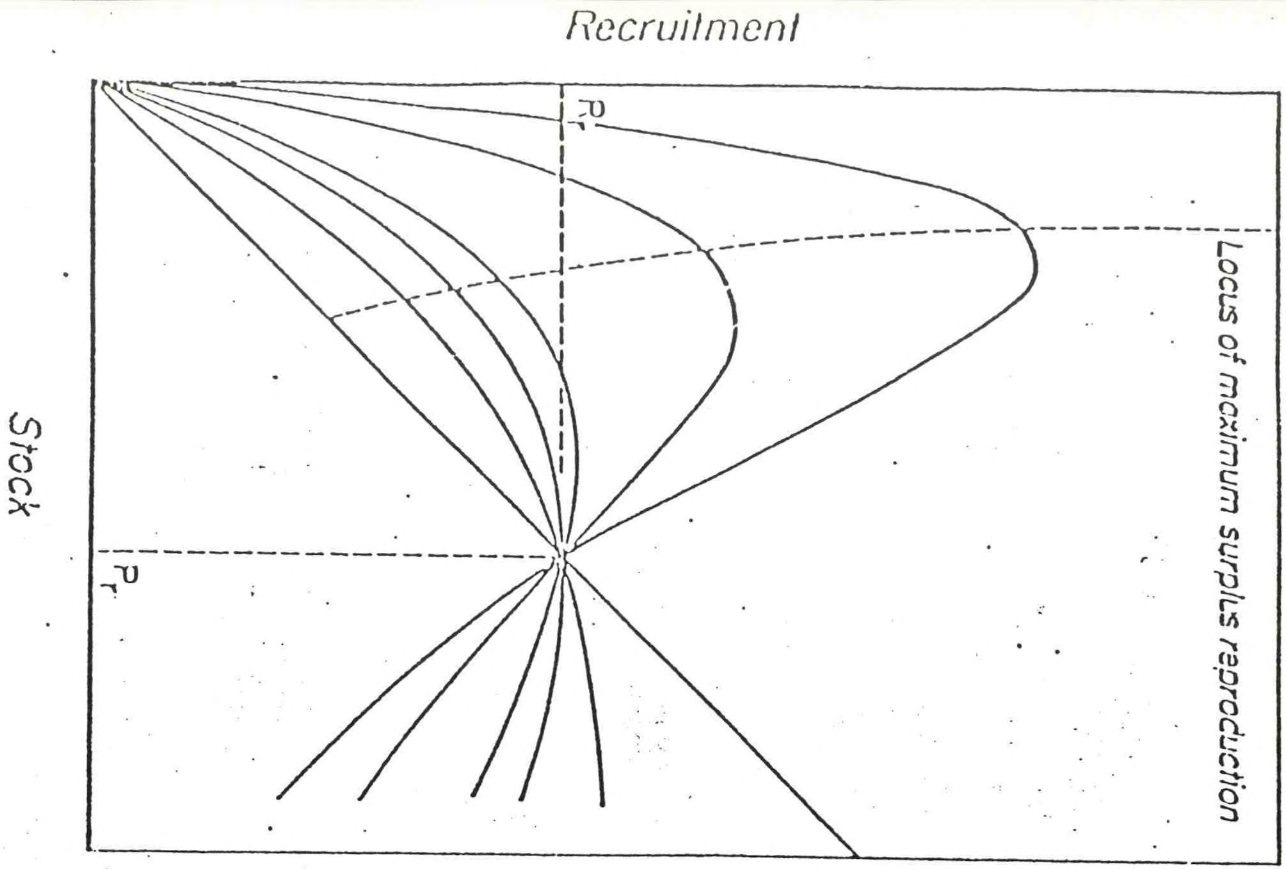


Figure 2.5.3 Family of Ricker stock-recruitment curves.

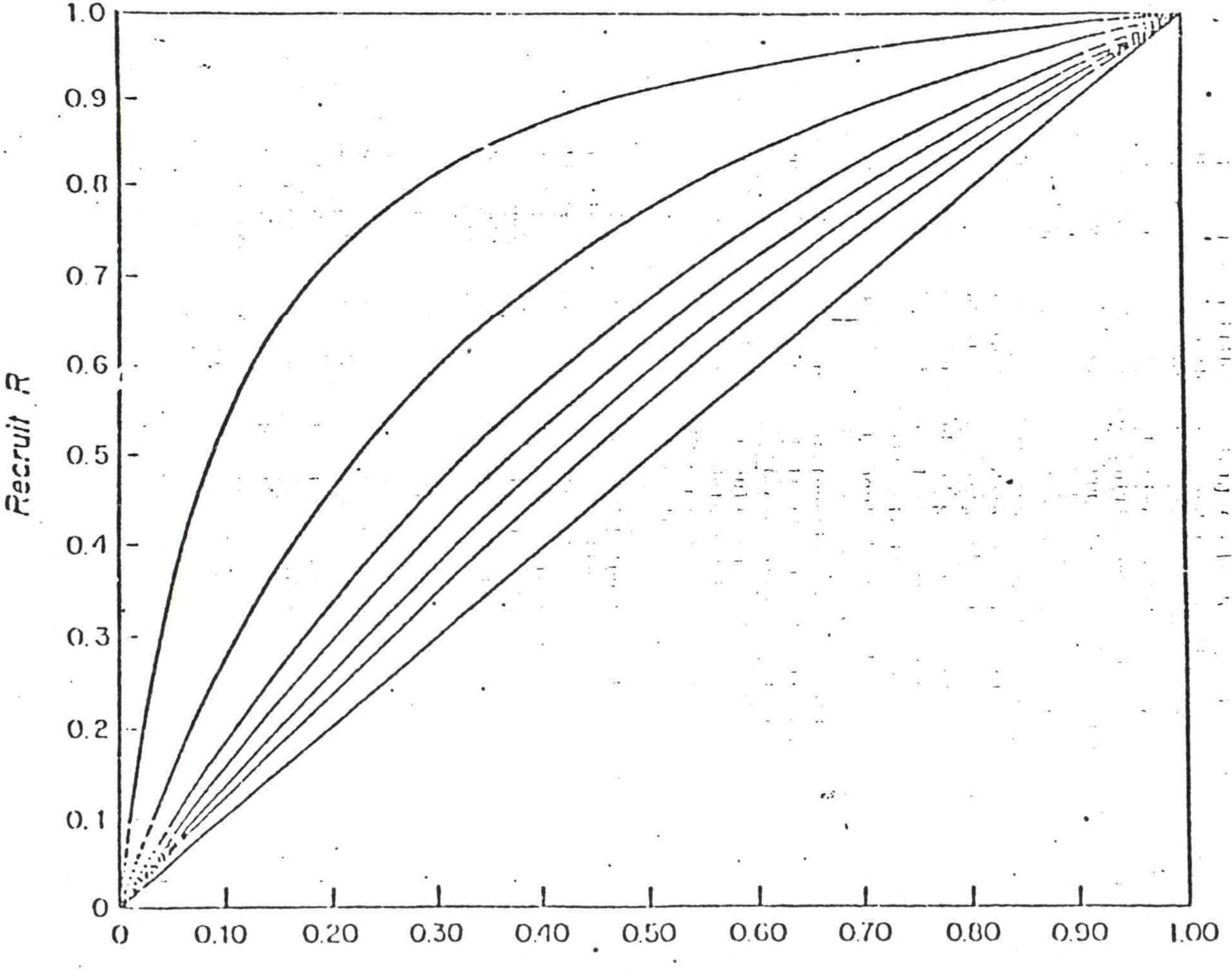


Figure 2.5.4 Family of Beverton and Holt stock-recruitment curves.

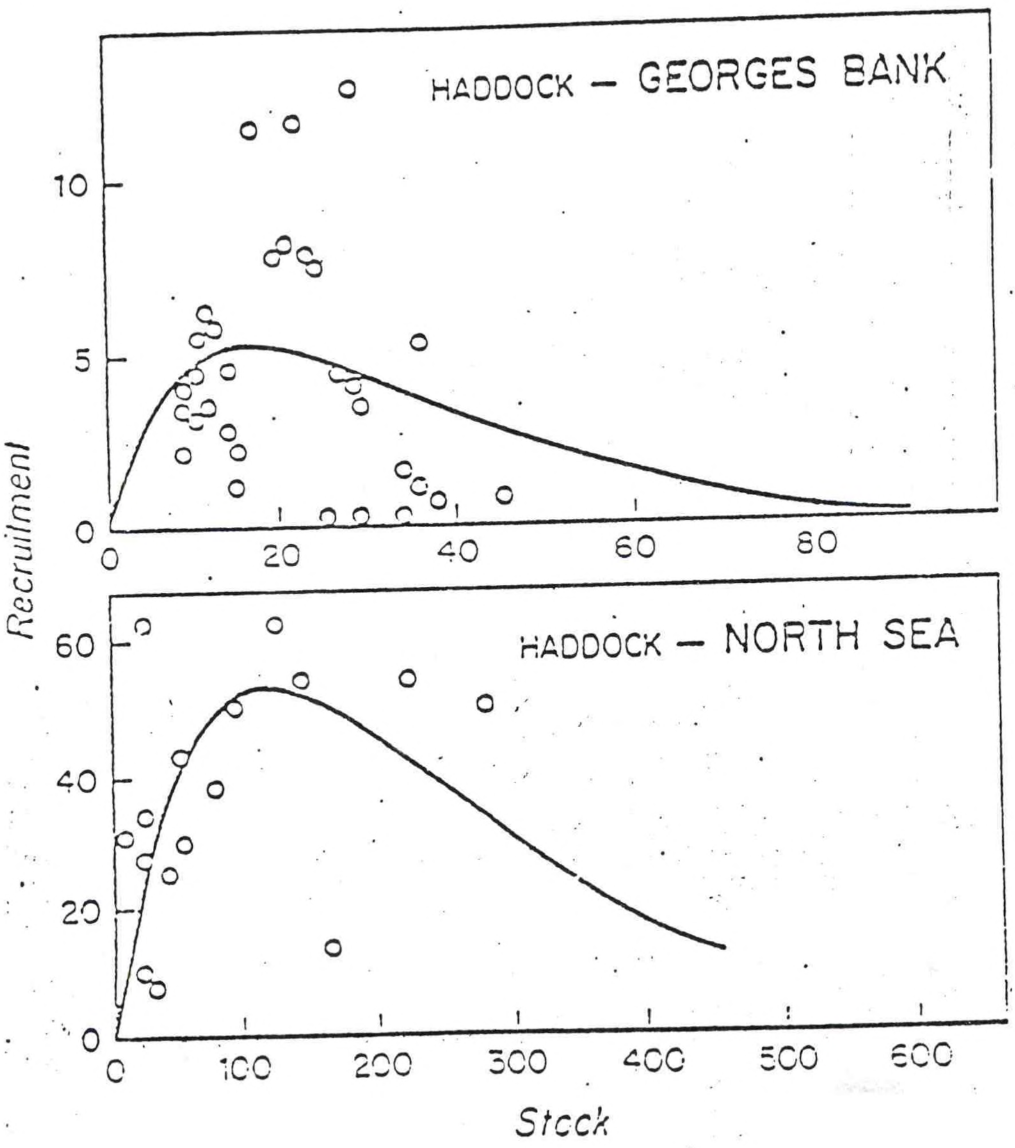


Figure 2.5.5 Haddock stock-recruitment data from the North Sea and Georges Bank fitted to a Ricker S-R curve.

In some cases, variability in recruitment unexplained by a S-R function can be explained by anomalies in abiotic conditions. For Atlantic menhaden, Nelson, Ingham, and Schaaf (1977) correlated deviations in recruitment from a Ricker S-R function with anomalies in zonal Ekman transport. The authors' hypothesis is that strong inshore transport increases the probabilit of eggs and larvae reaching inshore nursery grounds and thus enhance year-class strength. Sissenwine (1974, 1977c) found that correlations between temperature and recruitment for Southern New England yellowtail flounder were so strong that no relationship between spawning stock size and recruitment could be detected. Considerable care is necessary when interpreting correlations between biological phenomena (such as recruitment) and measures of climatic conditions when the mechanism responsible for the correlation is unknown. It is advisable to test such correlations on a second independen set of data. This points out the need for long-time series of biotic and abiotic data.

Assessment by projection based on current stock status

In the jargon of agencies responsible for fishery management, the term stock assessment means the application of fishery science to a stock of fish in order to evaluate or assess its current condition and predict its future condition relative to specific resource management decisions. Stock assessments have played an increasing role in management decisions of such international organizations such as ICNAF. Now with the extension of coasta state jurisdiction, management agencies of several individual countries (suc as Canada, Iceland, and the United States) are even more dependent on stock assessments.

Before one can evaluate current stock conditions, previous levels of abundance have to be estimated. Baranov's (1918) catch equation is used to estimate past stock size. The catch equation is the solution of a different equation expressing catch rate in number of fish instead of weight. The equation is

$$C_{ij} = \frac{N_{ij} F_{ij}}{Z_{ij}} (1-e^{-Z_{ij}})$$

where i = year
j = year class
C_{ij} = catch in numbers in year i for year class or cohort j
N_{ij} = size in numbers at the beginning of year i or year class j
F_{ij} = fishing mortality
M_{ij} = natural mortality
Z_{ij} = total mortality = $M_{ij} + F_{ij}$

If C_{ij}, F_{ij}, and M_{ij} (and therefore Z_{ij}) are known, then the above equation can be solved for N_{ij} numerically.

A second equation is applied in conjunction with the equation above,

$$N_{i+1,j} = N_{i,j}e^{-Z_{ij}}$$

By manipulating these equations together, N_{ij} and F_{ij} can be calculated for all past years of life of the cohort if the entire catch history of the cohort and natural mortality are known, and the fishing mortality in the last year that the cohort is fished (terminal F) is estimated or assumed. This procedure is called virtual population analysis (VPA) or cohort analysis. The mechanics of sequential computations with the catch equation were described by Ricker (1948). The method was popularized by Murphy (1965) and Gulland (1965). Solution of an approximate form of the catch equation was also called cohort analysis by Pope (1972). When the analysis is applied several years into the past, the results are generally insensitive to the estimated or assumed value of terminal F (Jones 1961).

These same two equations are also used to project into the future. If the current N_{ij} is known along with N_{ij} and F_{ij}, then N_{i+j} can be calculated for any particular C_i in the upcoming year. Unfortunately, errors in the current estimate of N_{ij} are propagated when projecting into the future. Therefore, projections are usually limited to a few years. In order to make projections for an entire population, the N_{ij}'s are summed over all year classes. Recruitment is accounted for by adding the recruiting cohort each year and projecting this along with all of the others. Possible catches in year i can be predicted for given target fishing mortality rates such as F_{msy}, and $F_{0.1}$ and the resulting stock size evaluated.

The resulting tabulation of various F_{ij} and $N_{i+i,j}$ and the sum of the $N_{i+1,j}$ for all cohorts provides the bases for management decisions. Furthermore, knowledge of the resulting stock by age and size allows the evaluation of changes in spawning stock size or potential egg production. Stock size and catch can also be expressed in weight by multiplying N_{ij} by the appropriate mean weight of individuals of the cohort or by substituting $G_{ij} + Z_{ij}$ for Z_{ij} where G_{ij} is the instantaneous growth rate and C_{ij} and N_{ij} are expressed in weight.

Virtual population methods are useful for estimating the past history of the fishery (as recent as perhaps 3 to 5 years ago depending on the fishing mortality rate) given catch-at-age data. For projecting into the future it is necessary to have an estimate of current fishing mortality or stock size and to predict recruitment from some independent source. Resource surveys are one source of independent information. For example, virtual population analysis can be used to estimate recruitment during a series of previous years. A functional relationship is then fit statistically between estimates of recruitment and survey catch rates of pre-recruit fish. Then using this relationship and the current survey catch rate of pre-recruits, recruitment in the upcoming year can be estimated.

Obviously, models relating recruitment to abiotic factors may provide useful information for population projections. Where recruitment estimates are not available the catch equation can still be used to project the status of the stock by assuming a value for recruitment based on the frequency distribution of observed past recruitment. For example, one can assume a recruitment level that is the lowest ever observed, a level exceeded 25% of the time, one exceeded 50% of the time, etc. Monte Carlo simulation can

be used to determine the distribution function of projected stock size for a particular future catch rate. The managers then have to decide what level of risk they wish to take.

The fishing mortality rates F_{ij}'s for the current year also have to be estimated from independent sources. The usual procedure is to divide a measur of relative abundance of the fully recruited fish (such as commercial or survey catch rate) into the total catch to obtain a measure of fishing effort (for commercial data) or relative exploitation rate (for survey data) and to functionally relate these to fishing mortality. The function is fit statistically to past estimates of fishing effort or relative exploitation rate and fishing mortality rate (calculated by VPA).

It is important to note here the inherent age specificity of F in these models. In reality F is usually size specific especially where size selectiv gear is used and thus F_{ij} for age j is a function of the size at age j.

Projected stock size is usually compared to past stock size. An estimate of the percent change in stock size is sometimes calculated for each level of catch considered by managers. Sometimes the projected stock size is compared to a previously established minimum stock size constraint. The minimum stock size might be the smallest size that has parented strong year classes in the past. In other cases an optimum stock size is chosen in order to stabilize the fishery, and increase availability of fish to particular user groups.

None of the above procedures explicitly include species interactions and environmental effects. Since the current stock condition reflects the past history of the stocks, these effects are included in the evaluation of the current stock status implicitly. For short-term predictions these other factors may have little effect. For longer-range prediction, the ability to include these factors explicitly could improve the assessments to the extent that data can demonstrate the validity of any relationship used. Environmental data may also be useful as an additional variable in stock-recruitment relationship studies which are needed to clarify the determination of minimum and optimum stock sizes. Presently, for longer-term simulation the best approach is to use recruitment generated from a probability distribution based on past observation. When populations of several species are simulated simultaneously, realistic results are obtained by using recruitment generated from a joint probability distribution function for all species. If the available data basis is inadequate to estimate the joint probability distribution, the sum of production resulting from recruitment of all species should be bounded within the historically observed range.

In no case in the Northwest Atlantic has a stock been managed on the basis of a Ricker or Beverton and Holt stock-recruitment model fit to observe data. Squid (Loligo) have been assessed taking into consideration the robustness of stock to different harvest levels relative to different assumptions about the parameters of a Ricker stock-recruitment model (Sissenw and Tibbetts 1977). General stock-recruitment considerations have been important to management on a qualitative basis, considering a very low level of spawning stock as a minimum below which the stock should not be reduced, and an optimum level sometimes defined as the average spawning stock during the years when a stock was producing at consistently high levels. These rather arbitrary levels are used to compare with the projected spawning stock sizes in providing advice to managers.

A summary of the current assessment studies is given in Table 2.5.1 taken from Sissenwine et al. (in press).

3. TOTAL ECOSYSTEM APPROACH

3.1 Basic Rationale

It has been clear for a long time that in order to understand natural fluctuations in fish production we need a much better functional understanding of marine ecosystems as a whole. This is because fish abundance is dependent directly or indirectly on complex interactions with all the major trophic levels as well as the physical environment in the sea. For example, the single most important process governing changes in fish production is recruitment, and a key aspect of this process is growth and survival through the egg and larval stages where the major factors controlling year-class success operate. Understanding variations in larval food supply requires knowledge of the linkages between the physical environment and primary and secondary production cycles. Further, estimating effects of predator-prey interactions on larval as well as juvenile and adult stages of fishes requires detailed knowledge of an extraordinarily complex food web involving many species and life forms on several trophic levels. In fact it now seems apparent that in order to predict long-term trends in fish production potential it will be necessary to gain a much better quantitative understanding of the basic biotic and abiotic processes (and interactions) controlling all the major biological components of the ecosystem. This implies measuring rates and manner of cycling energy and materials through an entire ecosystem and linking the dynamics of biological components to the dynamics of shelf circulation. In addition to the complexities of the natural system we must add the impacts of man in the form of fishing and degradation of the shelf environment due to pollution, etc. The scale and complexity of the problem is truly colossal. Nevertheless we must improve our level of understanding of the structure and function of whole ecosystems--by monitoring the performance of natural ecosystems in a quantitative way and by conducting experiments to obtain better estimates of the nature and rates of dynamic processes which are critical to our understanding of organic production of the ecosystem.

Methods of research on the adult finfish component have been under development for decades, and this is the part of the ecosystem on which we have the most complete data. Comprehensive and quantitative studies of other biological components and the physical and chemical characteristics of the New England shelf area have begun only recently, in the 1970's for the most part. Here we describe briefly our strategy of ecosystem research and its development to date, with emphasis on the NOAA-NMFS program.

Table 2.5.1 Current application of fishery assessments models to fisheries off the Northeastern Coast of the United States.

Stock	Yield per recruit	Equilibrium surplus production models	Virtual population analyses (VPA)	Stock Recruitment model considerations	Projections based on catch equation	Evaluation of relative stock changes
Cod Gulf of Maine	Beverton and Holt yield per recruit model used to choose range of Fs considered in assessment. Also evaluation of effects of size at entry	Evaluated from historic catch statistics. No quantitative model	None	None	None	F from earlier analyses related to survey cruise trends and catch; catches by market categories are reviewed over time for changes in size distributions
Cod Georges Bank Middle Atlantic	• •	Several generalized production models fit, but none are considered viable in view of historical catches	First approximation available - but sensitivity to potential errors in age composition of catch unknown	No model but historic stock sizes from VPA qualitatively used for evaluating minimum stock sizes appropriate from stock-recruitment standpoint	Done using estimates of size of recruiting year classes and current Fs for older year classes based on survey cruise VPA relationships	Commercial age/length frequencies are reviewed; F from earlier analyses reviewed relative to current cohort analyses; commercial landings by market categories reviewed
Haddock Gulf of Maine Georges Bank	• •	Good historical yield model - useful in evaluating long range potential	Analyses available	Stock recruitment model investigated but not developed enough to use explicitly; the frequency of strong year-classes relative to spawning stock size has been evaluated	analysis available	• •
Pollock Nova Scotia Gulf of Maine	• •	None	Available but based on limited aging	None	Current Fs estimated from survey-VPA relationships. Recruitment possibilities are chosen relative to historic year-class sizes	Commercial catch per unit effort and survey cruise trends evaluated.
Redfish Gulf of Maine	Currently consider YPR analysis from Nova Scotian shelf	A model to use with Walter's (1976) procedure for	None	None	None	Survey indices used; commercial catch/effort evaluated; survey and commercial length frequen-

Stock	Yield per recruit	Equilibrium surplus production models	Virtual population analyses (VPA)	Stock recruitment model considerations	Projections based on catch equation	Evaluation of relative stock abundance
Silver hake Gulf of Maine	See cod Gulf of Maine. Model has also been used in conjunction with VPA estimates to calculate maximum sustained yield	A model available that is useful in evaluating long range potential	Analysis available	See cod - Georges Bank	See cod - Georges Bank but data base stronger	Pre-recruit survey indices used
Silver hake Georges Bank	"	See cod - Georges Bank	"	"	"	"
Silver hake Southern New England - Middle Atlantic	"	"	"	"	"	"
Red hake Georges Bank	See cod - Gulf of Maine	None	"	None	See cod - Georges Bank	Commercial catch per unit effort not available; survey indices reviewed
Red hake Southern New England - Middle Atlantic	"	See silver hake Gulf of Maine	"	Qualitatively related to results of VPA analysis	"	"
Yellowtail flounder Georges Bank	" Ricker model also used	See cod Georges Bank	Very preliminary analysis available	Qualitative evaluation used	Yes, using Equations (31) and (32)	Commercial catch age compositions and catch per unit effort used; both total and pre-recruit survey catch rates used;
*Yellowtail flounder Cape Cod plus southern New England - Middle Atlantic	"	" (for Southern New England only)	Available only for early 1960's	Qualitative evaluation used; fit to Ricker stock recruitment is poor.	None	" Except no survey index for Cape Cod or commercial catch per unit effort for Middle Atlantic.

*Considered as two stocks but currently managed together

Stock	Yield per recruit	Equilibrium surplus production models.	Virtual population analyses (VPA)	Stock recruitment model considerations	Projections based on catch equation	Evaluation of relative stock abundance
Other flounders	None	None	None except for very preliminary one for fluke	None	None	Overall survey trends and changes in size composition reviewed relative to historical catches
Mackerel	see cod - Gulf of Maine	Walter's (1978) model where recruitment is modeled as an impulse has been applied	Analysis available	Qualitatively only	See silver hake - Georges Bank	see redfish
Sea herring Gulf of Maine	See cod Gulf - of Maine and see silver hake Gulf of Maine	None	"	Qualitatively only; minimum stock size concept used	Projection based on qualitative estimates of size at age 3 of each year-class in the fishery	Viable commercial indices not available; survey indices of low precision
Sea herring Georges Bank - Middle Atlantic	"	See cod Georges Bank	"	"	"	"
Sea herring Nova Scotia	See cod - Gulf of Maine	None	"	None	"	"
Loligo squid	Based on modification of Ricker's formulation	A model developed using yield per recruit combined with several hypothetical S-R curves	Preliminary analysis based on lengths	Used qualitatively	None	Commercial catch per unit effort and survey trends followed; population estimate of minimum biomass by areal expansion; length frequencies examined
Illex squid	"	"	"	Used qualitatively	None	"
Other finfish	No except for butterfish	No except for river herring and Butterfish	No except for very preliminary one for butterfish	None	None	Survey cruise trends; followed, commercial length frequencies revised; commercial catch rate for river herring revised

Stock	Yield per recruit	Equilibrium surplus production models	Virtual population analyses (VPA)	Stock recruitment model considerations	Projections based on catch equation	Evaluation of relative stock abundance
Total finfish plus squid	None	A Schaefer yield model in use	None	Qualitatively only	None	Survey trends followed and used with equilibrium yield model to assist in assessing current conditions
Surf clams	Beverton and Holt model used to evaluate size at entry	None	None	None	Catch relative to survey cruise indices used to evaluate F and the corresponding catch	Survey cruise trends followed; commercial and survey length frequencies reviewed
Ocean quahogs	None	None	None	None	None	Survey cruise trends evaluated
Northern shrimp	See cod - Gulf of Maine, Ricker method also used	None	None	None	F is estimated from State of Maine inshore survey	Length frequencies of survey and commercial catches evaluated

3.2 Monitoring the Ecosystem

A basic part of the research strategy is broad-scale monitoring of the state of the ecosystem to provide an empirical base against which theory and predictive models may be tested. In the early 1970's, NMFS established the Marine Monitoring Assessment and Prediction Program (MARMAP) to provide annual and seasonal monitoring of the distribution, biomass, and population structure of principal biota, and the physical environment, on a broad geographic scale. A brief description of the development and characteristics of this program and some results to date, are presented here.

Trawl surveys

Fishery statistics by themselves do not provide adequate information on biomass of all important fish species nor do they provide adequate pre-recruit estimates. Therefore another source of information was needed which would provide much more complete and unbiased measures of the changes in the size and structure of the finfish biomass as a whole. In addition there was a critical need for data on species interactions and environmental factors which might be related to recruitment fluctuations. The prototype MARMAP program had begun in 1963, when the Northeast Fisheries Center (NEFC) at Woods Hole, Massachusetts, began a comprehensive bottom trawl survey program designed to provide an annual quantitative inventory of fish populations on the continental shelf off New England. The development of these surveys and their value in assessments has already been described. Here we discuss briefly some results of food habit studies based on fish stomachs collected on the MARMAP trawl surveys.

From 1963-66 stomach contents of fish were examined at sea on trawl surveys and a qualitative evaluation of prey types was obtained for 65 species of fish. During the period 1969-72 fish were randomly selected from trawl catches and stomachs preserved for later examination in the laboratory. On the order of 30,000 stomachs have been examined from this later series (chiefly spring and fall surveys), and we now have a quantitative estimate of the mean stomach content (gm, wet weight) of each type of prey for 80 species of fish. A detailed summary of the food habits for many of the major species on Georges Bank is presented by Bowman, et al. (1976). Stomach sampling on MARMAP surveys has continued since 1973 on a routine basis, but more detailed information on predator size was obtained and these data are just now being summarized.

Food habits of 16 major species on Georges Bank from the 1969-72 series showed that five major taxa (crustaceans, pisces, polychaetes, echinoderms, and mollusks) accounted for 80 percent of the total diet by weight (Grosslein, Langton, and Sissenwine 1978). Crustaceans were the most widely preyed upon category of animals which is not unexpected since they are represented by both pelagic and benthic components of the ecosystem

(Figure 3.2.1). Fish are second in importance as prey and form a major part of the diet of spiny dogfish, goosefish, silver hake, Atlantic cod, white hake, pollock, and redfish (Figure 3.2.1). Mollusks are also important, particularly pelagic cephalopods, and it is quite likely that their real contribution to fish diets is grossly underestimated since it is common to find only the (squid) beaks in fish stomachs.

Despite the drastic decline in total finfish biomass off the northeastern US from the middle 1960's to the early 1970's, there appeared to be no major shifts in diets (percent occurrence) of the principal adult fishes (Grosslein, Langton, and Sissenwine 1978). Diet changes may have been significant for younger stages but these data are not yet available. Some implications of the food-habits data with respect to an energy budget for Georges Bank are discussed in the section on modeling.

Finally it should be noted that shellfish surveys are now part of the MARMAP program. For example, sea scallop and clam resources are surveyed on a regular basis with standardized dredges and stratified sampling schemes. Also from time to time there are special surveys for epibenthic organisms such as lobsters and crabs using underwater cameras, traps, etc. (e.g., Wigley et al. 1975). Comprehensive sampling of the entire benthos using grab samplers has been done over the whole shelf only on one occasion (Wigley and Theroux, in press). In the New York Bight more frequent sampling has been done in relation to polluted areas (Pearce et al., in press).

Plankton and hydrographic surveys

Plankton studies in the New England area over the past 50 years have generally been limited to observations over a one- or two-year cycle and a limited geographic area (Colton 1963; Cohen 1976). The MARMAP series was designed to provide a continuous and broad-scale time series sufficient to relate large-scale changes in plankton populations with changes in shelf circulation patterns or long-term temperature trends.

In 1968, ALBATROSS IV began taking a plankton tow at each bottom trawl station for the purpose of monitoring the general distribution of fish eggs and larvae. This "piggyback" plankton sampling on the trawl surveys continued until 1976 when separate bimonthly plankton surveys were initiated. In the standard MARMAP sampling protocol, zooplankton collections are made with 61-cm diameter bongo nets in a continuous oblique haul from ≤ 200 m to the surface at 1.5 knots. Paired bongos are used with 0.505-mm and 0.333-mm mesh apertures; at selected stations, a pair of 20-cm bongos with 0.165-mm and 0.253-mm mesh nets is attached to the wire above the larger bongos for sampling small zooplankton. In addition at each station, measurements of chlorophyll, nutrients, salinity, and temperature are made. Also C^{14} measurements of primary production are made daily on some cruises. The station pattern used for MARMAP plankton-hydro surveys since 1976 is shown in Figure 3.2.2.

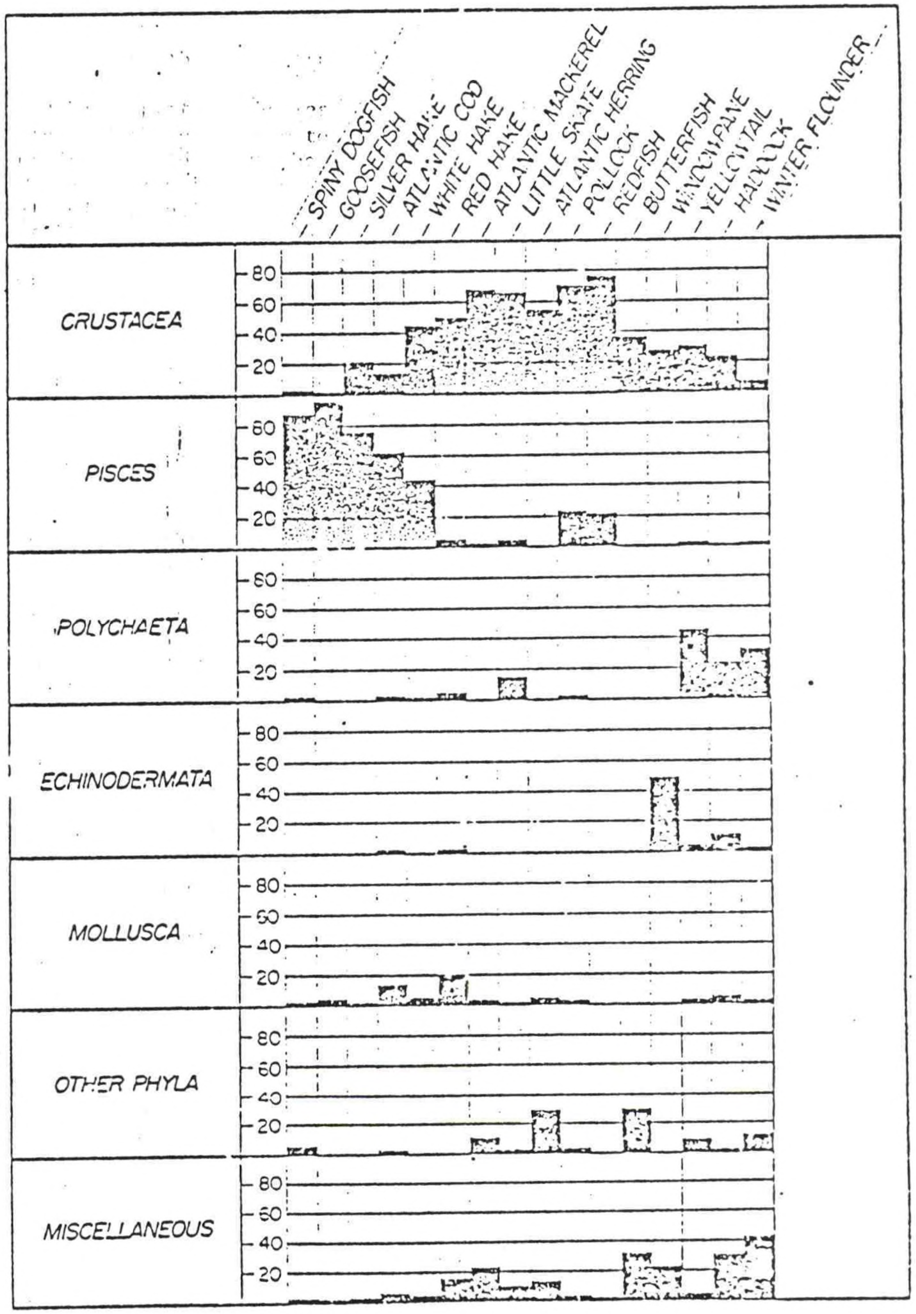


Figure 3.2.1 Prey composition of 16 fish species collected on Georges Bank in 1969-1972. Data expressed as percent by weight. (Figure 2.3, Grosslein, Langton, and Sissenwine 1976.)

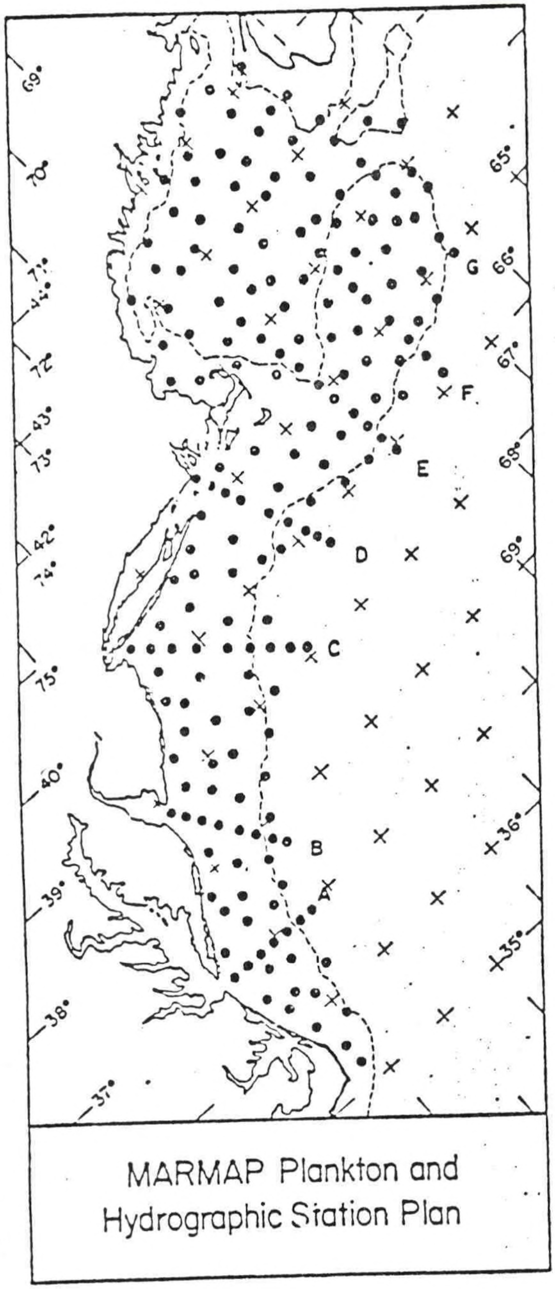
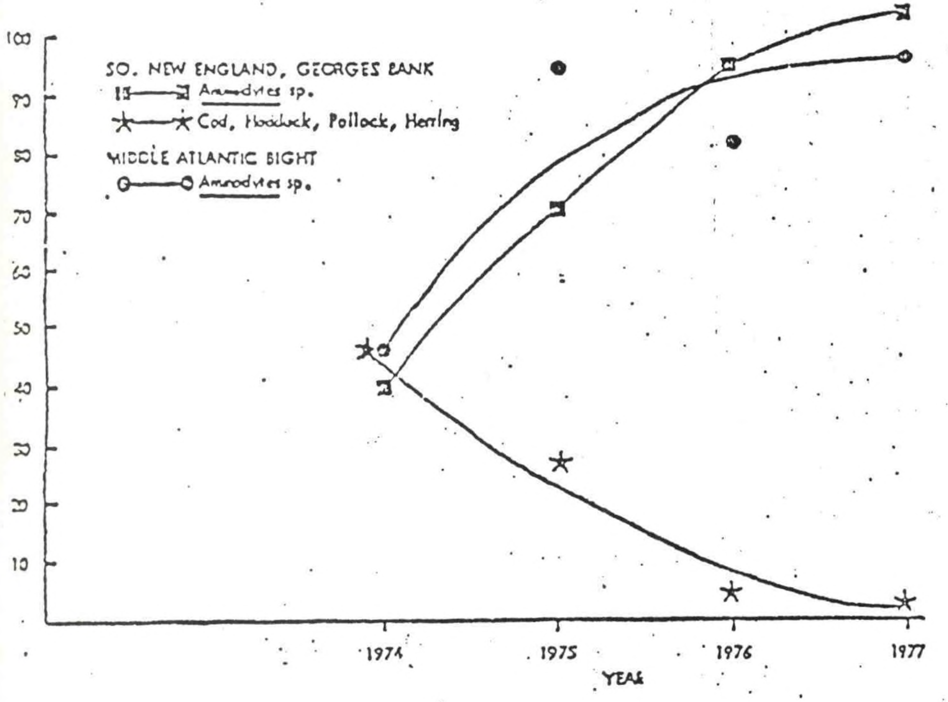


Figure 3.2.2 Plankton and hydrographic station pattern for NMFS

The most important observation so far on the MARMAP and related ICNAF plankton cruises is that primary production is very much higher on Georges Bank than previously thought, on the order of 400-500 gm C per m^2 per year, making it one of the most productive areas in the ocean (Cohen and Wright 1978). Further there is some evidence that this high level of production is maintained throughout much of the year (spring, summer, and autumn) through continuous mixing of the water on top of Georges Bank and by transport of nutrient-rich water onto the Bank from the deeper waters along both its northern and southern edges. More intensive studies (at least monthly cruises) will be required to document the nature of the seasonal primary productivity cycle and nutrient regeneration mechanisms on Georges Bank. However the bimonthly MARMAP coverage provides a basis for detecting gross changes from year to year and gradually adds to our understanding of the seasonal cycle.

The MARMAP zooplankton samples are providing very useful information on the large-scale seasonal and annual changes in abundance and distribution of fish larvae and the larger invertebrate zooplankton (only adults and copepodite stages III, IV, and V are retained in the standard 0.333-mm mesh nets). In a broad sense the series helps fill in gaps in our knowledge of the distribution and timing of spawning of fishes (Colton et al. 1977) as well as major changes in abundance, and it provides a gross measure of the seasonal and geographic variations in biomass and species composition of the invertebrate zooplankton populations. Of particular interest in recent years has been a large increase in the abundance of Ammodytes sp. in the ichthyoplankton. Since 1974 sand lance larvae have increased dramatically and consistently, from less than 50% of the ichthyoplankton constituents to more than 90% by 1977 (Smith and Sullivan 1978; and Figure 3.2.3). The increase in adult populations of sand lance (for which there is no fishery in the New England area) has been confirmed to some extent by the MARMAP trawl surveys but the variability of the trawl indices is extremely high. Thus the larval abundance indices appear to be more consistent estimates of spawning stock. The interest in sand lance arises from the fact that it is a potential competitor with the two major pelagic species, herring and mackerel, whose biomass is now at a low level (Grosslein et al. 1978). All three species depend upon copepods to varying degrees from larval to adult stages, and the increase in sand lance is considered a possible result of the decrease in the other two (personal communication, Ken Sherman).

Turning to the invertebrate components, spring and fall surveys since 1971 have shown a fairly typical structure of zooplankton populations in each year, that is, a consistent dominance by copepods which generally represented 90% or more of the zooplankton by numbers, with the remainder made up by chaetognaths, euphausiids, coelenterates, and larval cirripeds (Sherman 1978). Among the copepods there were usually only a half-dozen species contributing 1% or more to the total, and generally two species were overwhelmingly dominant, but these two species varied with season and geographic area. For example, in spring surveys, Calanus finmarchicus and Pseudocalanus minutus were consistently dominant in that order on Georges Bank and in the Gulf of Maine, but the order was reversed in southern New England. In autumn on Georges Bank, Centropages typicus replaced C. finmarchicus as the co-dominant with P. minutus. Changes in the timing of production cycles were observed for the dominant copepods in some years, and in autumn 1975 unusual abundance of



3.2.3 Changes in the percentage composition of Ammodytes spp. larvae the Georges Bank Southern New England, and Mid-Atlantic Bight sub areas the coastal ecosystem 1974-1977. Changes in the percentage composition also given for cod, haddock, pollock, and herring for the Southern England and Georges Bank subarea. (From Smith and Sullivan, 1978)

two copepod predators (the chaetognath Sagitta elegans and the coelenterate Nanomia cara) on Georges Bank may have contributed to the relatively low numbers of Centropages typicus observed in that year (Sherman 1978).

While it is possible to detect gross changes in the biomass and structure of zooplankton populations with the MARMAP series, it is not possible to document seasonal production cycles or estimate rates of growth and mortality with adequate precision. Similarly, major shifts in water-mass distribution and timing of seasonal stratification can be detected with the broad-scale surveys but finer-scale dynamics cannot be observed. The MARMAP series must be augmented with more intensive studies and some examples are described in the section on process-oriented studies.

Temperature and surface salinity observations are routinely made on all MARMAP trawl surveys, and as noted above more complete hydrographic sampling is accomplished on the plankton surveys. These data have provided good descriptions of the seasonal bottom temperature cycle as well as a recent warming trend in the Gulf of Maine region (Schopf 1967; Davis 1976), and also a broad-scale picture of the water mass distribution and major circulation patterns of the area (Pawlowski and Wright 1978). These and earlier monitoring cruises by Colton et al. (1968) represent an important base for "hindsight" modeling large-scale phenomena in the circulation of the shelf.

Pollution

Estimating effects of pollution on marine ecosystems is extremely difficult because we don't have adequate knowledge of the natural mechanisms controlling populations and because effects of pollutants and natural environment factors are often manifested in similar ways, ranging from subtle effects on food supplies, reproduction, and behavioral modifications to large-scale mortality of eggs, larvae, and even adults. A new NMFS/NOAA program called OCEAN PULSE is under development and is being designed to provide a basis for estimating effects of pollution on the marine ecosystem. Initial phases of the program involve baseline studies to document present levels and distribution of known contaminants in the marine environment and selected species among nekton, plankton, benthos, and microorganisms. The baseline studies will be followed by a program of monitoring selected test sites for chemical loading, with emphasis on comparisons between polluted and unpolluted areas in the Gulf of Maine, Georges Bank, and the Mid-Atlantic (Figure 3.2.4). In addition to the monitoring of chemical loading, coordinated laboratory and field studies will be conducted on selected organisms to investigate the sublethal effects of pollutants on their biochemistry, physiology, pathology, genetics, and behavior. Attempts will also be made to develop indices of the "health or condition" of marine populations at selected field locations, utilizing such characteristics as growth, relative "fatness" in terms of length-weight ratios or oil content, biochemical composition, etc.

Known pollutants include dredge spoils, chemicals, acids, heavy metals, sewage, heat, pesticides, and oil. The New York Bight area is the most heavily polluted part of the area under consideration and a great deal of research has already been done to document the sources and magnitude of pollution. Numerous examples of localized effects of pollutants on small segments of fish and shellfish populations have been reported for this area but there

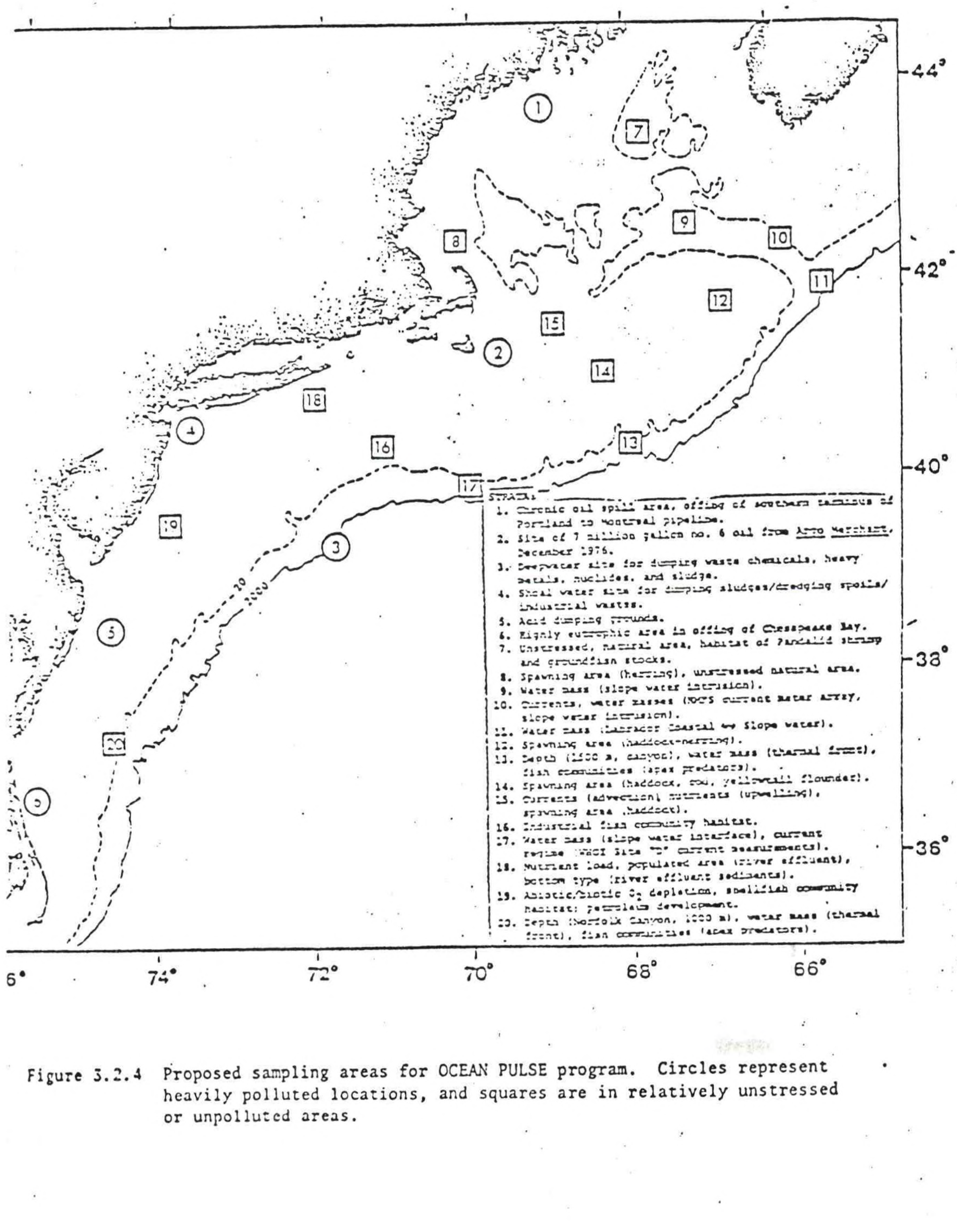


Figure 3.2.4 Proposed sampling areas for OCEAN PULSE program. Circles represent heavily polluted locations, and squares are in relatively unstressed or unpolluted areas.

is no specific evidence of widespread damage to major fishery resources that can be directly attributed to pollution (Sindermann 1976). This doesn't rul out the possibility that pollution is having a deleterious effect on fish production but it does serve to illustrate the difficulty of identifying specific impacts of pollution on fishes. The problem of measuring the impac on the various other biological components of the ecosystem, and the total effect on a stressed system, is one of enormous complexity. The OCEAN PULSE program together with the other ecological research described in this report represents a major step toward a long-term and sufficiently broad-scale research strategy which hopefully will provide real insight into the significance of pollution effects on marine ecosystems.

3.3 Process-Oriented Studies

The standard MARMAP surveys are adequate for macro-scale descriptions o biomass and gross population structure of plankton and finfish communities, and in the case of juvenile and adult fish production this can be estimated largely on an annual or quarterly basis (for which the 2-3 trawl surveys a year are reasonably adequate) and the techniques have already been outlined this paper, and are described by Sissenwine et al. (1978). However the MARM cruises are too far apart for quantitative estimates of plankton production cycles, rates of growth and mortality, and dispersal and feeding processes. More frequent sampling, on the scale of weeks--days--or even hours, is requi to estimate the rates of such processes, and thus the standard MARMAP survey must be augmented by a combination of meso- and micro-scale field studies together with laboratory experiments. Several of our principal plankton research projects are briefly described here to illustrate the problem of matching research strategy to the scales of time and space within which critical biotic and abiotic events occur.

Larval fish production

A major focus of our research program is placed on larval fish because factors controlling success of year classes in marine fish populations appea to operate in the larval stage. A necessary step toward gaining insight int the mortality mechanisms is to describe the production, dispersal, growth, feeding, and survival of larvae over a series of spawning cycles for selecte species and areas to determine the meso-scale events such as the geographic region and water masses within which the larval population lives, and the gross nature of the survival curves for the various stages of larval develop ment. This may be referred to as a meso-scale problem and is illustrated by the Georges Bank larval herring surveys which were conducted by ICNAF.

The approach of the ICNAF program was to concentrate sampling in the first 6 months of life on the Georges Bank - Gulf of Maine sea herring stock When the surveys were initiated in 1971, the plan was to cover the entire Georges Bank - Gulf of Maine area at least once a month from September to December to monitor larval production and intermixing of larvae from the various spawning sites (see Figure 3.3.1 for typical distribution pattern of stations and larval herring catches). During the first 2 years, minimum sampling at each station included oblique hauls with 60-cm bongos (0.505-mm and 0.333-mm mesh), temperature profiles, and surface salinities. Beginning in March 1973, the Federal Republic of Germany added night sampling of larva

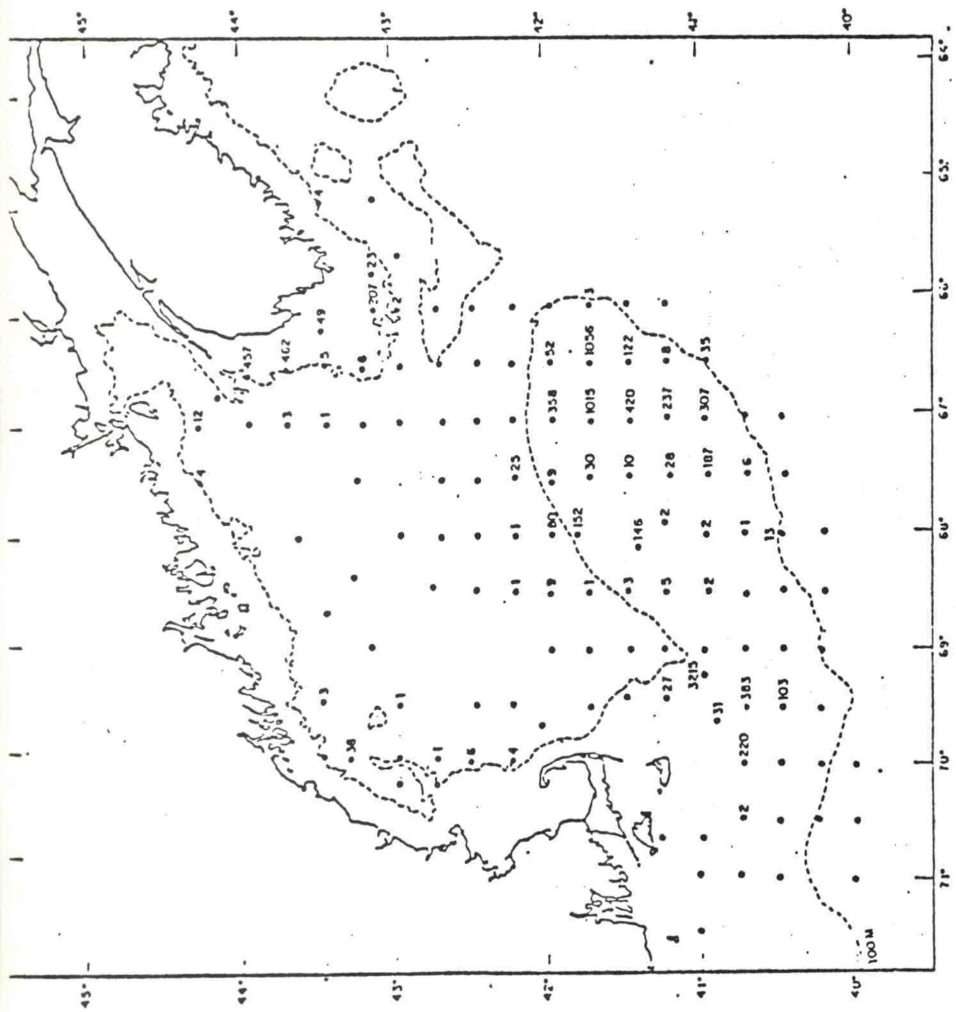


Figure 3.3.1 Typical pattern of stations and larval herring catches during 1971-74 ICNAF surveys.

herring with bongos and neuston nets, and in February 1974 the USA began the series of February cruises.

After the formation of the ICNAF Environmental Working Group in June 1974, interest developed in a more comprehensive and intensive investigation of factors controlling success of year classes. In the autumn of 1974, paired 20-cm bongos with smaller mesh sizes (0.253 mm and 0.053 mm) were added to the standard 60-cm bongos, and in subsequent years 0.253-mm and 0.165-mm mesh nets were used on the 20-cm bongos. In May 1975, the Working Group recommended that, in addition to monitoring larval herring production, more emphasis should be given to studying circulation in the Georges Bank - Nantucket Shoals area, and that concurrent studies of primary and secondary production should be initiated as well as fine-scale patch studies. Thereafter emphasis shifted to the Georges Bank - Nantucket area alone, since vessel support was insufficient for intensive sampling of the whole region (Figure 3.3.2). Sampling was expanded to include more complete hydrographic coverage (temperature, O_2, and salinity profiles at each station), and also nutrients, chlorophyll, and primary production when possible.

Plots of the distribution and abundance of herring larvae (numbers of larvae per $10m^2$ by size categories) provide a basis for estimating time and location of spawning and subsequent dispersal of larvae, as well as estimates of larval production. The frequency of surveys during the autumn - early winter period (an average of one cruise every 3 weeks from mid-September to mid-December) and the density of stations (one station per 250-300 $miles^2$) are adequate to describe general patterns of dispersal away from spawning sites in the Georges Bank - Nantucket Shoals area. Bumpus (1976) showed that larval dispersal is consistent with what is hypothesized about circulation on Georges Bank, namely strong tidal mixing coupled with a net westerly drift, and perhaps a clockwise gyre around the shoal part of Georges at least some of the time. The sampling intensity is not sufficient to measure short-term effects of storms nor to insure a complete record of possible losses of larvae from the perimeter of Georges Bank. However major losses appear to be relatively infrequent since throughout the 6-year time series significant numbers of larvae were seldom seen on the perimeters of the Georges Bank - Nantucket Shoals area. As the larvae get larger and older their distribution contracts more and more toward the central portions of Georges Bank, well inside the 100-m depth contour. Whatever mechanisms are operating to retain larvae on the Bank, one implication is that chances for their survival are best there.

Production of larvae < 10 mm was an order of magnitude greater in 1973 and 1974 than in 1971 and 1972, then dropped to an intermediate level in 1975, and to very low levels in 1976 and 1977 (Lough 1976). So far there appears to be little relation between the numbers of early-stage larvae produced and subsequent year-class strength; but we have only a few points of comparison since herring don't enter the adult fishery until age 3. The estimates of larval production do, however, correlate generally with the size of spawning stock estimates based on VPA estimates. Another indication that the production estimates are in the right ballpark is that within each season the mean abundance indices (on a per-cruise basis) show a systematic progression from low to high to low numbers during the September-December period, which is consistent with a concentrated spawning in one time and place. Also some indication of the actual precision in larval production estimates can be

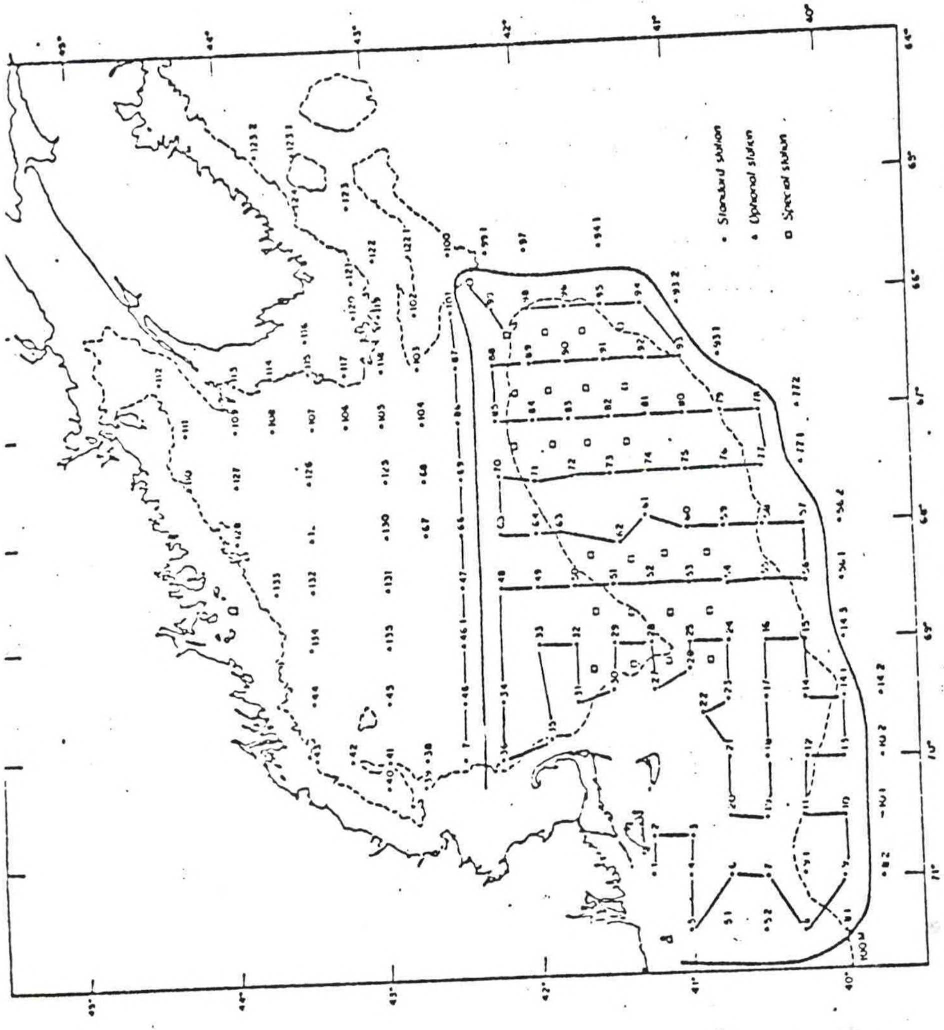


Figure 3.3.2 ICNAF larval herring survey sampling stations and standard cruise track. Coverage within heavy solid line emphasized since 1974.

obtained from the standard deviations of estimates of mean numbers of larvae on a per-cruise basis (Table 3.3.1). These and related data are considered further in the last section on statistical problems.

The most promising lead so far is that growth and mortality of larvae in the overwinter period may provide a clue as to the probable success of the year class. The 1975 year class shows preliminary indications that it may be a much larger year class than 1973 or 1974, and overwinter larval growth was much higher (and mortality lower) for the 1975 year class than for the other two.

Approximate growth and mortality estimates for three winter periods (December to February) in the Georges Bank area showed that mortality was substantially lower and growth higher in 1975-76 than in the previous two winters (Lough 1976). Mortality was about 4% per day in the first two winter as compared with 1.5% per day in the third winter, and growth was 2.5% and 3.5% per day in the first two winters as compared with 4% per day in the thir winter. Although no confidence limits were placed on these estimates, the magnitude of the differences was so large as to make it extremely unlikely they could be due to sampling errors alone. More refined estimates of growth and mortality are now in progress which take into account the following:

(1) Change from exponential to logarithmic form of the growth curve fo larger larvae, and more accurate classification of age vs. length based on larval otoliths.

(2) Specific length - dry weight regression curves for individual year (instead of pooled regression for 4 years).

(3) Separate estimates for larval subpopulations to reduce possible bi due to mixing of larvae from Georges Bank and Nantucket Shoals.

(4) Day/night analysis to clarify the avoidance problem, and adjust analyses accordingly.

(5) Correction for extrusion of small larvae from 0.333-mm samples.

An important limitation in net samples is the fact that most food orgar isms of smaller larvae are extruded through mesh as large as 0.333 mm. Col (personal communication) found that a substantial proportion of food items the guts of herring larvae (4-18-mm size range) consisted of organisms whic were not retained by 0.333-mm (or 0.253-mm) mesh nets; these included inver brate eggs, copepod nauplii, Oithona spp. and Pseudo-Paracalanus spp. copepodites. Even smaller mesh (0.165 mm) will not retain nauplii or even all copepodite stages of Pseudocalanus minutus.

Since matching up larval growth and survival with abundance and composition of food organisms may be one of the most important aspects of the recruitment process, consideration should be given to methods of obtaining some qualitative measures of all zooplankton constituents during large-scal surveys, at least on a sampling basis. Possibilities include special water samples from a plankton pump, or a special plankton sampler such as the un lating oceanographic recorder (UOR), a fancy version of the Hardy continuo

Table 3.3.1 Mean numbers of herring larvae per 10m² on Georges Bank, and associated standard deviations and coefficients of variation. For 37 standard ICNAF stations east of and including the transect on 68° west longitude (see Figure 2).

1972					1973					1974				
Cruise	Size (mm)	$\bar{X}$	SD	SD/$\bar{X}$	Cruise	Size (mm)	$\bar{X}$	SD	SD/$\bar{X}$	Cruise	Size (mm)	$\bar{X}$	SD	SD/$\bar{X}$
ARGOS	5-10	15	83	5.5	CRYOS	5-10	32	120	3.7	CRYOS	5-10	0	-	-
22-30 Sep	10-15	[illegible]	44	4.0	16-28 Sep	10-15	1	5	5.0	02-24 Sep	10-15	0	-	-
ARGOS	5-10	3	8	2.7	WIECZNO	5-10	489	1,5[illegible]	3.7	WIECZNO	5-10	291	1,050	3.6
12-28 Oct	10-15	30	60	2.0	29 Sep-20 Oct	10-15	397	1,578	3.9	27 Sep-18 Oct	10-15	0.4	1.5	3.8
WIECZNO	5-10	31	131	4.2	BELOGORSK	5-10	671	3,107	4.6	PROGNOZ	5-10	1,026	2,403	2.3
02-28 Oct	10-15	52	132	2.5	15 Oct-01 Nov	10-15	133	269	2.0	18-30 Oct	10-15	179	343	1.9
DOHRN	5-10	7	22	3.1	W. HERWIG	5-10	387	1,679	4.3	A. DOHRN	5-10	93	354	4.1
31 Oct-12 Nov	10-15	7	16	2.3	28 Oct-08 Nov	10-15	125	300	2.4	16-23 Nov	10-15	83	143	1.7
AL IV	5-10	0	-	-	AL IV	5-10	12	61	5.1	AL IV	5-10	1.1	4.6	4.2
02-20 Dec	10-15	1	4	4.0	04-20 Dec	10-15	6	14	2.3	04-19 Dec	10-15	59	168	2.8

1975					1976				
Cruise	Size (mm)	$\bar{X}$	SD	SD/$\bar{X}$	Cruise	Size (mm)	$\bar{X}$	SD	SD/$\bar{X}$
BELOGORSK	5-10	10	40	4.0					
25 Sep-08 Oct	10-15	-	-	-					
BELOGORSK	5-10	84	359	4.3	WIECZNO	5-10	0.5	1.5	3.0
17-30 Oct	10-15	52	133	2.6	14 Oct-03 Nov	10-15	5	18.7	3.7
A. DOHRN	5-10	85	267	3.1	A. DOHRN	5-10	0	-	-
01-18 Nov	10-15	85	161	1.9	15-29 Nov	10-15	0	-	-
AL IV	5-10	1	8	8	RESEARCHER	5-10	0	-	-
05-17 Dec	10-15	2	4	2	27 Nov-11 Dec	10-15	0	-	-

plankton recorder. In lieu of truly quantitative sampling, and perhaps in addition, it may be desirable to use small-mesh gear routinely for relative zooplankton, biomass indices as well as size frequencies of larger invertebrate forms. We have found that 0.253-mm mesh and even 0.165-mm mesh nets can be used routinely in the Georges Bank area in autumn without severe incidence of clogging. However, as indicated above, the problem of sorting increases rapidly as the mesh size decreases.

Primary and secondary production linkages

The monthly coverage achieved in the Georges Bank larval herring program is sufficient only to provide a rather gross index of zooplankton production cycles because development of some forms from juvenile to adult occurs within a period of two weeks or less. Still more intensive coverage is needed in both time and 3-dimensional space to provide estimates of zooplankton production cycles of sufficient precision to relate to feeding and survival of fish larvae, and to link the dynamics of zooplankton production to that of phytoplankton production. An example of the latter type of study is that by the Brookhaven National Laboratory on the 1975 spring phytoplankton bloom in the New York Bight region. Over a two-week period, on a section of the shelf south of Long Island, New York, a time series of measurements were made of temperature, salinity, irradiance, nutrients, chlorophyll, phytoplankton (species), particles, particulate nitrogen and carbon, zooplankton, primary production, respiration, and nitrate uptake. The study indicated that there was a maximum in primary production and a minimum in herbivore grazing stress at mid-shelf, and that these may have been related to the effects of internal waves formed at the shelf break and propagating shoreward (Walsh et al. 1977). The energy for these waves may arise from the semidiurnal tide in this region. Mixing from three storms during the two-week study and possible breaking of internal waves appeared to be mechanisms for replenishing nutrients. Nutrient recycling through herbivore excretion also appeared to be a major source of nutrients at that time. Both phytoplankton and zooplankton populations showed significant differences between inshore and offshore stations, and the characteristics of phytoplankton cells and chlorophyll in the inshore, mid-shelf, and offshore areas were consistent with the potential level of grazing represented by abundance and species composition of the zooplankton. Significant chemical and biological changes occurred during the two-week period particularly after the storms. The apparent initial effect of these events was to increase the nutrient content of the euphotic zone through mixing of the upper 50 m of the water column. At the shelf-break station in 90 m, phytoplankton doubled their standing crop 1-2 days after each of two storms, and then declined rapidly in each case, illustrating the rapid rate at which phytoplankton populations can respond to nutrient fluxes, and be grazed down by herbivores.

More comprehensive sampling than was possible in the Brookhaven study in both vertical and horizontal dimensions would be required to describe the dynamics of the zooplankton populations. However the key to understanding zooplankton dynamics obviously lies in studies where the phytoplankton and circulation dynamics are studied at the same time and on a scale of days and weeks, and meters and kilometers. Investigations like the one just described are now being conducted on Georges Bank as well as in the Mid-Atlantic by Brookhaven in cooperation with NMFS. The next step is to incorporate more intensive sampling of zooplankton including fish larvae.

Larval patch study

An example of a comprehersive "micro-scale" study including larval fish is the larval herring "patch" experiment scheduled for 3-4 weeks beginning in mid-October 1978 on Georges Bank. The purpose of the experiment is to measure the fine-scale dynamics of physical and biological mechanisms controlling growth, survival, and dispersal of recently hatched herring larvae and their zooplankton food, on northeast Georges Bank, a principal herring spawning ground. The experiment will involve intensive sampling of the horizontal and vertical structure of a patch of larvae and associated zooplankton and phytoplankton populations, and it will include direct measures of water motion using moored current meters, drifting buoys with drogues, and dye experiments. Eight vessels and five countries (USA, Canada, USSR, Poland, and Federal Republic of Germany) are scheduled to participate. Two vessels will provide a preliminary reconnaissance of possible patch locations. Once a patch is located, a third vessel will do hydrographic and current studies, and a fourth will monitor patch boundaries by continuous high-speed sampling with plankton nets. A fifth will sample vertical structure and horizontal patchiness of zooplankton and herring larvae with a large opening-closing sampler, and a sixth will study fine-scale structure and dynamics of zooplankton and phytoplankton populations and associated nutrient distribution using a large plankton pump, particle counters, and standard chemical, chlorophyll, and C^{14} analyses. A seventh vessel will quantitatively sample (bottom to surface) the fish larvae and larger zooplankton in the patch every 2-3 days using standard bongos. One of the first two vessels will provide hydrographic-zooplankton coverage over the whole of Georges Bank comparable to that for previous years in the ICNAF larval herring program--and similar standard surveys in the late fall, winter, and spring will follow the patch study to provide a follow-up on the fate of the herring larvae, and for comparisons of growth and mortality with previous years. Finally, an eighth vessel is scheduled to use midwater and bottom trawls in an attempt to capture larger predators of herring larvae.

It is expected that such a study can provide significant new insight into the dynamics of plankton patches and in particular help identify mechanisms which may be critical to survival of early-stage herring larvae. Emphasis is placed on the recently hatched larvae since there is general experimental evidence that initiation of feeding after hatching is a critical stage for larvae of a number of fish species (Laurence 1977). Studies of egg and larval patches for major spring-spawning fish species in conjunction with monthly MARMAP surveys are planned for the future.

Circulation studies

Understanding shelf circulation is of critical importance in the development of predictive models of fish production because physical transport and exchange processes control the seasonal cycles of primary and secondary production upon which fish production is ultimately based. Also they affect fish directly, e.g., through temperature effects on metabolism and behavior (particularly migration), timing of spawning, and dispersal of eggs and larvae. The status of knowledge regarding circulation off the northeast coast of the United States has recently been reviewed by Mooers (in press) and much of this section is taken from that paper.

The general circulation on the continental shelf and slope off the Northeast United States has been known in broad-scale terms since the early studies by Bigelow (1933) and Iselin (1939). Estimates of mean transport rates have only recently been deduced from surface and seabed drifters (Bumpu 1973) and so far are substantiated by relatively few direct current measurements and analytical results using box models. However since about the middl 1970's there has been a resurgence of interest in the shelf circulation on th part of oceanographers partly as a result of public concern over possible effects of the impending offshore gas and oil production, as well as gradual recognition of the importance of circulation to fisheries problems. A brief account of the major activities is presented here.

With respect to monitoring subsurface characteristics of shelf waters, the NMFS MARMAP surveys represent the only program committed to broad-scale annual and seasonal monitoring of shelf waters, but only limited physical and chemical measurements are possible on these cruises because the focus is on biological sampling. Temperature transects across the Gulf of Maine and the Mid-Atlantic shelf are also made on a routine monthly basis using XBT's on ships-of-opportunity as part of the MARMAP effort. In the near future monitoring capabilities may be considerably improved through technological advances in data sensing, logging, and telemetry. The NOAA Data Buoy Office (NDBO) now has several telemetering meteorological and oceanographic buoys operating on the Atlantic shelf and off the shelf of the United States. Also satellites are providing more frequent and dense coverage of the sea surface with IR and visable imagery, radar altimetry, and further active microwave data products are expected in the near future. Satellite coverage is particularly useful for monitoring surface temperatures, positions of ocean fronts, eddies and large-scale water mass movements, and may soon be able to sense surface chlorophyll densities.

In addition to the monitoring activities by NMFS noted above, there are also related environmental assessment studies which attempt to relate large-scale atmospheric and oceanographic events with fisheries. For example the severe winters of 1977 and 1978 on the east coast of the United States were related to unusually high mortalities of juvenile croakers in Chesapeake Bay, and white shrimp in South Carolina's coastal waters (Ingham 1978). Another example is the good correlation which was found between larval menhaden transport inshore to nursery grounds, and subsequent strength of year classes, and the wind-generated westward components of Ekman transport off the US east coast (Nelson et al. 1977).

Although the capabilities for monitoring are improving there is a significant need for a scientifically designed long-range program which will provide observations on large-scale phenomena required as specific inputs to circulation models whose outputs in turn must include scales of time and spa of critical importance to ecosystem models.

We now take a brief look at oceanographic studies aimed at estimating rates and processes governing circulation dynamics. In the New York Bight NOAA has recently conducted intensive studies of circulation including many direct current measurements at specific sites where pollutants are discharge and these results together with other studies by universities and private research groups are providing much new information on circulation in the Mid-Atlantic (Bowman and Wunderlich 1977; Hansen 1977). The Gulf of Maine and Georges Bank also are under intensive study now including direct current measurements by the US Geological Survey, Woods Hole Oceanographic Institution, NMFS, University of New Hampshire, and E G and G Company. And as noted above, Canada (Bedford Institute of Oceanography) is conducting intensive current work on Georges Bank as part of the ICNAF larval herring patch study; and they are also conducting intensive shelf dynamics studies on the Scotian Shelf just east of the Northeast Channel separating Georges Bank from the Scotian Shelf. Shelf and slope waters surge in and out of the Gulf of Maine through the Northeast and Great South Channels in response to storms, tides, and possibly offshore eddies, and our own NEFC fishery oceanographic group has recently completed the first definitive study of deep currents through the Northeast Channel (Ramp and Vermersch 1978).

A number of oceanographers in various agencies are now actively engaged in the development of preliminary circulation models for the Northwest Atlantic shelf region, and the new data inputs are being used as quickly as they become available. An informal workshop on the physical oceanography of the Gulf of Maine region was held in April 1977 to review recent results and to foster fruitful exchange of ideas between oceanographers and biologists (Beardsley 1977). A second workshop is scheduled for May 1979 in Halifax and is to include both the Gulf of Maine and the Scotian Shelf. These workshops are serving to provide an in-depth integration of ideas from physical and biological scientists never before achieved in this area. It is anticipated that a comprehensive research strategy will evolve, including long-term monitoring as well as coordinated meso- and micro-scale experiments on the critical dynamics of both physical and biological processes. In short, a marine ecosystem model of the region is the ultimate outcome.

3.4 Biological Modeling Approaches

Until very recently our efforts at NEFC in modeling were largely confined to short-term estimates of future abundance for the major fish populations, and first approximations of the total finfish yield-effort relationship as described earlier in this paper. In the past two years we have begun to look at production and biomass of other biological components of the ecosystem, and also to examine multispecies prey-predator interactions with emphasis on finfish as predators. A brief account is given here of a first approximation energy budget for Georges Bank and food web studies involving finfish, and our current plans for modeling effects of various fishery management strategies in relation to the food web affecting juvenile and adult fishes. More details are available in a report by Cohen et al. 1978).

Gross energy budget for Georges Bank

As a first step toward development of an ecosystem model for the shelf we prepared a first approximation static energy budget for Georges Bank for which we have the most comprehensive data. Estimates of average annual biomass and production of phytoplankton, zooplankton, benthos, and fish were calculated, and converted to Kcal/m^2/yr, and arrayed in the same manner as that for the North Sea after Crisp (1975)--see Figure 3.4.1. For the three components with empirical measures of production (phytoplankton, benthos, and fish), all

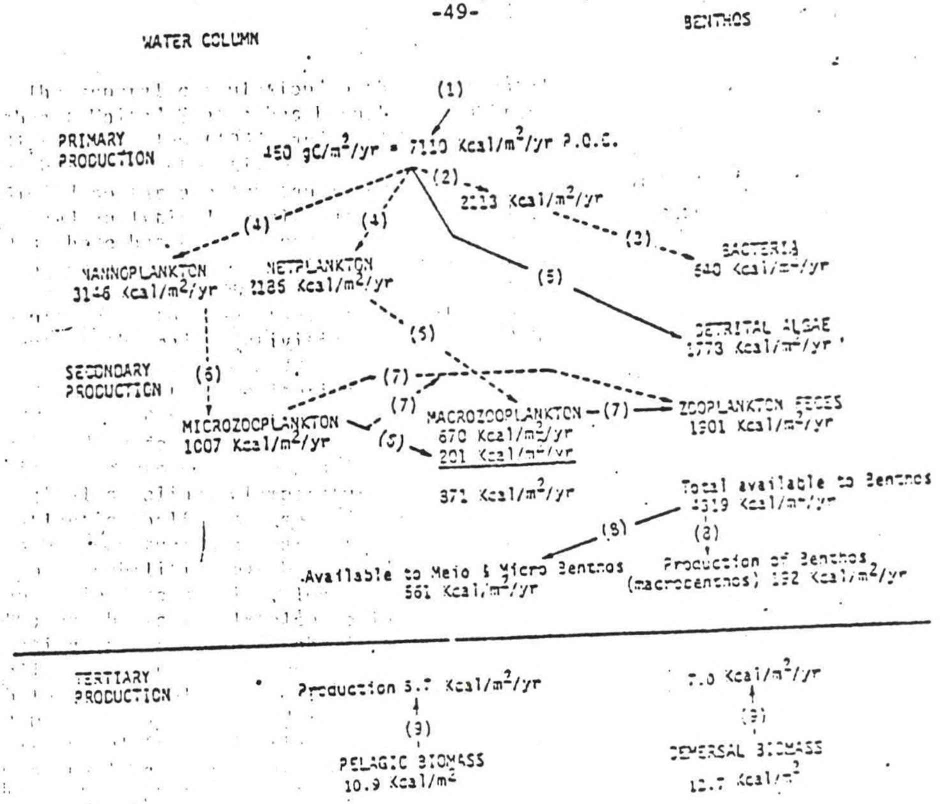


Figure 3.4.1 Energy budget for Georges Bank. Modified from Crisp (Figure 2, 1975).
In the above figure energy flow between trophic levels is linked by arrows, but
the direction of the arrow represents the logical derivation of the values given,
not the direction of energy flow, which is always from top to bottom of the page.
The double underlined values are based on observations, the continuous inter-
connecting lines are steps based on observed relationships, while the dotted
interconnecting lines indicate more speculative relationships. Numbers in
parentheses explain the relations observed or assumptions made.

(1) Data from NEFC larval herring cruises 14C measurements. Kcal/gC
based on a factor of 15.3 (Platt 1971).
(2) Estimate of D.O.C. from Choi (1972) that equivalent of 30% of P.O.C.
production is released as D.O.C.
(3) Assumption that 30% of D.O.C. is incorporated into benthic bacteria
or bacteria which are attached to particles and enter benthos
(Parsons and Seki 1970).
(4) Estimate of nano and net plankton production based on Malone's (1976).
observations that in N.Y. Bight 59% of primary production is
nanoplankton and 41% is net plankton.
(5) Based on the estimate that 75% of phytoplankton is eaten by zooplankton
(Crisp 1975). Remaining 25% is detrital phytoplankton due to
natural mortality.
(6) Assuming an ecological efficiency of 32% for herbivores 20% for
omnivores (Steele 1974). The longer food chain from nanoplankton is
based on Parsons and LeBrasseur (1970).
(7) Assumes assimilation efficiency is 70% for zooplankton, feces is
30% (Crisp 1975).
(8) Average wet wgt of benthos is 240 gm/m^2 (Wigley, unpublished data).
See text for details.
(9) Biomass data for nekton are from NEFC data. Production was determined
using P/B ratios. See text for details. Pelagics include herring
and mackerel; demersal includes all other finfish and squid.

showed higher production rates than the North Sea. The level of primary production of 400-500 gC/m^2/yr is substantially higher than that reported for the North Sea and there is evidence that this level of productivity may be maintained on Georges Bank from the time of the spring bloom through the summer and into early autumn, instead of rapidly declining after the spring bloom as has been thought to be the classical phytoplankton cycle (Cohen et al. 1978; Cohen and Wright 1978). Thus it is perhaps not surprising to find higher levels of benthos and fish production rates on Georges Bank than in the North Sea.

Partitioning of fish production into pelagic and demersal components revealed that pelagic fish production (rates) are similar in the two areas but demersal fish production is significantly higher on Georges Bank than in the North Sea. Crisp (1975) estimated the production of North Sea pelagic and demersal fish species in the mid-1960's as 8.0 and 2.5 Kcal/m^2/yr, respectively. Production of pelagics (herring, mackerel, and squid) on Georges Bank was 6.2 and 5.7 Kcal/m^2/yr during two periods of high (1964-66) and low (1973-75) biomass, respectively, and corresponding values for demersals were 11.0 and 7.0 Kcal/m^2/yr (Grosslein et al. 1978).

We shall update and refine the static energy budget for Georges Bank as new data become available on biomass and production of major biological components, and energy conversions between components. This may include better estimates of transport of production off the bank through migration of animals, and losses of plankton off the bank due to storms or warm core rings which impinge on the southern edge of the bank. In addition we need to include elements not yet included in the budget, particularly birds, mammals, and apex predators such as sharks, billfish, and tuna. Our data for nekton is already adequate to permit more sophisticated treatment which will eliminate some of the biases; this work is now in progress. It is unlikely that this approach will provide more than a very broad framework within which to evaluate other approaches for modeling energy flow. However, it may prove helpful in evaluating broad concepts about partitioning of energy among trophic or size categories through comparisons of different ecosystems such as Georges Bank and the North Sea. Also, it may help to identify gross errors in our assumptions or empirical estimates.

Energy budget based on food consumption

The next step will be to construct an energy flow model based on the energy balance equation at the level of the individual organism. That is, estimates of total food consumption will be balanced with growth, metabolism, reproductive products, and waste. Initially we will concentrate on fish because direct estimates of food consumption, growth, and reproductive products are feasible at least for representative species and life stages of fishes, and there is a good data base on fish food habits and extensive experimental data on metabolism for fish. Ultimately these data together with the available information on population size and structure from our MARMAP program will permit us to estimate average standing crop, production, and consumption of the finfish communities on an annual basis. For now, however, it is difficult to make direct estimates of food consumption by fishes because we do not have accurate estimates of digestion rates to convert our mean gut-content values into daily rations by prey category. The raw data for predator species must first be "calibrated" by an iterative analysis comparing theoretical energy requirements with empirical approximations. Some progress along these lines was made by Edwards and Bowman (1978) who examined possible bias from variable digestion rates of various prey types and sizes, and formulated a general model which among other things estimated annual amount of food consumed. Additional work appears necessary on this problem since the results of this model in terms of the biomass to consumption ratios, differ considerably from those consistent with the literature on metabolic requirements based on experimental results.

First approximations of food consumption by finfish on Georges Bank were made by Grosslein et al. (1978) utilizing estimates of growth production from VPA analysis and an energy balance equation with a metabolism function derived from experimental results on marine fish species. Both consumption and average biomass declined by about 42% between 1964-66 and 1973-75, but production declined by only 26%. The small reduction in production reflects primarily a decline in herring which have a low P/B ratio and the increase in squid which are assumed to have a high P/B ratio. Assuming that there had been no change in basic productivity during the period of study, the reduction in consumption would suggest that there may have been a substantial food surplus at the low point of the finfish biomass. However increased growth was observed only in a few species, which implies that the adult finfish biomass may not have been food-limited even at the higher biomass levels. Further analysis will be required to clarify this matter.

Food web modeling

In addition to using the food habits data for the energy flow model, we plan to use the data base to model the feeding interactions of whole fish communities. The ultimate objective of such a model would be to try to predict the long-term effects of alternate management strategies on the productive capacity, population structure (species and size composition) and stability of multispecies fish communities, taking into account the prey-predator and competitive interactions as well as stock-recruitment relationships. The first stage model is a deterministic trophic interaction simulation model designed to handle nonlinear relationships. Stochastic elements (e.g., recruitment functions, effects of storms, and other circulation dynamics) will be introduced as understanding of processes and linkages is established. The basic structure and characteristics of the first-stage model are outlined briefly here.

In a preliminary linear form the model is donor controlled; i.e., the energy flow ($F_{ij} = a\ x_i$) from donor compartment "i" to recipient compartment "j" is dependent on the state of the donor (x_i). In the nonlinear form, energy flows between compartments as a function of both donor (prey) and recipient (predator) compartments. The central element of the nonlinear model is a basic physiological mass balance equation:

$$I = G_T + G_R + R + M + E$$

he ingested food (I) is partitioned into tissue growth (G_T), reproductive aterial (G_R), respiration (R), maintenance (M), and waste elimination (E), ir manner similar to that in the Narragansett Bay model (Kremer and Nixon 978). When (R + M + E) > I, then starvation results and there is a drop in redator biomass and reduction in reproduction potential. The respiration and limination requirements (R + M + E) are functions of temperature,

$$C(t) = C_o e^{-r(t - t_o)},$$

here C_o is a constant at optimum temperature t_o and r is a fitting coeffi-ient (van't Hoff's rule). The amount of food the predator consumes to offset hese losses depends upon the prey abundance and composition. Two general eeding functions are being considered:

(1) $I = I_o(1 - e^{-KP})$, after Ivlev (1961)

(2) $I = I_o(\frac{P}{h + p})$, after Holling (1959)

where P = prey population

I_o = optimum ingestion rate

K and h are fitting constants.

he donor population consists of a multispecies array of prey. Following the ultispecies prey-predator model of Parrish (1975) our model makes ingestion a unction of the predator's preferences:

$$I = I_T(\frac{V_i P_i}{\Sigma V_i P_i}),$$

here V_i, P_i, I_k are preference, biomass, and ingestion of the ith prey, espectively, and I_T is the total food ingested.

rowth and mortality model for larval fish

Another major focus of our modeling efforts will be on studies of growth nd mortality of larval fish. This is important not only because major atural mechanisms controlling year-class strength operate at this stage, but lso because fish larvae are extremely sensitive to very low levels of some ontaminants (Rosenthal and Alderdice 1976).

A stochastic dynamic model of growth and mortality of winter flounder has ecently been constructed by Laurence and Beyer (MS 1978). Although the model eals only with mortality from starvation in experimental aquaria (predators ere absent), the assumptions and hence input parameters for feeding behavior, etabolism, and growth were based on extensive quantitative experiments in the laboratory. The key stochastic element in the model is the assumption that individual larvae encounter food organisms in a completely random fashion, i.e., according to a Poisson process. This assumption is not inconsistent with extensive and detailed observations of feeding behavior of winter flounder larvae in aquaria. The level and pattern of mortality simulated by the model are basically consistent with results obtained on a natural population of winter flounder larvae, making allowances for the fact that predation was also a factor in the field study.

Results of the larval herring patch study will be examined within the framework of this model, and in particular we hope to be able to gain some insight into the problem of partitioning larval mortality into its two basic components, starvation and predation.

4. SOME STATISTICAL PROBLEMS

The problems of sampling and interpreting sample data from biological populations are widely known. Organisms are generally not distributed in a homogeneous fashion, and in most cases we must use only partially effective sampling methods which sometimes perform erratically and whose average efficiency is generally unknown or known only approximately. In addition we seldom know the underlying distribution of the organisms with any precision--only that they are contagiously distributed with respect to the rather large scales of time and space we must deal with in the marine environment, and that their distribution or aggregational properties undoubtedly change from time to time in response to both biotic and abiotic environmental factors.

In this section we outline briefly some of the statistical characteristics of trawl and plankton catch data, and a few of the problems we face in their analysis and interpretation.

4.1 Characteristics of Trawl Catch Data

Throughout the preceding case history the criticality of the time series of the stratified random bottom trawl surveys in developing the understanding necessary for management of the Gulf of Maine, Georges Bank, Middle Atlantic ecosystem is obvious. Not only for direct measures of relative abundance but also for the estimation of population parameters. Therefore, considerable research has been devoted to trying to understand these data, e.g., Grosslein (1971), Pennington and Grosslein (1978). Numerous assessment studies have used statistical relationships between survey cruise catches to estimate from virtual population size (Clark in press).

The trends in haddock autumn survey catch per tow and stock size estimated for VPA are given in Figure 4.1.1. Although the trends are remarkably similar the relative availability of haddock in the survey would appear to have improved in recent years. This could be the result of some underreporting of catches in the latter (1977-78) period which would result in underestimates of recent stock size. The degree to which catches would have had to be underreported to achieve this has not been determined. An alternative hypothesis is that the form of the distribution of haddock changed with relative density as hypothesized by Clark and Brown (1977). This would mean different probability distribution functions for low and high densities would have to be used in the anal'sis. The frequency of numbers per tow in the trawl catches are given in Figure 4.1.2 bottom, from Clark and Brown (1977).

The above problems although intriguing and in need of solution present little problem for assessments. In contrast the pollock present very difficult problems for the most recent assessment (Clark, Burns, and Hayden 1978; Clark, Cleary, and Burns 1978). The catch per tow in kilograms is given in Figure 4.1.3. There appears to be evidence of a stable population if one ignores the high catches in 1970 and 1977. Furthermore, examinations of the catch in numbers per tow by age does not explain the large increases, i.e., they were not caused by recruiting year classes. Commercial catches do not account for the severe drop in the following year. It is possible that these points are just outliers, but if so, what rules should be developed to use on their interpretation of survey cruise series? One hypothesis is that the distributions of pollock could best be described by a distribution function such as a negative binomial and thus a transformation of ln (N + 1) could be used. Using this transformation and retransforming according to the following formula as suggested by Bliss (1967):

$$E\,(\overline{y}_{st}) = \exp\,(\overline{y}_{st} + S^2/2)$$

where $E\,(\overline{y}_{st})$ represents the estimated (retransformed) stratified mean catch per tow and $\overline{y}_{st}$ and S^2 represent the stratified mean and the estimated population variance in logarithmic units. This procedure brought the 1970 point in line with adjacent values but the 1970-78 still appears too high relative to adjacent points to be attributed to increases in abundance.

Clark, Cleary, and Burns (1978) described this situation as follows: Changes in the underlying probability distribution function associated with pollock are likely involved, as pollock aggregate in autumn in large spawning concentrations. If tows in a given year were taken in concentration areas when substantial spawning activity was occurring, the probability of very large or very small catches would obviously be increased as opposed to years in which survey scheduling relative to spawning activity was different. Consequently, the pronounced increases observed in 1969 and again in 1976-77 may result at least in part from distributional differences between years. Support for this hypothesis is provided by catch data for individual strata which indicate that catch rates were in fact extremely high in 1976 and 1977 in or adjacent to known spawning areas (Stratum 24 in 1976 and Stratum 26 in 1977) in comparison to the 1971-75 period. Consequently, the extent to which the 1976-77 USA autumn survey data reflect an actual change in abundance is uncertain at the present time.

The question still remains--how best to analyze these data?

4.2 Characteristics of Net Zooplankton Data

Some indication of the precision in estimates of larval production can be obtained from the standard deviations of estimates of mean numbers of larvae on a per-cruise basis. Data for the eastern Georges Bank spawning site were

CLARK and BROWN: CHANGES IN BIOMASS OF FINFISHES AND SQUIDS

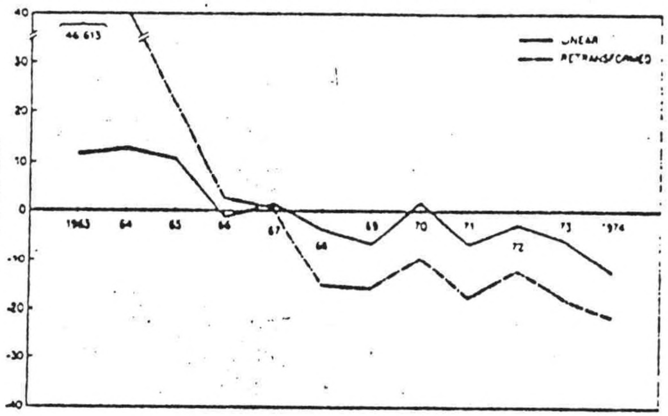


Figure 4.1.1

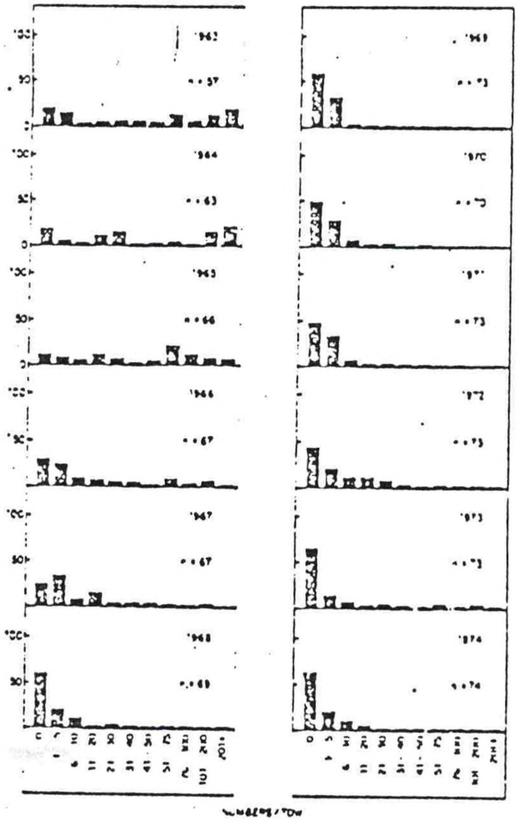


Figure 4.1.2

—Top. Trends in catchability coefficien calculated by year using untransformed and r transformed survey data, and bottom) distributio of stratified mean catch per tow in numbers expresse as relative percentages of the total number of surve tows by year for Georges Bank haddock.

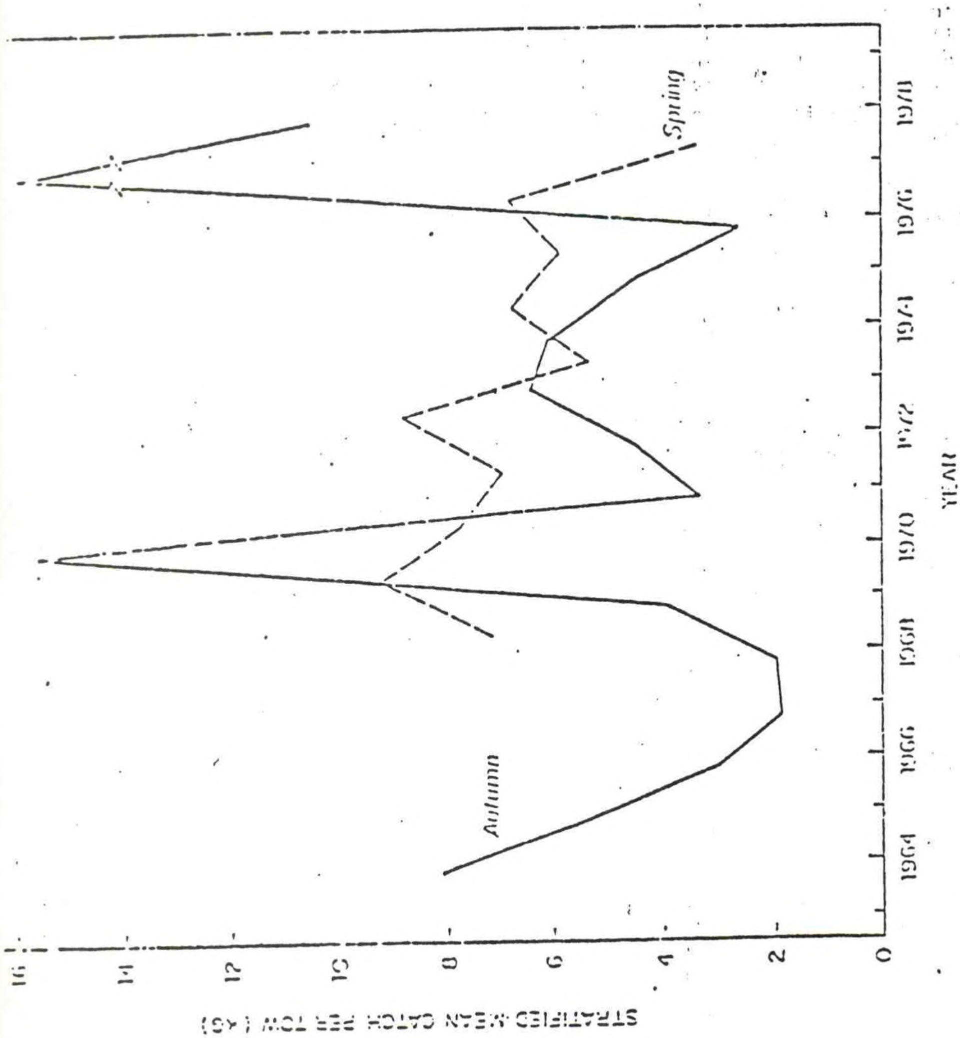


Figure 4.1.3 Stratified mean catch per tow (kg) of pollock in USA spring and autumn bottom trawl surveys for Georges Bank, the Gulf of Maine, and the Scotian Shelf (spring: Strata 13-42; autumn: Strata 24 and 26-42). Spring data for 1968-72 adjusted by a factor of 1.7 to account for differences in surface area between the "36 Yankee" and the "41 Yankee" trawls.

summarized for two size categories (5-10 mm, 10-15 mm) and all cruises in September through December 1972-76. There were 37 standard stations occupied on each cruise in the area from 68° west longitude to the eastern edge of Georges Bank (Figure 3.3.2). Means, standard deviations, and coefficients of variation (CV) for each larval size category and cruise are presented in Table 3.3.1. For the 5-10-mm length group, CV's ranged from 2.7 to 5.5 with a mean CV of 3.8, and comparable values of CV for the 10-15-mm group were 1.7-4.0 with a mean of 2.6; CV's for cruises with means ($\overline{X}$) less than or equal to 1 are not included in these ranges or mean values of CV. The large CV's are a result of highly skewed frequency distributions as illustrated for four cruises in Table 4.2.3. Although these CV's are large, they are not so large as to obscure the very large differences in larval production which have occurred on Georges Bank since 1971. Lough (1976) showed that production of larvae < 10 mm was an order of magnitude greater in 1973 and 1974 than in 1971 and 1972, intermediate in 1975, and virtually nil in 1976 (see Table 4.2.1). Another encouraging feature is the fact that within a given season the mean abundance indices almost invariably show a systematic progression from low to high to low numbers during the September-December period, which is consistent with a concentrated spawning in one time and one place (Table 3.3.1). Actually the production estimates referred to here represent the total for Georges Bank and Nantucket Shoals combined, but the relative differences between years are basically the same for eastern Georges Bank alone.

Another measure of variability which is of interest here was derived from a 1974 study of vertical distribution of herring larvae on Georges Bank. A series of simultaneous horizontal tows were made at 6 depths, every 2 hours for 40 hours, at a single location on Georges Bank in a concentration of recently hatched herring larvae. A total of 21 hauls were made and the CV's of mean larval densities (no./100m^3) for the 6 depths ranged from 0.6 to 1.6, with a mean of 0.9 (Table 4.2.2). The CV for the estimated mean abundance per 10m^2 (integrated over the water column) was 0.6. This level of within-station variability is not too large to obscure major differences in vertical distribution of larvae and is small enough so that one can place reasonable confidence in a single oblique haul such as one of the standard ICNAF hauls. That is, the implication here is that a grid pattern such as that used in the ICNAF program is adequate to detect major differences in larval distribution and abundance. However it is also clear that because of the highly skew distribution, significant improvements in precision on a per-cruise basis would require a very large increase in density of stations. If it becomes necessary to achieve higher precision of abundance estimates it would be more effective to increase the frequency of cruises rather than the density of stations per cruise. We have not yet tried to estimate the relative cost-benefit ratios for one or the other strategy in the larval herring program partly because we are still analyzing the seasonal estimates of growth and mortality. However it is obvious that certain types of studies (e.g., short-term phenomena such as dispersal vs. currents, larval feeding and mortality vs. absolute densities of zooplankton within a plankton patch) will require much more intensive sampling in time and space to produce definitive results.

In October 1977 the Polish research vessel WIECZNO sampled a patch of recently hatched herring larvae in the Nantucket Shoals area. Plots of individual catches (numbers per 10 m^2) showed that patch boundaries could be

Table 4.2.1 Summary of Georges Bank-Nantucket Shoals larval herring initial duration-corrected abundance and average seasonal mortality rates for the 1971-1977 seasons.

Season	Initial Larval Abundance (n·10[illegible]) (< 10 mm S.L.)	Mortality Coefficient (-Z) Sept.-Dec.	95% Confidence Interval	Mortality Rate ($1-e^{-Z} \cdot 100$ %/day)	Mortality Coefficient (-Z) Sept.-Feb.	95% Confidence Interval	Mortality Rate ($1-e^{-Z} \cdot 100$ %/day)
1971	20.78	0.0320	0.0166-0.0475	3.15	(No February Survey)		
1972	37.30	0.0491	0.0338-0.0644	4.79	(No February Survey)		
1973	256.05	0.0481	0.0332-0.0629	4.69	0.0498	0.0347-0.0649	4.86
1974	159.24	0.0436	0.0312-0.0560	4.26	0.0395	0.0319-0.0471	3.87
1975	61.96	0.0538	0.0413-0.0662	5.24	0.0277	0.0190-0.0364	2.74
1976	0.13	+0.0093	0.0238-0.0051	+0.94	+0.00026	0.0005-0.0090	+0.026
1977	9.06	0.0329	0.0186-0.0472	3.24	0.0355	0.0271-0.0432	3.49

Table 4.2.2 Abundance indices of recently hatched larval herring based on repeated sampling (21 hauls over a 40-hour period, with samples at 6 depths on each haul) at a single station on Georges Bank. Mean numbers/100m³ and standard deviations and coefficient of variation shown for each depth. Also data shown for the depth-integrated index (numbers/10m²).

Depth (m)	Mean number larvae per 100m³	Standard deviation	SD/Mean
1	453	709	1.6
10	1,027	922	0.9
20	1,470	1,074	0.7
30	2,232	1,350	0.6
50	2,126	1,473	0.7
80	[illegible]	643	0.9
Total no./10m²	11,516	6,861	0.5

ble 4.2.3 Frequency distributions of larval herring catches (no. per $10m^2$) on four ICNAF surveys on Georges Bank.

. of larvae per $10m^2$	WIECZNO 1973		BELOGORSK 1973		W. HERWIG 1973		PROGNOZ 1974	
	5-10	10-15	5-10	10-15	5-10	10-15	5-10	10-15
0	31	27	31	17	25	17	27	16
1-99	6	10	7	20	15	18	8	17
100-199	2		1	1		3	2	4
200-299	1			1		1		1
300-399	2	2		1	2	3		2
400-499		1		1		1		
500-599		1	1	1				
600-699	1	1						
700-799		2	1				1	2
800-899				1	1		1	
900-999		1		2				1
000-1,999			2			2		2
000-2,999			1		1		1	
000-3,999								
000-4,999							1	
000-5,999							1	
000-6,999	1						2	
000-7,999								
000-8,999								
000-9,999	1				1		1	
10,000			1					
tal frequency	45	45	45	45	45	45	45	45
	489	397	671	133	387	125	1,026	179
	1,833	1,578	3,107	269	1,679	300	2,403	343
$\sqrt{x}$	3.7	3.9	4.6	2.0	4.3	2.4	2.3	1.9

defined reasonably well since abundance of larvae in the patch were two orders of magnitude greater than background concentrations (Figure 4.2.1). Only one mode of larvae was observed with a mean length of 8.8 mm. The density distribution of herring larvae within the confines of the heaviest density contour (> 1,000 larvae per 10 m^2) was remarkably homogeneous with a negative binomial K of 2.52 which implies that a transformation ln (N + 1) should be appropriate. The frequency distribution of catches within the patch proper (≥ 1,000 larvae or more) is in fact not terribly far from normal:

catch (no's/$10m^2$)	f
< 900	3
901-1,000	3
1,001-2,000	5
2,001-3,000	8
3,001-4,000	1
4,001-5,000	2
5,001-6,000	1
6,001-7,000	1
> 7,000	0

It remains to be seen how long the integrity of such a patch is retained but it is very encouraging to see such coherence on a scale of 20 K_m over a period of several days. The problem in the patch study will be to devise (in real time) an objective procedure for deciding initially when the patch boundaries are reached, and ultimately when the "patch" ceases to exist. A proposed rule of thumb for use in the upcoming larval herring patch study is that when two consecutive hauls along a transect through a patch yield larval catches an order of magnitude lower than the highest catch along the transect, then the boundary is passed and a new transect in the reverse direction is begun. We are open to suggestions for a better decision rule.

After the patch study we hope to have better insight into the likelihood of encountering (or missing) a patch on the order of 10-20 km on a side, with the standard station pattern of the ICNAF sampling scheme of one station every 25-30 km (see Figure 3.3.2).

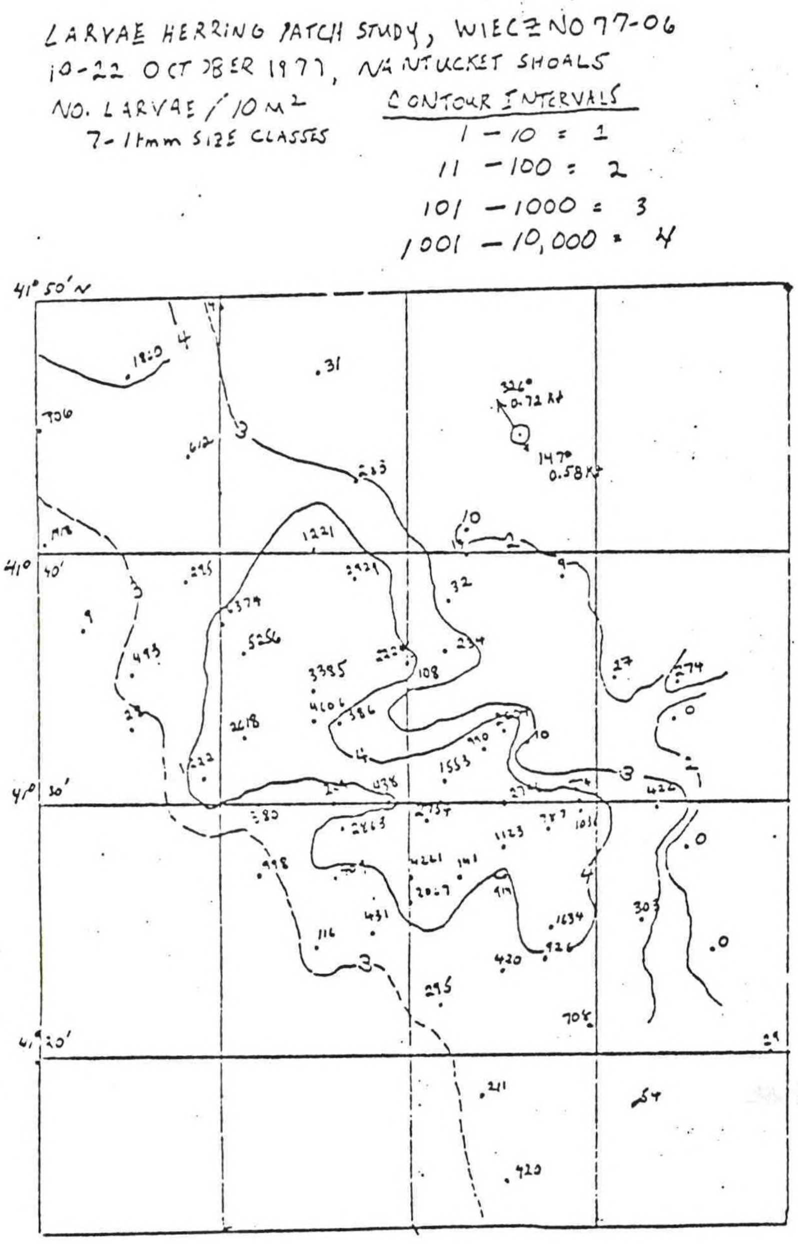


Figure 4.2.1 Patch of recently hatched herring larvae on eastern edge of Nantucket Shoals, October 1977.

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Food Requirements of Fish Stocks of the Gulf of Maine, Georges Bank, and Adjacent Waters. ICES C.M.1978/Gen:8 (Symp.). 8 pp.

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ITEM 7

International Council for the
Exploration of the Sea

C.M.1978/Gen:8 (Symp.)

Food Requirements of Fish Stocks of the Gulf of Maine, Georges Bank, and Adjacent Waters

By

K. Sherman,[1] E. Cohen,[2] M. Sissenwine,[2] M. Grosslein,[2]
R. Langton,[2] and J. Green[1]

[1]National Marine Fisheries Service
Northeast Fisheries Center
Narragansett Laboratory
Narragansett, Rhode Island 02882
USA

[2]National Marine Fisheries Service
Northeast Fisheries Center
Woods Hole Laboratory
Woods Hole, Massachusetts 02543
USA

Abstract

Food consumption and production of fish stocks in the Gulf of Maine, Georges Bank, Southern New England, and Mid-Atlantic continental shelf waters are described in relation to primary productivity estimates for the areas. Comparisons are made between theoretical estimates of fish production in relation to primary productivity as outlined recently by Sheldon et al. (1977) and recent empirical estimates based on an energy balance equation and estimates of biomass derived from VPA and research vessel data. Empirical data on food consumption is examined among areas in relation to differences in primary production-fish production ratios. Comparisons are also made with recent production and consumption estimates for North Sea fish stocks.

Introduction

Since the early works of Bigelow (1926), Riley (1946), and Clarke (1946), little attention has been focused on the energetic linkages among primary, secondary, and fish production off the U.S. east coast. Using average values for ecological efficiencies and productivity, Ryther (1969) estimated that one million metric tons of fish were produced annually in the area from the Nova Scotian shelf to Hudson Canyon. Total finfish biomass estimates of about six million metric tons for the period 1968-1969 are given by Clark and Brown (1977), based on research vessel trawl-surveys and catch-data for a slightly larger area. This large biomass of finfish has in the period since 1968 declined by approximately 65% to a level of 2.5 million metric tons in 1974-1975. Most of the decline is correlated with fishing effort (Clark and Brown, 1977).

The impact of a reduction of three-and-one-half million metric tons of finfish biomass on the productivity of the ecosystem off the northeast coast is presently the subject of an extensive investigation by the Northeast Fisheries Center. As part of the study, initial estimates have been made of the food requirements of the fish stocks in the area in an attempt to clarify the importance of food availability as a factor in governing fish production.

Food Base

Initial estimates of the principal prey items utilized by 17 of the more abundant pelagic and demersal fish off the northeast coast based on the examination of approximately 70,000 stomachs are summarized in Edwards and Bowman (1978) and Grosslein et al. (1978). The major pelagic species are herring, and mackerel; squid are also included as pelagic species although concentrations can be found along the bottom, where they are vulnerable to bottom trawling. Herring and mackerel feed principally on euphausids, copepods, chaetognaths, pteropods, fish eggs, and appendicularians. Data for squid, although incomplete, suggest that fish, euphausids, and squid are the predominant prey items. Of the 14 demersal species examined, four are principally fish eaters--silver hake, cod, spiny dogfish, and goosefish. Three prey almost exclusively on benthic crustaceans--white hake, red hake, and little skate. Four species--haddock, and windowpane, yellowtail, and winter flounders--concentrate on benthic invertebrates including polychaetes and echinoderms, and three species--pollock, redfish, and butterfish--prey on pelagic crustaceans, particularly euphausids (Table 1).

The food habits of eight species of fish were examined for gross differences in diet between three geographic areas off the northeast coast--Gulf of Maine, Georges Bank, and Southern New England. These eight species were selected because they cover the spectrum of feeding types, ranging from benthic to pelagic predators, and/or because of their overall importance as part of the finfish biomass in a specific area. The species considered are: Atlantic cod, haddock, yellowtail flounder, silver hake, Atlantic mackerel, Atlantic herring, pollock, and redfish. An examination of the food habits of these species revealed no remarkable differences in diet between areas for any given species (Table 2). There are some instances where a change in the species composition of prey reflects the changing distribution of available prey but this does not necessarily represent a change in feeding tactics by the predator. If anything the conclusion one must draw is that the food habits are remarkably constant for any given species.

Food Requirements of Fish Stocks off the Northeast Coast

Recent estimates have been made of the food requirements of the fish biomass off the northeast coast. Edwards and Bowman (1978) using caloric values for the dominant prey items, and a model of energy requirements for the biomass of fish in the Gulf of Maine, Georges Bank, and Southern New England areas calculated energy requirements for the biomass of finfish during a period of high abundance 1963-1965 and for a low biomass period 1972-1974. Their values reflect a substantial difference in energy requirements for the stocks decreasing from $89,783 \times 10^3$ metric tons of food per-year in the early period to $51,215 \times 10^3$ metric tons per-year for the more recent time-frame (Table 3).

Theoretical Food Requirements of Fish Stocks off the Northeast Coast

In an attempt to partition the amount of energy consumed by fish and the amounts available to other components of the ecosystem, the theoretical primary productivity to fish relationships were calculated according to the method developed by Sheldon et al. (1977). This approach, uses the sizes of predators, and their prey, and the efficiencies of their interactions to estimate the production at any trophic level using standing stock and growth estimates of different size ranges. We have used this method to calculate the fish production of the Gulf of Maine, Georges Bank, Southern New England, and Mid-Atlantic waters based on estimates of primary production in these areas. Sheldon et al. (1977) assume an average doubling time of phytoplankton of 2 days and a standing stock of fish that is about 70% of the phytoplankton standing stock resulting in an estimate of phytoplankton production 260 times fishery production for waters of the Gulf of Maine. These assumptions were also used in our calculations for Georges Bank. The ratios of fish to phytoplankton biomass differ both for Southern New England and the Middle Atlantic. The values for these areas were determined by solving the equation $P=rS$ for S; where P=production of phytoplankton, r=instantaneous growth rate and S=phytoplankton standing stock (Sheldon, 1977). The standing stock of phytoplankton was then compared with that of fish in the period before stocks declined (1964-1966). The value for r in the equation was calculated from the doubling time. A reasonable value for doubling time under field conditions is 2 days, based on the work of Epply (1972). The production value in the equation is our best estimate of the primary productivity for each area. Carrying out the calculation we found that the fish biomass was 100% of the phytoplankton biomass in Southern New England and 36% in the Middle Atlantic region. Adjusting the phytoplankton production by the biomass ratios leads to the phytoplankton production being 180 times the fish production in Southern New England and 500 times greater in the Middle Atlantic. The fish production based on the phytoplankton production is about 11 g wet wt/m^2/yr in the Gulf of Maine, 29 g wet wt/m^2/yr in Georges Bank, 14 g wet wt/m^2/yr in Southern New England, and about 6 g wet wt/m^2/yr in the Middle Atlantic area. In addition, a calculation of primary production needed to support the fish stocks was carried out using this method. Estimates of fish production were made using an energy balance equation described in Grosslein et al. (1978; Table 5) based on biomass data for the Gulf of Maine, Georges Bank, and Southern New England for the period before overfishing (1964-1966) and in recent years (1973-1975) when the stock levels were lower. The biomass of herring of the Georges Bank and the Gulf of Maine stock was estimated by virtual population analysis using catch data and assumptions compatible with the most recent assessment of the stocks. Biomass density was obtained by dividing population estimates by the area of Georges Bank and Nantucket Shoals (69,773 km^2) and Gulf of Maine (61,487 km^2). The average density of herring in Southern New England was estimated by adjusting the density of the Georges Bank-Nantucket Shoals area by the ratio of the area of Nantucket Shoals to all of Southern New England. This results in 25% of the Georges Bank stock being attributed to Southern New England.

Estimates of mackerel biomass for ICNAF SA 3-6 were reported by Anderson and Paciorkowski (1978). These estimates were divided by the total area of SA 3-6 (448,000 km^2). The density so calculated was assumed to apply to each of the four areas considered. The density of all finfish and squid on Georges

Bank, excluding the principal pelagics (herring and mackerel) as reported in Grosslein et al. (1978) were used. The population estimates reported in Clark and Brown (1977) for all of SA 5-6 (excluding herring and mackerel) minus population estimates on Georges Bank based on Grosslein et al. (1978) were used to calculate the average density for the Mid-Atlantic, Southern New England and Gulf of Maine areas combined. These values were adjusted according to the relative mean catch per tow in autumn bottom trawl surveys in order to obtain estimates for each of these areas separately. The production is lower calculated this way (Grosslein et al., 1978) than that computed using the method of Sheldon et al. (1977). For example, on Georges Bank the production ranges from 17.5 to 12.7 using P/B ratios (1964-1966 to 1973-1975) versus 28.8 g wet wt/m^2/yr as given in Table 5.

Our calculations show that there is a surplus of primary production over the amount necessary to support fish production even at 1964-66 levels. Using the approach of Sheldon et al. (1977) and the fish production value for Georges Bank of 17.5 g/m^2/yr, the amount of primary production required to support this level of fish production is only 273 gC/m^2/yr as shown in Table 4. Our present estimate of mean annual primary production for Georges Bank is 450 gC/m^2/yr. There is also a surplus in the Gulf of Maine and Middle Atlantic (Table 4).

When we consider the changes in biomass, production, and consumption between the 1964-1966 and 1973-1975 periods, significant quantities of available food are not accounted for by consumption. The surplus from each area for the different fish types is given in Table 5. In each area for finfish, squid and herring, there is less food consumed now than before overfishing began. It is possible that species less vulnerable to our sampling methods such as Ammodytes are increasing in the Georges Bank, Southern New England region (Smith et al., 1978; Meyer et al., 1978).

Environmental Considerations

Schlitz (personal communication) has estimated that as much as 30% of the water on Georges Bank may be advected off the bank during the year, this includes transport to the southwest along the shelf-slope front as well as water advected across the front due to calving (Wright, 1976) and water pulled off of the bank by Gulf Stream rings. The major loss appears to be a southwest transport along the front; an experiment involving the NEFC, USGS, and WHOI is planned for next year to measure this transport. In addition, storms are responsible for large quantities of near surface water being advected off of the bank. This was shown very clearly in the offshore transport to the southwest of the Argo Merchant oil by predominant northwest winds. If 30% of the primary production is lost with the water, the primary production of approximately 300 gC/m^2/yr would suffice to support the 1964-1966 fish production.

Long-Term Trends

An examination of research vessel trawl surveys and fish-catch data for the period 1963 through 1977, although indicative of significant changes in biomass levels, revealed no major differences in species composition. No large build-up of other demersal or pelagic species to replace those that declined in the early 70's is apparent, with the possible exception of sand lance, which appears to have been increasing steadily since 1974 (Smith et al., 1978). The reductions in mean weight of fish (kg) observed during the heavy exploitation period of the early 70's is now approaching the mean weight of the stocks prior to heavy exploitation. The data do not indicate any significant shifts to smaller sizes in fish collected on the trawl surveys. Nor is there any apparent evidence of a significant shift in food habits (Grosslein et al., 1978).

For the Georges Bank area production and consumption values were calculated for the high biomass 1964-1966, and low biomass periods (1973-1975). Both consumption and average biomass declined by about 40%. Production declined only 26%, reflecting a reduction in herring which has a low P/B ratio and an increase in squid, which has a high P/B ratio. Both pelagic and demersal species declined, unlike the condition in the North Sea (Grosslein et al., 1978).

Comparison with the North Sea

Recent studies of fluctuations in the relative abundance of pelagic and demersal fishes in the North Sea have suggested that decreases in the pelagic biomass (herring and mackerel) have released sufficient food energy to support an increased biomass of demersal species (Jones and Richards, 1976) thus implying a sustained level of production of prey organisms. In the Northwestern Atlantic the decline has been in both the pelagic and demersal stocks (Table 5) with no apparent change in the availability of food organisms. Grosslein et al. (1978) have pointed out that the consumption rates of Georges Bank appear higher than the North Sea for both high and low biomass periods. Similarly, calculations presented here showed that Southern New England and the Gulf of Maine stocks also have higher consumption rates than the North Sea. Estimates of finfish food requirements for the North Sea were about 59 Kcal/m^2 during the period 1959-1961 (when the adult finfish biomass of the major stocks was 6.4 million tons), and 40 Kcal/m^2 during the period 1968-1970 when the total biomass was on the order of 4.8 million tons (Jones, 1976; Jones and Richards, 1976). In contrast stocks of the Gulf of Maine and Southern New England had consumption estimates of 71 and 95 Kcal/m^2, respectively, during the high biomass period and 49 and 58 Kcal/m^2 during the low biomass period. The differential consumption between the two areas would be less if consumption of squid and juvenile fish were incorporated in the North Sea estimates. It is interesting to note that the decrease in total consumption over all four Northwestern Atlantic areas of 37% according to the calculations presented here agrees well with the decrease of 43% calculated from Edwards and Bowman's (1978) results, which were derived by different methods.

For the later period (1968-1970) the level of exploitation (50%) assumed for pelagics in Crisp's (1975) study would seem too low relative to the data presented on biomass and catch in the two studies by Jones (1976) and Jones and Richards (1976). A higher level would seem more realistic and this would decrease production estimates somewhat in the North Sea. By way of comparison, application of the B/P ratios for the Northwest Atlantic region to the biomass data for the North Sea (pelagic and demersal) yields a substantially smaller estimate of production for the North Sea. It would be useful to examine these production estimates for the two areas in more detail.

Stock Recovery

If we assume that the level of primary and secondary production has remained fairly stable since the early 1960s, then recovery of the fish stocks to former abundance levels should be fairly rapid from an ecosystem point of view, given reasonable fishery management regulations. No large-scale change has been observed in feeding habits of the principal fish stocks or in the species composition of their prey. The most significant change in prey was limited to the increasing abundance of Ammodytes (sand lance). The consequences of this increase will be monitored closely over the next several years. Size changes that have been observed are related to the loss of larger sizes of fish to increased fishing exploitation. Recently, evidence of increasing mean weights have been observed (Grosslein et al., 1978).

Given the large reduction in consumption, it would appear that the ecosystem off the northeast coast is not food-limited for medium size fish. Our initial estimates of food requirements while useful need to be refined for different size categories of predators and prey. The availability and abundance of food to larval and juvenile stages, for example, is critical to growth and survival (Lasker, 1975; Laurence, 1974, 1977). Studies are presently underway to obtain a better understanding between plankton and the survival of the early-life history stages of fish.

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Table 1. Stomach contents of fish collected on Georges Bank from 1969 through 1972. The data is expressed as a percent of the total stomach contents by weight for each species. The number of fish examined, the percent of empty stomachs, mean weight of prey per stomach, and the mean predator length are included at the bottom of the table for each species of fish. (From Grosslein et al., 1978.)

Predators / Prey groups	Pollock		Redfish		Butterfish		Windowpane		Yellowtail		Haddock		Winter flounder	
CRUSTACEA	70.7		77.9		37.5		25.6		32.2		23.7		8.3	
Caridean shrimp		3.3		-		-		26.7		2.5		0.7		-
Penaeid shrimp		-		0.2		-		-		-		-		-
Anomuran crabs		-		-		0.1		-		0.7		0.9		0.2
Brachyuran crabs		-		-		-		-		-		0.2		0.3
Astacidean		-		-		-		-		-		-		-
Euphausiids		63.2		44.4		7.5		-		-		5.5		-
Mysids		0.1		-		-		-		-		0.2		-
Caprellid amphipods		-		-		-		-		0.1		-		-
Gammaridean amphipods		-		0.1		0.3		-		9.1		9.9		2.7
Hyperiid amphipods		-		0.1		0.6		-		-		-		-
Isopods		-		-		-		-		0.5		0.2		-
Copepods		-		-		0.1		-		-		-		-
Cumaceans		-		-		-		-		0.1		-		-
Cirripeds		-		-		-		-		-		-		-
Unidentified		2.1		33.1		29.2		1.9		19.2		6.1		5.1
PISCES	23.6		20.6		-		-		0.1		-		0.1	
Clupeidae		0.9		-		-		-		-		-		-
Scombridae		-		-		-		-		-		-		-
Pleuronectiformes		-		-		-		-		-		-		-
Gadidae		0.5		-		-		-		-		-		-
Cottidae		-		-		-		-		-		-		-
Ammodytidae		-		-		-		-		-		-		-
Fish eggs		-		-		-		-		-		-		-
Unidentified		22.2		20.6		-		-		0.1		-		0.1
POLYCHAETA	0.1	0.1		-	-	-	-	-	46.4	46.4	23.9	23.9	33.0	33.0
ECHINODERMATA	-		-		-		50.3		2.2		12.5		0.3	
Asteroids		-		-		-		-		-		0.2		0.1
Ophiuroids		-		-		-		-		-		9.3		0.1
Echinoids		-		-		-		50.3		-		2.5		0.1
Holothuroids		-		-		-		-		-		0.5		-
Unidentified		-		-		-		-		2.2		-		-
MOLLUSCA	1.7		-		-		-		1.3		6.2		1.0	
Gastropods		0.1		-		-		-		0.1		0.4		0.3
Pelecypods		-		-		-		-		1.1		5.2		0.7
Cephalopods		-		-		-		-		-		-		-
Pteropods		1.6		-		-		-		-		-		-
Unidentified		-		-		-		-		0.1		0.6		-
CHAETOGNATHA	-	-	-	-	7.5	7.5	-	-	-	-	-	-	-	-
TUNICATA	0.1	0.1	-	-	21.4	21.4	-	-	0.3	0.3	-	-	2.6	2.6
CNIDARIA	1.0	1.0	-		-		-		10.6		0.1	0.1	13.9	
Hydrozoans	-	-		-		-		-		-		-		3.9
Anthozoans	-	-		-		-		-		10.6		-		10.0
SIPUNCULIDA	-	-	-	-	-	-	-	-	-	-	-	-	-	-
NEMERTEA	-	-	-	-	-	-	-	-	0.1	0.1	-	-	-	-
ANIMAL REMAINS	2.3	2.8	1.5	1.5	33.3	33.3	21.1	21.1	3.0	3.0	10.0	10.0	22.1	22.1
SAND AND ROCK	-	-	-	-	-	-	-	-	3.8	3.8	23.6	23.6	18.7	18.7
Number of stomachs		197		54		67		30		709		408		71
% empty		3.6		31.5		40.3		60.0		28.5		8.6		25.4
$\bar{X}$ wt per stomach(g)		12.3		1.0		0.2		0.6		0.4		5.8		1.8
$\bar{X}$ length (cm)		38		29		17		22		31		47		40

Table 1. Continued.

Predators / Prey groups	Spiny dogfish		Goosefish		Silver hake		Atlantic cod		White hake		Red hake		Atlantic mackerel[2]		Little skate		Atlantic herring[1]	
CRUSTACEA	1.3		0.1		20.5		16.6		45.5		52.8		67.3		66.2		54.4	
Caridean shrimp		-		0.1		4.6		3.8		37.4		17.7		11.5		9.9		-
Penaeid shrimp		-		-		-		-		-		-		-		-		-
Anomuran crabs		0.4		-		-		3.1		1.0		14.0		0.1		25.1		-
Brachyuran crabs		0.4		-		-		5.8		0.4		4.6		-		6.4		-
Astacidean		-		-		-		0.1		-		-		-		-		-
Euphausiids		-		-		13.2		0.4		4.8		2.5		51.3		-		51.2
Mysids		0.1		-		-		0.7		-		-		2.2		-		-
Caprellid amphipods		-		-		-		-		-		0.1		-		-		-
Gammaridean amphipods		-		-		0.1		0.5		0.1		3.7		0.1		10.0		0.1
Hyperiid amphipods		-		-		-		-		-		-		-		0.1		-
Isopods		-		-		-		-		-		1.7		-		2.2		-
Copepods		-		-		-		-		-		-		1.9		-		1.9
Cumaceans		-		-		-		-		-		-		-		-		-
Cirripeds		-		-		-		-		-		-		-		-		-
Unidentified		0.4		-		2.6		2.2		1.8		8.5		0.2		12.5		1.2
PISCES	88.9		97.2		78.2		60.7		43.0		6.2		0.8		4.9		-	
Clupeidae		6.0		-		-		30.2		-		4.1		-		-		-
Scombridae		16.9		20.9		-		-		-		-		-		-		-
Pleuronectiformes		12.2		-		-		5.1		-		-		-		0.7		-
Gadidae		-		24.2		-		2.5		11.5		-		-		-		-
Cottidae		-		5.2		-		2.7		-		0.3		-		1.3		-
Ammodytidae		-		-		-		0.1		-		-		-		-		-
Fish eggs		2.8		-		-		3.6		-		0.3		-		-		-
Unidentified		51.0		46.9		78.2		11.5		31.5		1.5		0.8		2.9		-
POLYCHAETA	0.2	0.2	-	-	-	-	1.1	1.1	0.1	0.1	2.4	2.4	-	-	15.6	15.6	-	-
ECHINODERMATA	-		-		-		0.4		-		0.2		-			-	-	
Asteroids		-		-		-		0.4		-		0.2		-		-		-
Ophiuroids		-		-		-		-		-		-		-		-		-
Echinoids		-		-		-		-		-		-		-		-		-
Holothuroids		-		-		-		-		-		-		-		-		-
Unidentified		-		-		-		-		-		-		-		-		-
MOLLUSCA	1.6		2.4		0.6		15.2		7.5		20.0		1.0		0.2		2.5	
Gastropods		0.1		-		-		4.4		0.1		20.0		-		-		-
Pelecypods		-		-		-		9.2		-		-		-		-		-
Cephalopods		1.5		2.4		0.6		-		7.4		-		0.6		0.2		-
Pteropods		-		-		-		-		-		-		0.4		-		2.5
Unidentified		-		-		-		1.6		-		-		-		-		-
CHAETOGNATHA	-	-	-	-	-	-	-	-	-	-	-	-	2.3	2.3	-	-	23.6	23.6
TUNICATA	-	-	-	-	-	-	-	-	-	-	-	-	7.9	7.9	-	-	0.1	0.1
CNIDARIA	-				-		0.7		-		-		-		-		0.1	
Hydrozoans		-	-	-		-		0.7		-		-		-		-		0.1
Anthozoans		-	-	-		-		-		-		-		-		-		-
SIPUNCULIDA	6.2	6.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
NEMERTEA	0.2	0.2	-	-	-	-	-	-	-	-	-	-	-	-	0.2	0.2	-	-
ANIMAL REMAINS	1.6	1.6	0.3	0.3	0.7	0.7	2.9	2.9	3.9	3.9	18.5	18.5	20.2	20.2	12.9	12.9	14.3	14.3
SAND AND ROCK	-	-	-	-	-	-	2.4	2.4	-	-	0.1	0.1	-	-	-	-	-	-
Number of stomachs		152		25		236		517		128		195		56		174		98
% empty		22.4		44.0		26.3		6.5		28.9		23.1		37.5		10.3		21.4
$\bar{X}$ wt per stomach(g)		19.3		132.1		4.5		29.9		6.3		1.7		0.6		2.2		0.4
$\bar{X}$ length (cm)		67		55		30		50		45		33		27		44		26

[1] Includes some data from 1974.

[2] All mackerel data are from 1974.

Table 2. Stomach contents of fish collected in three areas--Southern New England, Georges Bank, and Gulf of Maine--from 1969 through 1972. The data is expressed as a percent of the total stomach contents by weight for each species. The number of fish examined, the percent of empty stomachs, mean weight of prey per stomach, and the mean predator length are included at the bottom of the table for each species of fish.

	Atlantic Cod			Haddock			Yellowtail Flounder			Silver Hake		
	Southern New England	Georges Bank	Gulf of Maine	Southern New England	Georges Bank	Gulf of Maine	Southern New England	Georges Bank	Gulf of Maine	Southern New England	Georges Bank	Gulf of Maine
CNIDARIA	-	0.7	-	-	0.1	0.2	0.1	10.6	1.9	-	-	-
Anthozoans	-	-	-	-	-	-	0.1	10.6	1.9	-	-	-
Hydrozoans	-	-	-	-	-	-	-	-	-	-	-	-
ANNELIDA	6.4	1.1	0.2	4.5	23.9	13.1	34.6	46.4	27.7	1.0	-	-
NEMERTEA	-	-	-	-	-	-	0.4	0.1	-	-	-	-
CRUSTACEA	20.7	16.6	25.5	81.9	23.7	13.2	47.2	32.2	27.9	36.7	20.5	21.3
Gammaridean Amphipods	1.6	0.5	0.1	2.1	9.9	1.6	19.8	9.1	11.8	1.1	0.1	-
Caprellid Amphipods	-	-	-	-	-	-	0.9	0.1	0.8	-	-	-
Hyperiid Amphipods	-	-	-	-	-	-	-	-	-	-	-	-
Caridean Shrimp	1.1	3.8	4.0	1.2	0.7	7.3	3.0	2.5	-	16.3	4.6	6.2
Penaeid Shrimp	-	-	-	-	-	-	-	-	-	-	-	-
Anomuran Crabs	3.3	3.1	0.2	0.9	0.9	0.3	-	0.7	-	-	-	-
Brachyuran Crabs	12.7	5.8	15.8	0.8	0.2	0.5	1.1	-	0.1	-	-	0.1
Astacideans	-	0.1	-	-	-	-	-	-	-	-	-	-
Euphausiids	-	0.4	1.2	-	5.5	1.5	-	-	-	14.4	13.2	12.4
Mysids	-	0.7	-	-	0.2	-	-	-	-	0.7	-	0.2
Cumaceans	-	-	-	-	-	-	0.5	0.1	-	0.1	-	-
Copepods	-	-	-	-	-	-	-	-	-	-	-	-
Isopods	-	-	-	-	0.2	0.1	0.4	0.5	0.4	-	-	-
Unidentified	2.0	2.2	4.2	76.9	6.1	1.9	21.5	19.2	14.8	4.1	2.6	2.4
MOLLUSCA	1.8	15.2	0.6	0.7	6.2	1.5	1.5	1.3	-	0.8	0.6	1.3
Gastropods	1.3	4.4	0.3	-	0.4	0.4	0.2	0.1	-	-	-	-
Pelecypods	0.4	9.2	-	0.7	5.2	0.8	1.2	1.1	-	-	-	-
Cephalopods	-	-	0.3	-	-	-	-	-	-	0.8	0.6	1.3
Pteropods	-	-	-	-	-	-	-	-	-	-	-	-
Unidentified	0.1	1.6	-	-	0.6	0.3	0.1	0.1	-	-	-	-
ECHINODERMATA	0.3	0.4	0.4	1.4	12.5	56.6	2.0	2.2	21.2	-	-	-
Asteroids	-	-	-	0.1	0.2	-	-	-	-	-	-	-
Ophiuroids	-	-	-	-	9.3	43.9	-	-	-	-	-	-
Echinoids	-	-	-	1.2	2.5	9.9	-	-	-	-	-	-
Holothuroids	-	-	-	0.1	0.5	2.8	-	-	-	-	-	-
Unidentified	0.3	0.4	0.4	-	-	-	-	-	-	-	-	-
PISCES	64.2	60.7	70.0	-	-	1.7	0.4	0.1	-	58.8	78.2	76.2
Ammodytidae	-	0.1	-	-	-	-	-	-	-	-	-	-
Clupeidae	32.8	30.2	19.8	-	-	-	-	-	-	-	-	32.0
Scombridae	6.4	-	8.5	-	-	-	-	-	-	29.6	-	27.9
Pleuronectiformes	3.7	5.1	0.3	-	-	-	-	-	-	0.1	-	-
Gadidae	-	2.5	5.7	-	-	-	-	-	-	11.7	-	1.4
Cottidae	1.1	2.7	-	-	-	-	-	-	-	0.1	-	-
Fish Eggs	-	8.6	0.2	-	-	-	-	-	-	-	-	-
Unidentified	20.2	11.5	35.5	-	-	1.7	0.4	0.1	-	17.3	78.2	14.9
CHAETOGNATHS	-	-	-	-	-	-	-	-	-	0.1	-	-
TUNICATES	-	-	-	-	-	0.2	4.3	0.3	7.5	-	-	-
ANIMAL REMAINS	5.7	2.9	2.9	8.5	10.0	11.0	8.0	3.0	4.7	2.6	0.7	1.2
SAND AND ROCK	0.9	2.4	0.4	3.0	23.6	2.5	1.5	3.8	9.1	-	-	-
No. Stomachs Analyzed	79	817	364	27	408	266	1428	709	44	707	236	409
% Empty Stomachs	6.3	6.5	9.3	11.1	8.6	9.0	21.5	28.5	29.5	33.7	26.3	34.7
$\bar{X}$ wt. per Stomach (g)	46.6	29.9	31.3	4.1	5.8	6.6	0.5	0.4	0.9	1.6	4.5	5.8

Table 2. Continued.

	Atlantic Mackerel			Atlantic Herring			Pollock			Redfish		
	Southern New England	Georges Bank	Gulf of Maine	Southern New England	Georges Bank	Gulf of Maine	Southern New England	Georges Bank	Gulf of Maine	Southern New England	Georges Bank	Gulf of Maine
CNIDARIA	-	-	-	-	0.1	-	-	1.0	-	-	-	-
Anthozoans	-	-	-	-	-	-	-	-	-	-	-	-
Hydrozoans	-	-	-	-	0.1	-	-	-	-	-	-	-
ANNELIDA	-	-	-	-	-	-	-	0.1	-	-	-	0.1
NEMERTEA	-	-	-	-	-	-	-	-	-	-	-	-
CRUSTACEA	5.8	67.8	-	27.7	54.4	99.8	-	70.7	68.7	-	77.9	97.3
Gammaridean Amphipods	-	0.1	-	0.1	0.1	0.1	-	-	-	-	0.1	-
Caprellid Amphipods	-	-	-	-	-	-	-	-	-	-	-	-
Hyperiid Amphipods	0.4	-	-	-	-	-	-	-	-	-	0.1	-
Caridean Shrimp	0.1	11.5	-	1.6	-	-	-	3.3	59.4	-	-	20.4
Penaeid Shrimp	0.1	-	-	-	-	-	-	-	-	-	0.2	-
Anomuran Crabs	-	0.1	-	-	-	-	-	-	-	-	-	-
Brachyuran Crabs	-	-	-	-	-	-	-	-	-	-	-	-
Astacideans	-	-	-	-	-	-	-	-	-	-	-	-
Euphausiids	3.6	51.8	-	0.3	51.2	99.6	-	65.2	6.8	-	44.4	74.3
Mysids	-	2.2	-	-	-	-	-	0.1	-	-	-	-
Cumaceans	-	-	-	6.2	-	-	-	-	-	-	-	-
Copepods	1.2	1.9	-	16.5	1.9	-	-	-	-	-	-	0.2
Isopods	-	-	-	-	-	-	-	-	-	-	-	-
Unidentified	0.4	0.2	-	3.0	1.2	0.1	-	2.1	2.5	-	33.1	2.4
MOLLUSCA	57.8	1.0	-	6.6	2.5	-	-	1.7	0.1	-	-	0.2
Gastropods	-	-	-	-	-	-	-	0.1	-	-	-	-
Pelecypods	-	-	-	-	-	-	-	-	-	-	-	0.2
Cephalopods	-	0.6	-	-	-	-	-	-	0.1	-	-	-
Pteropods	57.8	0.4	-	6.6	2.5	-	-	1.6	-	-	-	-
Unidentified	-	-	-	-	-	-	-	-	-	-	-	-
ECHINODERMATA	0.8	-	-	-	-	-	-	-	-	-	-	0.5
Asteroids	-	-	-	-	-	-	-	-	-	-	-	-
Ophiuroids	0.3	-	-	-	-	-	-	-	-	-	-	0.5
Echinoids	-	-	-	-	-	-	-	-	-	-	-	-
Holothuroids	-	-	-	-	-	-	-	-	-	-	-	-
Unidentified	0.5	-	-	-	-	-	-	-	-	-	-	-
PISCES	3.6	0.8	-	1.1	-	-	-	23.6	30.2	-	20.6	0.5
Ammodytidae	2.2	-	-	0.6	-	-	-	-	-	-	-	-
Clupeidae	-	-	-	-	-	-	-	0.9	3.1	-	-	-
Scombridae	-	-	-	-	-	-	-	-	-	-	-	-
Pleuronectiformes	-	-	-	-	-	-	-	-	-	-	-	-
Gadidae	-	-	-	-	-	-	-	0.5	2.4	-	-	-
Cottidae	-	-	-	-	-	-	-	-	-	-	-	0.2
Fish Eggs	0.7	-	-	-	-	-	-	-	-	-	-	0.3
Unidentified	0.7	0.8	-	0.5	-	-	-	22.2	24.7	-	-	-
CHAETOGNATHS	0.8	2.3	-	57.4	28.6	-	-	-	-	-	-	-
TUNICATES	6.2	7.9	-	0.1	0.1	-	-	0.1	-	-	-	0.1
ANIMAL REMAINS	25.0	20.2	-	7.1	14.3	0.2	-	2.8	1.0	-	1.5	1.3
SAND AND ROCK	-	-	-	-	-	-	-	-	-	-	-	-
No. Stomachs Analyzed	193	56	-	198	98	28	-	197	181	-	54	579
% Empty Stomachs	30.6	37.5	-	15.2	21.4	25.0	-	3.6	16.6	-	31.5	38.2
$\bar{x}$ Wt. per Stomach (g)	0.4	0.6	-	0.3	0.4	1.2	-	12.8	24.2	-	1.0	1.5

Table 3. Percentage gross efficiency,[1] biomass,[2] mean fish length, and estimated food consumption[2] for the periods 1963-1965, 1968-1969, and 1972-1974. (From Edwards and Bowman, 1978.)

Species	% gross efficiency	1963-1965			1968-1969			1972-1974		
		Biomass	Mean length (mm)	Food consumed annually	Biomass	Mean length (mm)	Food consumed annually	Biomass	Mean length (mm)	Food consumed annually
Silver hake	8.7	999.4	250	11,487	414.4	140	4,763	522.7	141	6,008
Atlantic herring	13.7	3,565.5	281	26,026	1,136.7	267	8,297	309.8	252	2,261
Spiny dogfish	6.1	1,002.3	720	16,431	1,024.4	676	16,973	362.2	640	5,938
Haddock	15.0	783.2	335	5,221	253.8	430	1,692	160.9	318	2,120
Red hake	15.2	279.2	329	1,837	185.5	279	1,220	84.0	261	553
Pollock	13.8	216.2	600	1,567	213.4	685	1,546	245.1	505	1,776
Thorny skate	5.8	272.0	508	4,690	289.4	537	4,990	236.8	537	4,083
Atlantic cod	11.9	155.7	575	1,308	105.6	628	887	141.2	453	1,187
Redfish	12.2	165.3	243	1,335	287.4	246	2,356	195.3	250	1,601
Little skate	9.5	146.3	431	1,540	43.2	425	455	97.1	404	1,022
Butterfish	10.5	147.9	150	1,409	168.0	137	1,600	160.5	120	1,529
Winter skate	10.5	128.7	525	1,226	40.4	539	385	82.6	513	787
Atlantic argentine	10.2	26.3	251	258	11.0	319	108	8.3	209	81
Winter flounder	14.1	71.1	336	504	36.2	305	257	37.9	329	269
Yellowtail flounder	12.6	76.8	317	610	94.0	283	746	40.9	312	325
Barndoor skate	11.6	115.6	730	997	9.7	693	84	11.1	688	96
Ocean pout	29.0	105.0	504	362	36.0	385	124	27.0	325	93
Goosefish	6.6	73.6	566	1,115	37.2	533	564	47.0	367	712
American plaice	20.5	63.9	292	312	39.4	306	192	28.3	255	138
Atlantic mackerel	11.6	471.5	270	4,065	3,266.4	157	28,159	1,418.1	261	12,225
Alewife	13.3	102.0	230	767	43.0	225	323	29.0	179	218
White hake	11.6	35.0	485	302	50.0	415	431	71.5	473	616
Longhorn sculpin	5.5	11.2	230	204	17.7	236	322	7.4	228	135
Windowpane	7.9	32.7	157	414	27.0	239	342	39.0	204	494
Scup	18.7	68.0	62	364	37.6	133	201	78.9	112	422
Witch flounder	15.6	18.1	400	116	25.6	442	164	15.4	422	99
Fourspot flounder	6.2	8.7	295	140	3.5	269	56	5.4	250	87
Sea raven	5.9	2.9	313	49	1.3	266	22	1.6	270	27
Other fish	11.9	610.1	117	5,127	719.8	111	6,049	751.3	87	6,313
Total biomass		9,719.8		89,783	8,664.6		83,308	5,349.5		51,215

[1] Percent gross efficiency calculated for 300-mm fish.

[2] Biomass estimates and food consumption in metric tons x 10^3.

Table 4. Estimate of fish production from primary production values using method of Sheldon et al. (1977).

	Gulf of Maine	Georges Bank	Southern New England	Mid-Atlantic Area
Primary Production $gC/m^2/yr$	150-200(1)	450(2)	150(3)	150-200(4)
Fish Production(5) g wet $wt/m^2/yr$	9.6 - 12.8	28.8	13.9	5.0 - 6.7
Fish Production(6) g wet $wt/m^2/yr$				
1964-1966	7.0	17.5	9.2	4.1
1973-1975	5.6	12.7	6.8	3.7
Primary production based on fish production from				
1964-1966	109.2	273.0	99.0	123.0
1973-1975	87.3	198.1	73.0	111.0

(1) Value from C.S. Yentsch personal communication.

(2) Value from Cohen & Wright (1978).

(3) Value from Ryther (1969).

(4) Walsh et al. (1977).

(5) Conversion of .06 gC = 1 g wet wt., Mullin et al. (1966).

(6) Based on P/B derived from Grosslein et al. (1978).

Table 5. Production, consumption, P/B ratio based on biomass estimates for pelagic and demersal fishes in the Gulf of Maine, Georges Bank, Southern New England, and the Mid-Atlantic Bight for high biomass (1964-66) and low biomass (1973-75) periods.

	1964-66					1973-75					1964-66 - 1973-75
	P/B^1	C/B^1	Biomass^2	Prod.^{3}	Consumption	P/B^1	C/B^1	Biomass^2	Prod.^{3}	Consumption^3	Consumption Difference
Gulf of Maine											
Fin-Squid	.55	4.8	9.9	5.4	47.5	.68	4.8	6.2	4.2	29.8	17.7
Herring	.29	4.6	3.9	1.1	17.9	.29	4.6	1.6	0.5	7.4	10.5
Mackerel	.34	4.3	1.4	0.5	6.0	.34	4.3	2.7	0.9	11.6	-5.6
TOTAL			15.2	7.0	71.4			10.5	5.6	48.8	22.6
Georges Bank											
Fin-Squid	.55	4.8	20.7	11.4	99.4	.68	4.8	14.9	10.1	71.5	27.9
Herring	.29	4.6	19.3	5.6	88.8	.29	4.6	6.0	1.7	27.6	61.2
Mackerel	.34	4.3	1.4	0.5	6.0	.34	4.3	2.7	0.9	11.6	-5.6
TOTAL			41.4	17.5	194.2			23.6	12.7	110.7	83.5
Southern New England											
Fin-Squid	.55	4.8	12.4	6.8	59.5	.68	4.8	7.8	5.3	37.4	22.1
Herring	.29	4.6	6.5	1.9	29.9	.29	4.6	2.0	0.6	9.2	20.7
Mackerel	.34	4.3	1.4	0.5	6.0	.34	4.3	2.7	0.9	11.6	-5.6
TOTAL			20.3	9.2	95.4			12.5	6.8	58.2	37.2
Mid-Atlantic Bight											
Fin-Squid	.55	4.8	6.5	3.6	31.2	.68	4.8	4.1	2.8	19.7	11.5
Mackerel	.34	4.3	1.4	0.5	6.0	.34	4.3	2.7	0.9	11.6	-5.6
TOTAL			7.9	4.1	37.2			6.8	3.7	31.3	5.9

[1] All P/B and C/B ratios derived from Table 4.14, Grosslein et al. (1978).

[2] Biomass expressed as g wet wt/m^2.

[3] Consumption and production expressed as g wet wt/m^2/yr.

MARMAP, A Fisheries Ecosystem Study in the NW Atlantic: Fluctuations in Ichthyoplankton-Zooplankton Components and Their Potential for Impact on the System. Paper Presented to the Advanced Ocean Measurements Workshop I, Held at the Belle W. Baruch Institute for Marine Biology and Coastal Research, University of South Carolina, Sponsored by Office of Naval Research, Dept. of Navy, October 24-28, 1978. 38 pp.

K. Sherman

ITEM 8

MARMAP, A Fisheries Ecosystem Study in the NW Atlantic: Fluctuations in Ichthyoplankton-Zooplankton Components and Their Potential for Impact on the System

by

Kenneth Sherman
National Marine Fisheries Service
Northeast Fisheries Center
Narragansett, R. I. 02882

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Abstract

Initial results of a fishery ecosystems study based on time-series surveys of fish, plankton, benthos, hydrography, fish catch data, and ancillary process-oriented projects are described for the continental shelf area off the northeast coast of the U. S. The study is conducted from the Gulf of Maine to Cape Hatteras as part of the MARMAP Program of NMFS. The region has been subjected to heavy fishing mortality over the past decade. During the 1968 to 1975 period the biomass of principal fish species declined by 50% over this region of the continental shelf. The full impact of the removal of several million metric tons of predators from the continental shelf ecosystem is not known. Two major questions are being addressed: (1) Does the reduction in the stocks of important predator species--herring, mackerel, cod, haddock, hake, and others--release secondary production to be consumed by short-lived, fast growing, smaller, less desirable species? (2) What are the probabilities associated with the return of over-exploited species to former abundance levels? Ecosystem studies now underway by the Northeast Fisheries Center focus on the biological and environmental factors controlling mortality, recruitment, survival, and productivity of the fish stocks on the continental shelf. Changes in population levels of ichthyoplankton and zooplankton detected on MARMAP surveys are discussed in relation to potential impact on the ecosystem. Preliminary evidence suggests that the recent (1974-1977) increase in sand lance abundance may be indicative of a shift in dominance among the fish species in the Northwest Atlantic. Emphasis is given to the importance of time-series studies at all levels in the ecosystem in relation to emerging theory, which holds that stressed ecosystems favor the development of fast growing, short-lived, and generally less desirable commercial species, like sand lance. Comparisons are made between primary productivity and fish biomass in the North Sea, Mid-Atlantic Bight, and Georges Bank. The higher fish biomass of Georges Bank is attributed to the higher primary productivity of the area. The importance for accelerating studies of secondary production in both the benthos and zooplankton in order to better understand fish-plankton-benthos relationships is stressed.

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from the onset of larval hatching up to juvenile development on target species. Herring has been the target species since 1971 in studies of recruitment processes off the northeast coast. Microscale studies of larval herring growth and predator-prey studies are planned for 1979.

Fisheries Ecosystem Studies off the Northeast Coast of the U. S.

The fishery resources off the northeast coast of the United States support a fish-catching and processing industry contributing a billion dollars annually to the economy of the coastal states from Maine to North Carolina. These resources are now, under the terms of the recently passed Fisheries Management and Conservation Act,[1] subject to management by the New England and Mid-Atlantic Regional Fisheries Management Councils. The Councils are required to develop management plans for the resources under their jurisdiction that ensure optimal sustained yields based on ecological, economic and social considerations. Input for the ecological decisions are to be based on the "best scientific information available."

The best and most sought after scientific information from a fisheries management point of view is the accurate prediction of future stock sizes and the effects of different levels of fishing on the continued production of economically viable resource populations. This need has not changed since the early days of whaling, when the U. S. Wilkes Expedition of 1838 was supported by Congress to improve our knowledge of Pacific whaling areas. Henry Bigelow was supported, in part, by Federal funds when in the 1920's he investigated the fish, plankton, and oceanography of the Gulf of Maine for the U. S. Fish Commission with an end to improving the fishing industry. Subsequent studies on both sides of the Atlantic focused on the yields of single

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[1] Fisheries Conservation and Management Act of 1976, U.S.A. (FCMA) Public Law No. 94-265, 94th Congress H.R. 200, April 13, 1976.

species, not from any lack of intellectual awareness of the interaction and interdependence of species, but rather from the constraints of meager budgets provided to support fishery research organizations. Those days are passed. But the early orientation to single species assessments has not been easily shed. "Special" interests will continue to demand information on particular species, and we will need to continue providing single species estimates of abundance levels.

Under the FCMA some 2.2 million square miles of contiguous ocean water falls under the jurisdiction of the U. S. as a Fisheries Management Zone. At present only 150,000 square miles of the zone, most of which is off the northeast coast, is being systematically monitored for seasonal, areal, and annual changes in plankton, fish, benthos, and hydrography. There are no shortcuts to obtaining the comprehensive population and environmental information required to improve forecasts of fish abundance within the FMZ. A balanced approach is needed that allows for: (1) a time-series of observations in the form of routinized multispecies fish, plankton, benthos, and hydrographic monitoring surveys, (2) a systematic collection of fish-catch data, and (3) ancillary process oriented studies dealing with linkages among plankton production, benthos production, and the influence of the environment on the productivity of fish resources to ensure that the most critical spatial and temporal processes are, in fact, being monitored adequately for forecasting purposes. This kind of fisheries ecosystem program, called MARMAP for marine resources monitoring, assessment and prediction, is conducted by the National Marine Fishery Service on the continental shelf from the Gulf of Maine to Cape Hatteras.

During the past decade this region of the continental shelf including the Gulf of Maine, Georges Bank, Southern New England, and the Mid-Atlantic Bight has been subjected to extreme fishing pressure. From 1968 to 1975 the biomass of the principal fish species declined approximately 50% (Figure 1); much of the decrease in biomass correlates with increased fishing effort, indicating an overfishing condition (Clark and Brown, 1977). Environmental conditions, coastal pollution, inter- and intra-specific competition may also have contributed to the decline, but no quantitative estimate of this mortality is now available.

The full impact of the removal of several million metric tons of predators from the continental shelf ecosystem is not known. Significant questions remain unanswered. Does the reduction in the stocks of important predator species--herring, mackerel, cod, haddock, hake, and others--release secondary production to be consumed by short-lived, fast growing, smaller, less desirable species? What are the probabilities associated with the return of over-exploited species to former abundance levels? Studies are now underway by the Northeast Fisheries Center (NEFC) to address these questions. They focus on the critical linkages among the principal food species of fish and the recruitment, survival, and productivity of the fish stocks on the continental shelf from the Gulf of Maine to Cape Hatteras.

Multispecies Assessments

Studies of single species alone do not provide the kind of assessment information required for effective management of multispecies fisheries operating at different trophic levels. While it is important to continue these studies, they are now being pursued within a broader matrix that measures interactions in changing abundances among the species in the ecosystem. Single-species yield models have recently been augmented with multispecies models that are ecologically sensitive (Regier and Henderson, 1973; Parrish, 1975; Lavaestu et al., 1976; Anderson and Ursin, 1977). These models deal with multispecies fishery interactions at different trophic levels. They are important approximations of the consequences of predator-prey dynamics based on fishery imposed selective mortality, and hold promise for providing a basis for the management of marine ecosystems. If ecosystem models are to assume an appropriate role in the management of marine resources, it will be necessary to overcome present deficiencies in: (1) understanding relationships between stock-size and recruitment, (2) identifying the linkages between primary, secondary, and fish production; and (3) quantifying predator-prey dynamics.

Predator-Prey Interactions

Predator-prey interactions are complex. They reflect a series of interrelationships that can change significantly the abundance of important fish stocks. A schematic representation of the predator-prey interactions for eight of the more abundant species of fish and squid off the northeast coast of the U. S. is given in Figure 2. It is presented as a qualitative example of the complexity of the known interactions between fish and their prey. In addition, the significant changes in the size of prey consumed as a fish moves through larval, juvenile, and adult stages of development compound the difficulty in sorting out predator-prey relationships. The feeding habits of codfish illustrate the problem. Codfish larvae feed principally on microzooplanktonic copepods, crustacean eggs, pteropods, Fig. 2

and larvae of meroplankton. As juveniles they feed on macrozooplankton including euphausids and amphipods, and as adults, fish become a principal food (Figure 3).

In stressed marine ecosystems it has recently been suggested that shifts in the abundances of predators can lead to significant changes in the species composition and size structure of the prey populations (Steele and Frost, 1977). The degree to which species shifts in abundance can result in changes to fish production of the continental shelf ecosystem is now the subject of an expanded research effort by the Northeast Fisheries Center. For example, it appears that the predatory consumption levels of a single species, the silver hake, is sufficient to consume 30% of all fish produced on the continental shelf of the northeast coast (Edwards and Bowman, 1978). Aspects of this research, including recent evidence of changes in abundance among ichthyoplankton and zooplankton species is given in the present report.

MARMAP Surveys

With the exception of relatively small groups of fishery scientists in the United States and elsewhere, particularly in Western Europe, society has not yet come to grips with the magnitude of the effort confronting the scientific community in its attempt to provide information on resource populations that can support management options within the fisheries management zones on both sides of the Atlantic. Fishery science is undergoing major changes in the approach to improving assessment of the abundance levels and forecasting potential yields of fish stocks inhabiting these zones. The new approach represents a balance between the more traditional studies of biological and physical processes as they relate to productivity of coastal waters and coastal populations, and the requirement for committing ships and personnel to fisheries-independent time-series surveys of annual changes in the productivity levels of plankton, fish, and benthos populations. Time-series surveys are dull, routinized, but absolutely necessary for measuring population, environmental, and pollution changes over time and space and sorting out the causes of these changes with respect to fishing mortality, natural mortality, or mortality caused from the increasing introduction of pollutants into the continental shelf ecosystem. In addition to the surveys carefully controlled ecosystem experiments are now being conducted in very large enclosures containing the smaller population components of the pelagic ecosystem. The best example of this effort is in the Controlled Ecosystem Experiments sponsored by the National Science Foundation. The CEPEX operation is conducted as a multidisciplinary study of the interactions of primary and secondary and tertiary trophic levels of a northwest temperate deep-water embayment in British Columbia under the effects of physical-chemical changes. Findings of this study will have application to our investigations of fishery ecosystems by providing more insight to the critical functions that need to be measured on the time-series surveys. Other technical advances in hydroacoustics, remote sensing, and electronic data processing when applied to the time-series approach will undoubtedly contribute significantly to increased efficiencies and reduced costs of the MARMAP surveys.

In 1971 a systematic macroscale sampling of zooplankton and ichthyoplankton was initiated by the Northeast Fisheries Center, NMFS in the Gulf of Maine, Georges Bank, Southern New England, and Mid-Atlantic Bight during bottom trawl surveys in autumn and spring. In 1976 the zooplankton-ichthyoplankton surveys were expanded to bimonthly coverage of the areas to examine the zooplankton-fish linkages including: (1) changes in the distributions, abundance, and growth of juvenile and adult fish, and (2) larval fish growth and mortality in relation to their planktonic prey and predators. MARMAP surveys are conducted systematically at stations selected from a stratified random design for fish, shellfish, benthos, phytoplankton, ichthyoplankton, and zooplankton. Bottom trawl surveys for fish are conducted in spring and autumn, and since 1977, in summer. Two shellfish surveys are made annually. Benthic sampling is limited, contingent on the analyses of 25 years of collections now being completed at the Woods Hole Laboratory of NEFC. Surveys of zooplankton-ichthyoplankton, phytoplankton, primary productivity, and hydrography are conducted on a bimonthly basis for a total of six surveys per year. The survey data is augmented with a comprehensive system for obtaining catch data at each of the major fishing ports from Cape Hatteras to the Gulf of Maine. As required, special surveys are conducted to deal with specific problems (e.g., tagging, feeding, current meter deployment and retrieval, vertical distribution studies of ichthyoplankton, samplings for sharks and other large predators). Mesoscale studies of larval mortality have been done jointly with other countries for larval herring. Plans are now underway for microscale "patch-studies" to study factors controlling larval survival from examination of larval predator-prey relationships within the water column. The area under investigation is extensive, requiring a heavy logistic commitment. The MARMAP studies are being conducted jointly with scientists and ships of the Federal Republic of Germany, German Democratic Republic, Poland, and the USSR.

Ichthyoplankton-Zooplankton Monitoring

All ichthyoplankton-zooplankton collections are made with 61-cm diameter bongo nets towed obliquely through the water column between 1.5 and 3.5 kts. At each location nets with 0.505-mm and 0.333-mm mesh apertures are used; at selected stations a 20-cm bongo sampler is fitted with 0.165-mm and 0.253-mm mesh nets and positioned above the larger bongo frame to sample the microzooplankton. Sample processing is done at the Narragansett Laboratory of NMFS under the supervision of Mrs. Ruth Byron, at the Polish Plankton Sorting Center, Szczecin under the direction of Dr. Leonard Ejsymont.

Observational Protocol

The four areas on the continental shelf surveyed--Gulf of Maine, Georges Bank, Southern New England, and Mid-Atlantic Bight--are shown in Figure 4. At each station tows are made for zooplankton and ichthyoplankton. Measurements are made of chlorophyll, nutrients, salinity, and temperature. During each survey of the continental shelf C^{14} measurements of primary production are made daily.

Although the 1971 through 1977 time-series of ichthyoplankton-zooplankton collections is not yet fully sorted and identified several findings are particularly noteworthy and will be reported here.

Ichthyoplankton

Shifts in the abundance of fish species may be established in the egg and larval stages of fish. Reduction in abundance can be caused by: (1) a decline in the size of the spawning biomass of traditionally abundant resource species below the competitive advantage threshold with incoming recruits of other species, (2) shifts in spawning periodicity causing a mismatch between newly hatched larvae and optimal densities of their planktonic prey, (3) changes in environmental and climatic events leading to mass mortalities from shifts in circulation away from nursery areas, and (4) increased embryonic and larval mortality levels imposed by chronic releases of hazardous substances over principal spawning areas.

Ichthyoplankton Pulses in Abundance

On the average, peak spawning of the principal species follows a temporal and spatial pattern that may serve as a critical adaptive mechanism for survival. Based on recent observations reported by Colton et al., (1978) spawning peaks of larvae tend to be successive rather than simultaneous (Table I). For example, among the 11 most common gadids, only two species overlap with respect to both spawning area and time--cod, *Gadus morhua*, and haddock, *Melanogrammus aeglefinus*, on Georges Bank in March. It should be mentioned, however, that the peak of haddock spawning is more prolonged beginning in February and extending through March. Among the pelagic species mackerel, *Scomber scombrus*, reach peak spawning in the Mid-Atlantic Bight in May, and in June in the western Gulf of Maine. The butterfish, *Peprilus triacanthus*, is at peak spawning in southwest Georges Bank in June and July. The peak spawnings of the remaining pelagics also differ. Menhaden, *Brevoortia tyrannus*, reach their peak from September through November in the Mid-Atlantic Bight, and Atlantic herring, *Clupea harengus*, in October-November on Georges Bank and western Nova Scotia, with less intensive spawning in the Gulf of Maine. It is, however, the deviation from average conditions that will have an important influence on the size of a year-class.

Measures of these deviations can not be made without a time-series of observations over the continental shelf. This data-base is just now being developed.

Shifts in Abundance of Ammodytes Larvae

In the southern half of the survey area--Southern New England and the Mid-Atlantic Bight and Georges Bank--significant changes in the species composition of ichthyoplankton have been detected during the 1974-1977 period (Smith et al., 1978). Since 1974, the increase in abundance of sand lance[2] has been sharp and consistent, increasing from below 50% of the ichthyoplankton constituents in 1974 to a peak of over 90% of the larval fish assemblage in early spring, 1977. Abundance of cod, haddock, pollock, and herring larvae for the same period, declined from a level of approximately 50% of the ichthyoplankton to less than 10% in 1977 (Figure 5). The increase has been widespread along the shelf with principal centers of abundance spreading from off the Maryland and Delaware coasts in 1974 to encompass most of the southern half of the survey area in 1977 (Figure 6). The increase in abundance, although of lower magnitude, was also evident in the Gulf of Maine. On Georges Bank the increase in numbers of sand lance larvae followed a similar upward trend in 1974, 1975, and 1976, but showed a decrease in 1977.

Fig. 6

The sand lance preys on zooplankton in larval, juvenile, and adult stages (Bigelow and Schroeder, 1954). With respect to feeding, it can be considered a competitor of two other important pelagic species,

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[2] The taxonomic status of the sand lance, Ammodytes spp., has not been resolved. More than one species may be in the collections.

herring and mackerel. Sand lance and herring co-occur as larvae and adults. In the North Sea herring have been reported to prey heavily on larval sand lance. Mackerel reaches peak spawning in May-June limiting any potential competition between the larvae of both species; they could be food competitors in the juvenile and adult stages. The extent of mackerel predation on sand lance is not known. With the decline in the biomass of herring and mackerel, feeding conditions for sand lance would have improved greatly and the probability of high mortalities through predation would be reduced. The sand lance is also abundant in the nursery areas of cod and haddock larvae and may be a serious competitor for zooplankton food. The full impact of an apparent increase in abundance of a zooplankton predator in relation to other pelagic and demersal species is not yet clear. Studies on interspecific competition among sand lance, herring, mackerel, cod, and haddock are continuing.

Zooplankton and Fisheries

Since the early work of Bigelow fifty years ago little attention has been given to a systematic assessment of the changes in the biomass and species composition of the zooplankton off the northeast coast of the U. S., and how the changes relate to fish distribution and production. Studies over the past five decades have generally been limited to observations over a one or two year cycle and over a limited geographic area. Reports of these studies have been summarized by Colton (1963). As recently as 1976, information on seasonal changes in zooplankton standing stock was limited to a rather confused series of data compiled from the available literature in which both spring and autumn were depicted by different authors as annual peak periods of zooplankton abundance (Cohen, 1976).

Zooplankton Pulses in Biomass Abundance, 1977

The present analysis includes a summary of the standing stock of biomass and species composition of the most abundant zooplankters in 1977 in the Gulf of Maine, Georges Bank, and Southern New England. Biomass values are based on displacement volumes of the 0.333-mm mesh samples. Species composition reflects the relative abundance of only the larger zooplankton constituents (adults and copepodites III, IV, V) retained by the relatively coarse meshes of the 0.333-mm bongo net.

Statistical profiles of the biomass data were prepared for the 1977 data including calculations of the mean, median, range, standard deviation, variance, and coefficient of variation. A list of cruises and dates on which these data are based is given in Table II. Sampling locations during the 1977 MARMAP surveys are shown in Figures 7a to 7f. The variances of the biomass values exceeded the means in each of the surveys. In recognition of the skewness in the data, median values were used to depict trends in biomass changes (Table III).

During 1977, six surveys were completed. The standing stock of zooplankton was estimated from surveys made in early, mid, and late spring; in summer; and in mid- and late-autumn. Seasonal pulses in zooplankton abundances in Southern New England and Georges Bank were similar. Median values increased from < 25 cc/100 m^3 in early spring to between 60 cc/100 m^3 and 70 cc/100 m^3 in mid-spring. The greatest seasonal pulse was in late-spring, reaching 80 cc/100 m^3 to 130 cc/100 m^3, followed by a decline to approximately 50 cc/100 m^3 in summer, and a continuing decline through autumn to 27 cc/100 m^3. In the Gulf of Maine median zooplankton volumes increased from an early spring low of 13 cc/100 m^3 to a late-spring high of 60 cc/100 m^3. The zooplankton level is apparently maintained between 50 and 60 cc/100 m^3 through summer, followed by a second pulse that reached an annual high in mid-autumn of 55 cc/100 m^3. By late-autumn, zooplankton levels declined to 42 cc/100 m^3 (Figure 8).

Changes in the magnitude of the seasonal pulses in abundance of zooplankton were compared among seasons for each of the areas with the Kruskal-Wallis Analysis of Variance; between season differences in abundance were also compared. Differences in zooplankton standing stock characterized by median values were significantly different for the volumes in each of the three areas ($P < .0001$). Between-season tests for significance were made for each of the areas. Of the 15 pairs of comparisons made, four were not significantly different ($P > 0.05$)--mid-autumn and late-autumn in Southern New England; mid-autumn and late-autumn on Georges Bank; and between summer--mid-autumn and mid-autumn--late-autumn in the Gulf of Maine.

The among area differences in zooplankton standing-stock were tested for significance. Of the six comparisons made, the early-spring and summer zooplankton levels were not significantly different (Table IV).

Seasonal differences in biomass are most significant in late-spring. The peak spring pulse in abundance on Georges Bank is 1.6 x greater than in the Gulf of Maine and 1.4 x greater than in Southern New England. By summer the biomass along the entire area off New England is at a similar level of moderate abundance (50 cc/100 m^3). By mid-autumn, areal similarity changes and the lowest biomass is in Southern New England and the highest in the Gulf of Maine with values in Georges Bank at an intermediate level.

Zooplankton Species Composition

Among the 51 taxa in the samples, copepods were the most abundant, constituting 75 percent or more of the zooplankton. Our sampling may not have been sufficiently frequent to detect any major increase in cohorts of copepod populations produced during the inter-survey periods. The zooplankton standing-stock values for summer and autumn in the Georges Bank and Southern New England areas, therefore, should be considered minimal. Other zooplankters including chaetognaths, euphausids, coelenterates, larval cirripeds, cladocerans, salps, pelecypods, appendicularians, and ostracods occurred over a wide area but in low densities ($\overline{<}$ 20% of the zooplankton/survey/area). Larval cirripeds were swarming on Georges Bank in early-spring and in Southern New England waters in mid-spring. Chaetognaths were most numerous on Georges Bank in summer and late-autumn; pulses of chaetognath abundance occurred in late-spring and summer in Southern New England. Cladoceran pulses were particularly high in summer and autumn on Georges Bank and pelecypods swarmed in late-fall on Georges Bank (Table V).

Copepod Species Composition

The total zooplankton in each of the three areas surveyed was dominated by three species--*Calanus finmarchicus*, *Pseudocalanus minutus* and *Centropages typicus*. Indices of species abundance were based on changes in population densities (e.g., median numbers per 100 m^3 per survey), percentage composition of all copepod species, and a modified Fager and McGowan index of dominance:

$$D = \frac{S(100)}{N}$$

where: D = % dominance

S = Number of stations where the species represent $\geq$ 50% of the total copepod fauna

N = Number of stations

In addition to the three dominant species, the copepod Metridia lucens persisted in the samples, particularly in the deeper waters of the Gulf of Maine, but in relatively low numbers. Other species were dominant at only one or two locations. In this regard the status of Oithona similis is not clear. This small copepod was undersampled in the 0.333-mm mesh net, along with the naupliar and early copepodite stages of other species. Based on the frequency of Oithona in larval fish stomachs, it is likely to be among the dominant species in fine-mesh samples (0.153 mm and 0.253 mm) presently archived at Narragansett (Table VI).

Seasonal abundances for the C. finmarchicus, P. minutus, and C. typicus are plotted in Figures 9a-9c. Cumulative population increases are considered "pulses." They represent continuous production for several cohorts and do not represent an index of turn-over rate.

Calanus finmarchicus Pulses

In the Gulf of Maine, C. finmarchicus is at a high level of abundance throughout most of the year. Median values ranged between 30,000 and 60,000/ 100 m^3/season from mid-spring through autumn. On Georges Bank C. finmarchicus pulses to an annual maximum in late-spring (ca 100,000/m^3); it declines sharply in abundance from summer through late-autumn (1,000/100 m^3). In Southern New England waters C. finmarchicus undergoes an initial pulse in late-spring (ca 150,000/100 m^3) and an abrupt decline continuing to an annual low in late-autumn (< 200/100 m^3). Among area values in *C. finmarchicus* abundance for each of the seasons were significantly different ($P < .0001$); comparisons of abundance levels between the sampling periods were different in Southern New England and Georges Bank except for the mid-autumn to late-autumn period. In the Gulf of Maine differences seasons were significant between early and mid-spring and late-spring. Standing-stocks among the three areas were significantly different in early-spring among all three areas. The other differences reflected highest abundance levels of *C. finmarchicus* in the Gulf of Maine in summer and autumn ($P < .0001$). A summary of Kruskal- Wallis Chi Square (X^2) values and associated probabilities is given in Table VII.

Pseudocalanus minutus Pulses

This small calanoid undergoes an annual pattern of abundance similar to *C. finmarchicus* in all areas. On Georges Bank and in the Gulf of Maine numbers of *P. minutus* increase from an early-spring annual low to a late-spring high; abundance is reduced from late-spring through summer. A secondary weaker pulse in abundance is reached between mid- and late-autumn. Abundance levels for each of the areas were different among the seasons ($P < .001$); in early and mid-spring standing-stocks of *P. minutus* were different in each of the areas. In Southern New England the summer to early-autumn decline was not significant. However, the increase in abundance shown between mid- and late-autumn was significant ($P < .05$). On Georges Bank the pulses in abundance increasing from an early-spring low to a late-spring high were significant; however, the level of abundance from summer through late-autumn was not significantly different. In the Gulf of Maine early seasonal differences were different with increasing densities of *P. minutus* through late-spring; autumn levels were similar. The among area differences shown in Figure 9 were significant in each of the survey periods, except for late-autumn (Table VII).

Centropages typicus Pulses

The center of *C. typicus* abundance is in Southern New England. In each of the areas sampled *C. typicus* increased steadily in abundance from an early spring low to a mid- to late-autumn pulse of approximately 25,000/100 m^3.

Differences in *C. typicus* abundance among seasons were significant for each of the areas ($P < .0001$). In Southern New England the early to mid-spring decline was significant, as were the increases from late-spring through summer. On Georges Bank, abundance levels increased significantly from late-spring through late-autumn. The general increase shown for the Gulf of Maine was based on too few occurrences to test for significance. The among area differences for each of the seasons were significant with the exception of late-autumn values (Table VII).

Zooplankton Pulses in Abundance and Larval Fish Survival

The probability for successful larval growth is enhanced from spring through autumn by the combined and nearly continuous production of eggs, nauplii, and copepodites of the three dominant zooplankton species--*C. finmarchicus*, *P. minutus*, and *C. typicus*. The standing-stock of copepods is reduced during summer.

Survival and growth of larvae produced in successive spring and autumn spawnings is likely dependent on the match/mismatch in time and space of the cohort production of *C. finmarchicus* and *P. minutus* in spring, and *P. minutus* and *C. typicus* in autumn. Cod, haddock, mackerel, and flatfish larvae spawned in spring optimize survival potential by spawning on the ascending limb of the spring copepod production curve. Herring spawnings are supported by *P. minutus* production in autumn (Sherman and Honey, 1971). In sumer it would appear that growth and survival of hake and other first-feeding larvae may be dependent on the dynamics of *C. typicus* production.

In spring, successive pulses in abundance from early-spring through late-spring of *P. minutus* and *C. finmarchicus* are indicative of accelerated production of copepod eggs, nauplii, and copepodites; the presence of early developmental stages (copepodites) in our samples is noted, although no actual counts are made as they are undersampled in the 0.333-mm mesh used in the bongo sampler. Early developmental stages of *C. typicus* are in our summer and mid-autumn samples, and *P. minutus* copepodites are in the mid-autumn samples.

In the Gulf of Maine, the initial spring pulse is provided by increases in the abundance of *C. finmarchicus* and *P. minutus*, followed by a summer through mid-autumn pulse of *C. typicus* abundance and a third pulse from mid- to late-autumn of *C. typicus*. On Georges Bank *C. finmarchicus* and *P. minutus* generate the initial pulse in copepod abundance. This is followed by a second pulse extending from late summer through mid-autumn of *C. typicus*. In Southern New England waters *C. finmarchicus* and *P. minutus* generate an early to late-spring pulse. The annual *C. typicus* pulse is advanced over Georges Bank and the Gulf of Maine areas, beginning in late-spring and continuing to a late-autumn maxima for the second major seasonal pulse in copepod abundance in Southern New England. *P. minutus* undergoes a slight increase in abundance in late-autumn that represents a third, but minor, copepod pulse.

1971-1975 Zooplankton Time-Series

Zooplankton Biomass.--An initial examination of the zooplankton sampled during the fall and spring bottom trawl surveys has been completed. Samples analyzed are from the 0.333-mm mesh standard MARMAP bongo sampler collected at 39 or more locations on Georges Bank during each of the seasons. Biomass values were determined by displacement volumes and oven-dry weights. Good agreement was found between the two sets of values in each of the years ($r \geq 0.717$), except for spring 1971 ($r = 0.548$).

Statistical profiles of the biomass data were prepared including calculations of the mean, range, median, standard deviation, variance, standard error, and coefficient of variation. The variances of the biomass values exceeded the mean in each of the seasons. In recognition of the skewness in the data, plots were made using median values to depict trends in biomass changes (Figures 10 and 11). In autumn, the biomass increased from moderate levels in 1971-1972 (26 and 29 cc/100 m^3) to a high in 1973 (42 cc/100 m^3) and declined in 1974 to 25 cc/100 m^3 and a low of 19 cc/100 m^3 in 1975. The 1973 values were the highest among the five years of the time-series. The Mann-Whitney U test was used to examine between-year differences in biomass for both seasons. Volumes in 1973 were significantly higher than in each of the other years and the 1975 volumes were significantly lower ($P \leq 0.05$).

In spring the volumes were lowest in 1971-1972, and were not significantly different ($P > 0.05$) between-years. Volumes in 1973 and 1974 were similar ($P > 0.05$). Both were significantly greater than 1971-1972 ($P < 0.05$). In 1975 the biomass was significantly higher than in other years ($P < 0.05$) (Sherman et al., 1978).

Species Composition.--The zooplankton sampled on the 1971-1975 bottom trawl surveys were dominated by a few species. Copepods were the predominant taxa, ranging from 88% of the zooplankton in 1972 to 94% in 1971. In spring, *Calanus finmarchicus* and *Pseudocalanus minutus* were dominant in each of the years. Their abundance varied among the years; they were most numerous in the spring of 1973, 1974, and 1975. Population densities of *C. finmarchicus* were lowest during the 1971 and 1972 surveys, when percentages of adults to copepodites were highest, $\geq$ 41%. In the succeeding years the surveys were later in the "biological" sense for *C. finmarchicus*. Large-scale cohort production was well underway with the percentages of adults to copepodites reduced to 3%, 8%, and 2% respectively, for 1973, 1974 and 1975. The percentage difference of adults to copepodites did not exceed 64% for the smaller *P. minutus*. It is likely that the low densities of copepods in 1971 and 1972 were the result of a delay in the onset of spring swarming characteristic of *C. finmarchicus* on Georges Bank (Bigelow, 1926), rather than a reflection of a change in levels of secondary production.

In autumn copepods were the principal zooplankters. The species *Centropages typicus* and *Pseudocalanus minutus* were dominant in each of the years (Sherman et al., 1978). Median densities of *C. typicus* populations were highest in 1972 and 1973. Highest volumes for the five-year period occurred in 1973. The abundance of the mysid *Neomysis americana* (median 7,000/100 m^3) in addition to the high numbers of *C. typicus* combined to increase the biomass of zooplankton in 1973 over values observed during the other years of the survey. The hydrographic and biological factors controlling the size of the zooplankton populations are not fully understood. Work on this problem is continuing. A significant factor that could have contributed to the low numbers of *C. typicus* in autumn, 1975, was the abundance of the chaetognath, *Sagitta elegans*, and the coelenterate, *Nanomia cara* on Georges Bank, two important copepod predators. The presence of unusually dense concentrations of *N. cara* on Georges Bank in the fall and winter of 1975 caused loss of fishing time and income to coastal fishermen operating in the Gulf of Maine and Georges Bank; evidence of *N. cara* feeding on copepods during this period has been reported recently (Rogers et al., 1978).

Annual Zooplankton Pulses

Observations of monthly changes in zooplankton abundances in the offshore waters off the U. S. coast are limited. Based on earlier studies, Cohen (1976) attempted to depict an annual cycle for the Gulf of Maine-Georges Bank area (Figure 12). The trend of displacement volumes shown in his Figure indicates a spring peak in May-June. In addition, from another source, Cohen shows highest annual values in September. Recent MARMAP findings are consistent with the spring peak; no evidence of an autumn peak was found in the 1977 volume data. However, increases were observed in our 1977 data for the copepods, *C. typicus*, on Georges Bank and in the Gulf of Maine, and *P. minutus* in Southern New England in autumn.

In coastal waters of the Gulf of Maine the monthly trends in zooplankton displacement volumes show an April minimum, followed by an increase in late spring to a July peak, a decline in August and a secondary peak in October followed by a decline in December (Figure 13). The microzooplankton--e.g., copepod eggs, crustacean nauplii, and copepodites--were most abundant in summer and autumn; in winter and early spring, the zooplankters were predominately adults (Sherman et al., 1976).

The fluctuations in abundance of zooplankton along the inner margin of the Gulf of Maine coast are likely the result of local environmental conditions rather than any large-scale advective processes. In early spring onset of stratification triggers the spring phytoplankton bloom followed by rapid production of copepod cohorts. Meroplankton can swarm and assume dominance over the background abundance of copepods for limited periods. Over the entire annual cycle copepods are the dominant zooplankters in coastal waters. Of the 19 species common to the Central Gulf of Maine coastal area, nine are numerous, but only one, *Pseudocalanus minutus*, is abundant in all seasons, and is an important food of larval herring. Survival of larval herring may be related to the synchronous development of *P. minutus* cohorts and the first feeding of larval herring. *P. minutus* is the most abundant species, of the proper size to be ingested by small herring larvae in Gulf of Maine coastal waters, that is undergoing high rates of cohort production in synchrony with first feeding larvae (Figure 14). *Temora longicornis*, also increases in abundance in autumn but is too large to be eaten by young larvae. The other abundant species--*Acartia clausi* and *C. finmarchicus*--are declining in abundance in autumn, and are predominantly in the late copepodite and adult stages (Sherman and Honey, 1971; Sherman et al., 1976).

In the coastal band from Cape Ann to Machias Bay, 36 species of copepods are found, but only seven are numerous--*Acartia clausi*, *A. longiremis*, *Centropages typicus*, *Calanus finmarchicus*, harpacticoid spp., *Pseudocalanus minutus*, and *Temora longicornis*. The most important environmental factor shaping the distribution of the species is depth of water rather than any particular range of salinity of temperature. Four species are abundant in shoal areas of the coast--*A. longiremis*, *A.*

clausi, harpacticoid spp., and *T. longicornis*. The other three species--*P. minutus*, *C. finmarchicus*, and *C. typicus*--decline in abundance from offshore to inshore. Densities of copepods are greatest in the western area where conditions for feeding and growth are better in the stratified waters than in the turbulent vertically mixed waters in the eastern area (Sherman, 1970).

Zooplankton and Fish Distributions

In addition to playing a critical role in the survival, growth, recruitment, and mortality of larval fish, zooplankton can be a dominant influence on migrations of adult populations. Pavshtics (1963) and Zinkevitch (1967) have reported that movements of herring between the Mid-Atlantic Bight and Georges Bank follow progressive seasonal swarming of zooplankters as the vernal bloom moves from west to east along the coast in the frontal zones between coastal, slope and shoal waters around the periphery of Georges Bank. This apparent relationship may hold promise for forecasting herring and mackerel movements along the coast (Figure 15). Fig. 15

Information on the movements of pelagic fish in coastal waters is scanty. Adult herring are fished on Jeffreys Ledge and other shoals within the Gulf in autumn. Herring feeding in these areas appear to favor larger zooplankton particles including the copepods *Calanus finmarchicus* and *Centropages typicus*. It is unlikely that adults feeding on large calanoids which are most numerous beyond the headlands would move into the coastal embayments.

Larval Physiology and Feeding Studies

Physiological and predator-prey studies of fish species off the northeast coast are now underway by NEFC on the quality and densities of food required for optimal survival and growth of larval fish under controlled laboratory and field conditions (Laurence, 1974; 1977a). Experiments have been conducted with larval cod, haddock, scup, tautog, and winter flounder. Recently, growth and mortality models have been developed for winter flounder, Pseudopleuronectes americanus, that considers temperature, prey density, and larval size (Laurence, 1977b; Beyer and Laurence, 1978).

Recent hypotheses developed from models describing the quantity, and quality of food required by fish larvae for survival and growth have been tested in the sea. Off the California coast, dinoflagellates of the proper size and nutritional value for rapid growth of larval anchovy were found to co-occur with anchovy in horizontal and vertical patches. However, if upwelling is early it appears that the synchronous relationship can be unbalanced. Patches of dinoflagellates can be dispersed in the early upwelling and replaced by copepodites which may be too large for the anchovy to ingest thereby reducing the survival potential of first feeding larvae (Lasker, 1975). Laboratory studies of winter flounder growth based on empirical models indicate that densities of food required for rapid growth usually exceed values reported in the literature (Laurence, 1975). Patches of larval fish food of the proper density (2.0 cal/l) have recently been observed in estuarine and embayment areas in Southern New England (Laurence, personal communication). Both observations confirm the importance of microdistributions in the sea. If we are to understand the relationships between food availability and larval fish survival, our approach to sampling needs to include systems for measuring microdistributions of larvae, their predators, and food utilizing pumps, particle counters, and other "real-time" methods.

Secondary Production Estimates

The relationship of zooplankton numbers to biomass and productivity rates is under investigation. Available information, unfortunately, is fragmentary. Secondary production based on older stages of *C. finmarchicus* in spring was recently estimated at 79.46 mg carbon/m^2/day by Green et al. (1977). The instantaneous growth method was used in the calculation from the formula:

$$P = \frac{W_B - W_A}{t} \frac{(N_1 + N_2)}{2}$$

Where: W_A = weight at the beginning of a stage

W_B = weight at the end of a stage

t = stage duration in days

N_1 = count of organisms in a stage

N_2 = count of organisms in succeeding stage

The production rates for each of five surveys made during the spring generations of *C. finmarchicus* populations were used to estimate total production for the 100 day period of the surveys. As was pointed out by Green et al. (1977) the values were of the same order of magnitude, 46 mg C/m^2/day, estimated for *C. finmarchicus* in the North Sea by Mullin (1969) and 77 mg C/m^2/day reported for *Acartia tonsa* by Heinle (1966). Studies are now underway in the Northeast Fisheries Center to refine the estimates of secondary production by enlarging the number of species examined and extending the analyses to all of the growing seasons.

Biochemical Studies

Studies of larval fish condition have been traditionally based on morphological differences. The procedure is time consuming and subject to bias from preservative-distortion. A rapid biochemical method has been developed that provides an index of condition based on RNA/DNA ratios (Buckley, 1977).

Emerging Ecosystem Theory in Relation to Plankton Studies in the NW Atlantic

Trophodynamic studies of larval survival will need to take into account the early modelling of the production cycle developed by Riley (1941, 1946, 1947); Riley and Bumpus (1946); and Riley et al. (1949). They have not been used effectively in the Gulf to forecast conditions principally for lack of systematic input parameters that would allow for prediction in annual, seasonal, and/or more frequent time scales. Since the early studies of primary production of the Woods Hole and Bingham groups we have experienced a hiatus in making systematic observations. Some beginnings are underway. Matrices of information are being developed now for key elements in the ecosystem. Our goal is to develop a food budget for Georges Bank, and to continue satisfying our most critical information voids by expanding our effort from Georges Bank to the inner Gulf of Maine and Mid-Atlantic area. Progress is being made on defining the benthic communities on the shelf (Williams and Wigley, 1977). Examples of distributions of benthic species are given in Figure 16. Fig. 16 Changes in fish distribution and abundance are monitored with bottom trawl surveys conducted over the shelf for the past 15 years (Grosslein, 1969; Grosslein and Bowman, 1973). A generalized pattern of species mixtures along the shelf in spring and autumn is given in Figure 17. The MARMAP oceanographic effort includes the monitoring of current systems, temperature, and salinity changes and the effects of the movement of water masses on the fish stocks in the area. Surface temperature and salinity charts have been prepared for the bottom trawl surveys (Pawlowski et al., 1978) (Figure 18). In addition, new information on water movements Fig. 18 is now becoming available from moored current meters monitoring flow in the northeast channel of Georges Bank (Figure 19). High velocity in flow Fig. 19 from the Scotian Shelf into the Gulf of Maine and Georges Bank areas has been observed directly for the first time.

Primary Productivity Studies and Fish

Significant activity is now underway in the New York Bight. A group headed by John Walsh of Brookhaven National Laboratory is now investigating the energy flux of the Bight and principal driving forces of the system. Nutrient enrichment through storm mixing appears to be the principal mechanism for recycling nutrients within the ecosystem in spring (Walsh et al., 1976). The dominant forcing function of the wind-stirred water column is similar to the upwelling system off the Oregon coast. Other similarities between the two systems were also observed in annual primary productivity, food chain diversity, and fish biomass (Table VIII). Table [illegible]

In contrast to the coastal Oregon and the New York Bight area similarities, differences can be found in a preliminary comparison of the New York Bight, Georges Bank, and the North Sea. The estimated levels of primary productivity range from 100 $gC/m^2/yr$ for the North Sea to 150-200

$gC/m^2/yr$ for the New York Bight, and 400-500 $gC/m^2/yr$ for Georges Bank. The latter value has recently been reported by Cohen et al. (1978), based on C^{14} measurements made during MARMAP surveys in 1975. The estimated average production of fish biomass for the three areas increases from a low of 10 $mt/km^2/yr$ for the North Sea to 15 $mt/km^2/yr$ in the New York Bight, and a high of 19 $mt/km^2/yr$ for Georges Bank (Figure 20). Fig. 20

The extremely high value for Georges Bank primary production is now being reexamined critically. A series of C^{14} measurements have been made in the area in 1976. Preliminary evidence supports the high value.

Observations of Stressed Ecosystems in the Northwest Atlantic

Recently Steele and Frost (1977) described a model of a stressed ecosystem, wherein overall levels of primary production are not affected by stress. But significant shifts in species composition were in evidence. In a stressed system the production of small fast growing species is favored over the larger species. The theoretical basis for the model is supported by the authors with field data describing long-term changes in the plankton of the North Sea based on Continuous Plankton Recorder data. In addition, recent experimentation in stressed large-volume plastic enclosures have shown a shift from essentially large-celled diatom populations to smaller dinoflagellates following dosings with copper and petroleum hydrocarbons (Steele and Frost, 1977; Thomas and Seibert, 1977).

In addition to plankton changes in the North Sea, described by the IMER group in Plymouth, Ursin (1977) reported a decline in mackerel and herring stocks in the North Sea coincident with an increase in the biomass of fast growing and shortlived species--sprat, Norway pout, and sandeel (Figure 21). Although much of the data is preliminary in nature, the implication is clear. In a summary statement describing the results of the Symposium on the "Changes in the North Sea Fish Stocks and their Causes," Hempel (in press) reported that changes in food and predation of fish larvae may have been the key to the observed increases in growth and recruitment of cod and haddock. The decline in herring and mackerel abundance

Fig. 21

> ". . . was at least partly responsible for improved living conditions for young gadoids and that fast growing, short lived fish with higher ecological efficiency took the place of the slower growing (but higher priced) species which altogether caused a higher productivity of the total fish population in the North Sea."

Implications of Biomass Changes in the Northwest Atlantic

In the Northwest Atlantic off the U. S. coast the changes in the size of the fish biomass over the past eight years have been dramatic. Recent estimates of primary production levels indicate that Georges Bank is far more productive than previously estimated. Considerable effort is now being directed to verify the higher values. Given that the value is reasonable, then we would look for evidence of changes at levels below the primary-production "lid." Significant shifts have occurred among the fish species. Mackerel and herring stocks have declined, and "coincidentally" the abundance of sand lance, a short lived, fast growing species with high-ecological efficiency, has increased dramatically in abundance, particularly in the Southern New England and Mid-Atlantic Bight areas.

Some between year and among area differences in zooplankton abundance have been detected. However, the causes for the changes in zooplankton densities are not clear. It will be important in the future to partition zooplankton mortalities into environmental and predator compartments. This is a difficult but important task.

The implications of these kinds of species shifts is clear. Resource managers, now more than ever before, need to evaluate the consequences of multispecies interactions and be able to sort out the impacts resulting from the removals of presently unfished "ecological species" (e.g., four-bearded rockling, and/or sandeels in favor of "commercial" species (e.g., cod, haddock, herring, flounders, and mackerels). Proper evaluation is dependent on the best scientific advice available, and to this end it is necessary to re-evaluate how best to get on with studying marine ecosystems from a fishery management perspective.

Available evidence from the northeast Atlantic indicates that fluctuations of fish biomass as documented in the Symposium on the Changes in the North Sea Fish Stocks were of several orders of magnitude, and measurable with the present methods of combining, and analyzing data from fish-catches and fisheries-independent assessment surveys of fish stocks and their environments. In the northeast Atlantic, largely through the framework of ICES, catch-data is systematically reported and joint international surveys for demersal, and pelagic adults, juvenile, and larval fishes are conducted, usually for target species. Measurements of pollutants, primary production, hydrography and zooplankton biomass, species composition and productivity are generally studies of limited areas and/or relatively short-duration. The exception, is the Continuous

Plankton Recorder surveys of the North Atlantic underway for nearly three decades.

The approach in the northwest Atlantic is largely an evolution of ICNAF joint international studies to support the total fish biomass management regime adopted in 1973. Standardized MARMAP surveys are underway for monitoring population changes of fish, plankton, shellfish and benthos, and hydrography by the Northeast Fisheries Center.

Principal focus in the MARMAP ecosystem study is on the early life stages of fish (Figure 22). Estimates are being made of the magnitude of the size of the spawning biomass of a stock based on abundance and mortality estimates of eggs and early stage larvae. To support the activity, a major commitment has been made to conduct in cooperation with other countries a "patch" study in 1979. The operations will be conducted on Georges Bank on a microscale level using new sampling strategies including pumps, to observe the relationships among fish larvae, their prey and predators in relation to growth and survival. Macroscale ichthyoplankton-zooplankton surveys of up to 6x/yr are continuing to monitor temporal and spatial changes in: (1) fish spawning and estimates of larval fish production, (2) changes in zooplankton abundance and species composition, and (3) changes in hydrography and their effects on fish. The common denominator to the studies is energy flow among the principal species. An initial energy budget has been developed by Cohen et al. (1978) for Georges Bank. Serious deficiencies exist in several of the key components. One of the most significant is in the fragmentary nature of the secondary production component, both in the zooplankton and benthos. The initial stimulus for developing the budget was in fact to

Fig. 22

identify the weakest components and develop the necessary research initiatives to overcome them.

Principal focus over the next several years in the MARMAP program will be on predator-prey interactions at all trophic levels. To date approximately 70,000 stomachs have been examined to frame the most critical questions. Preliminary evidence suggests that silver hake *Merluccius bilinearis*, plays a principal role in regulating the ecosystems (Edwards and Bowman, 1978). Also, the estimate of turnover rate of benthos and plankton will be refined. The degree to which primary production serves as the probable "lid" on the ecosystem now needs to be examined carefully. Studies of primary production will be accelerated in an effort to confirm or modify the extremely high values attributed to Georges Bank, and the impact of these values on the fish stocks. The MARMAP studies are serving to improve primary production estimates, and provide a better understanding of the links between plankton and fish production.

January 31, 1979

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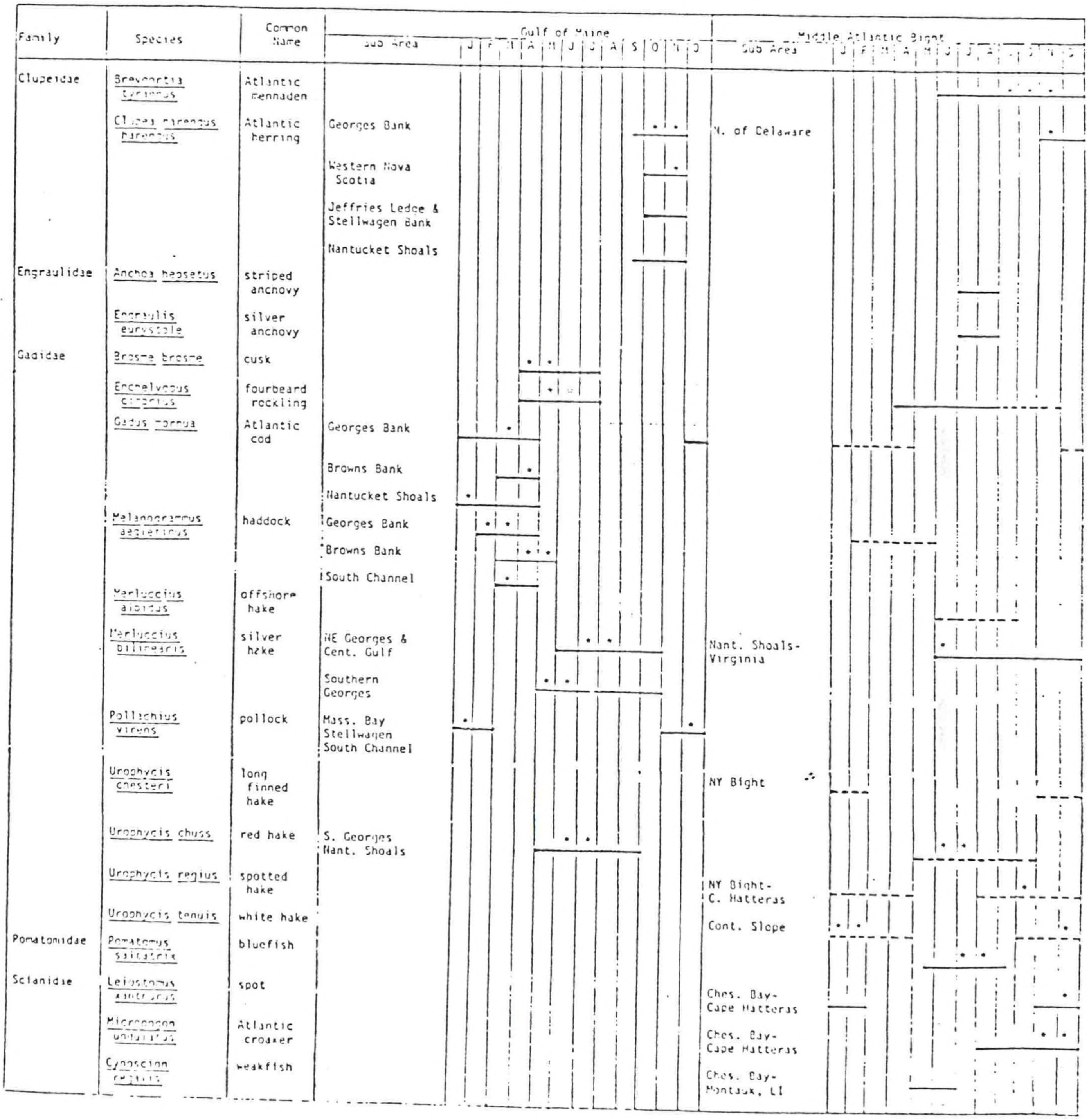
Table I. Principal spawning areas and times of marine fishes, Cape Sable to Cape Hatteras. From Colton, et al. (1978).



Family	Species	Common Name	Gulf of Maine Sub Area	Middle Atlantic Bight Sub Area
Clupeidae	*Brevoortia tyrannus*	Atlantic menhaden		
	Clupea harengus harengus	Atlantic herring	Georges Bank	N. of Delaware
			Western Nova Scotia	
			Jeffries Ledge & Stellwagen Bank	
			Nantucket Shoals	
Engraulidae	*Anchoa hepsetus*	striped anchovy		
	Engraulis eurystole	silver anchovy		
Gadidae	*Brosme brosme*	cusk		
	Enchelyopus cimbrius	fourbeard rockling		
	Gadus morhua	Atlantic cod	Georges Bank	
			Browns Bank	
			Nantucket Shoals	
	Melanogrammus aeglefinus	haddock	Georges Bank	
			Browns Bank	
			South Channel	
	Merluccius albidus	offshore hake		
	Merluccius bilinearis	silver hake	NE Georges & Cent. Gulf	Nant. Shoals-Virginia
			Southern Georges	
	Pollachius virens	pollock	Mass. Bay Stellwagen South Channel	
	Urophycis chesteri	long finned hake		NY Bight
	Urophycis chuss	red hake	S. Georges Nant. Shoals	
	Urophycis regius	spotted hake		NY Bight-C. Hatteras
	Urophycis tenuis	white hake		Cont. Slope
Pomatomidae	*Pomatomus saltatrix*	bluefish		
Sciaenidae	*Leiostomus xanthurus*	spot		Ches. Bay-Cape Hatteras
	Micropogon undulatus	Atlantic croaker		Ches. Bay-Cape Hatteras
	Cynoscion regalis	weakfish		Ches. Bay-Montauk, LI

Table I. (Continued)

Family	Species	Common Name	Gulf of Maine													Middle Atlantic Bight												
			Sub Area	J	F	M	A	M	J	J	A	S	O	N	D	Sub Area	J	F	M	A	M	J	J	A	S	O	N	D
Labridae	*Tautoga onitis*	tautog																			—	•—	—	—				
	Tautogolabrus adspersus	cunner	Mass. Bay S. Georges Nant. Shoals					•—	•—	- -	- -										—	•—	—	—				
Scombridae	*Scomber scombrus*	Atlantic mackerel	W. Gulf Cape Cod Bay					—	•—	- -						Cape Cod-Chesapeake Bay				—	•—	—						
Scorpaenidae	*Sebastes marinus*	redfish	Scotian Shelf & Cent. Gulf					—	•—	•—	—																	
Triglidae	*Prionotus carolinus*	northern searobin														Block Island-Cape Hatteras					—	—	—	—	—	—	—	
Cottidae	*Myoxocephalus octodecem-spinosus*	longhorn sculpin		•—	- -									—	•—													
Ammodytidae	*Ammodytes* sp.	sand lance		•—	•—	—	- -								—		•—	—										•—
Stromateidae	*Peprilus triacanthus*	butterfish	SW Georges Nant. Shoals					—	•—	•—	—										—	—	•—	•—	—	—		
Bothidae	*Citharichthys arctifrons*	Gulf Stream flounder	SW Georges Nant. Shoals						- -	- -	•- -	- -								—	—	—	•—	—	—	—	—	
	Hippoglossina oblonga	fourspot flounder	Nant. Shoals-South					- -	- -	- -											—	—	•—	—	—	—		
	Paralichthys dentatus	summer flounder	Nant. Shoals-South	- -	- -	- -	- -						- -	- -	- -		—	—	—	—					—	•—	—	—
	Scophthalmus aquosus	windowpane	Georges Bank Nant. Shoals-South					- -	- -	- -	- -									—	—	—	—	—	—	•—	—	—
Pleuronectidae	*Glyptocephalus cynoglossus*	witch flounder					—	•—	•—	—	—					Cape Cod-Delaware Bay					•—	•—	—	—				
	Hippoglossoides platessoides	American plaice			—	•—	•—	—								South of Martha's Vineyard				- -	- -							
	Limanda ferruginea	yellowtail flounder	Browns Bank					—	•—	—										—	•—	•—	—	—				
			Georges Bank Nant. Shoals-South			—	•—	•—	—	- -																		
	Pseudopleuronectes americanus	winter flounder	Georges Bank			- -	- -	- -	- -																			

——— Known spawning season.

- - - - - - Uncertain spawning season.

•Peak spawning.

Table II. Cruises and dates of sampling in each of the areas surveyed in 1977.

Survey	Dates	Vessels	Cruise	Area	No. of Samples Analyzed
Early Spring	3 Mar- 8 Apr	*Goerlitz* *Delaware II*	77-01 77-03	Southern New England	29
				Georges Bank	30
				Gulf of Maine	25
Mid-Spring	13 Apr- 20 May	*Albatross IV* *Delaware II*	77-02 77-05	Southern New England	30
				Georges Bank	23
				Gulf of Maine	30
Late Spring	17 May- 17 June	*Nogliki* *Delaware II* *Delaware II*	77-02 77-05 77-07	Southern New England	30
				Georges Bank	31
				Gulf of Maine	30
Summer	30 July- 3 Sept	*Yubileiniy*	77-02	Southern New England	36
				Georges Bank	21
				Gulf of Maine	28
Fall	18 Oct- 12 Nov	*Argus*	77-01	Southern New England	30
				Georges Bank	20
				Gulf of Maine	24
Late Fall	12 Nov- 13 Dec	*Mt. Mitchell* *Kelez*	77-11 77-11	Southern New England	18
				Georges Bank	20
				Gulf of Maine	30

Table III. Zooplankton biomass values (cc/100 m^3) based on displacement volumes of 0.333 mm mesh samples. Included are values for mean, median, range, standard deviation, variance, and coefficient of variation.

Area	Cruise	Date	Mean	Median	Range	S.D.	Var.	C.V.(%)
SNE	"Del" 77-03 and "Goerl" 77-01	Mar-Apr '77	32.57	21.96	2.95-111.66	28.23	799.61	87
GB	"Goerl" 77-01	Mar-Apr '77	24.87	20.32	1.36-92.22	19.34	373.91	78
GOM	"Goerl" 77-01	Mar-Apr '77	37.40	13.54	4.53-249.30	54.05	2,921.78	145
SNE	"Del" 77-05 and "Alb" 77-02	Apr-May '77	63.56	59.68	3.25-172.13	45.21	2,043.51	71
GB	"Alb" 77-02	Apr-May '77	85.31	68.12	20.39-277.25	61.11	3,734.38	72
GOM	"Alb" 77-02	Apr-May '77	40.90	32.64	10.48-133.82	25.93	650.06	64
SNE	"Del" 77-05 "Nog" 77-02	May-June '77	100.56	81.55	14.68-324.88	63.24	39,999.52	63
GB	"Nog" 77-02 "Del" 77-07	May-June '77	179.66	126.97	16.72-790.90	176.96	31,314.61	98
GOM	"Nog" 77-02 "Del" 77-07	May-June '77	81.09	59.95	16.03-199.21	52.89	2,797.33	65
SNE	"Yub" 77-02	Aug. '77	66.95	50.15	20.18-243.45	38.34	1,470.31	57
GB	"Yub" 77-02	Aug. '77	50.79	49.22	10.68-105.68	22.15	467.38	44
GOM	"Yub" 77-02	Aug. '77	52.48	48.64	19.95-97.33	20.44	402.84	39
SNE	"Argus" 77-01	Oct.-Nov '77	26.84	23.58	9.55-55.79	12.73	156.64	47
GB	"Argus" 77-01	Oct-Nov '77	38.57	40.40	12.24-142.05	28.60	777.54	74
GOM	"Argus" 77-01	Oct-Nov '77	61.45	54.64	6.87-140.72	31.49	950.23	51
SNE	"Kelez" 77-11	Nov-Dec '77	26.16	19.63	6.66-53.78	18.30	316.31	70
GB	"Kelez" "Mt.M" 77-11	Nov-Dec '77	30.31	27.10	9.29-102.55	20.90	415.00	69
GOM	"Kelez" "Mt.M" 77-11	Nov-Dec '77	49.94	42.31	6.01-115.39	25.26	616.71	50

GB=Georges Bank; SNE=Southern New England; GOM=Gulf of Maine.
"Alb"="Albatross IV"; "Wiecz"="Wieczno"; "Belog"="Belogorsk"; "Ant. D"="Anton Dohrn"; "Res"="Researcher"; "Goerl"="Goerlitz"; "Del"="Delaware II"; "Nog"="Nogliki"; "Yub"="Yubileiniy"; "Mt.M"=Mt. Mitchell".

Table IV. Kruskal-Wallis Chi-Square (X^2) and probability values for among season, between season, and among area comparisons of zooplankton volumes--Southern New England, Georges Bank, Gulf of Maine.

Southern New England		Among Season Differences Georges Bank		Gulf of Maine	
X^2	Probability	X^2	Probability	X^2	Probability
67.15	$P < .0001$	73.05	$p < .0001$	31.62	$p < .0001$

Between Season Differences

	X^2	
Southern New England		
Early Spring--Mid Spring	8.37	$P < .0038$
Early Spring--Late Spring	24.55	$P < .0001$
Late Spring--Summer	7.56	$P < .0060$
Summer--Mid Autumn	31.72	$P < .0001$
Mid Autumn--Late Autumn	0.62	$P > .05$*
Georges Bank		
Early Spring--Mid Spring	23.83	$P < .0001$
Early Spring--Late Spring	37.59	$P < .0001$
Late Spring--Summer	18.80	$P < .0001$
Summer--Mid Autumn	6.40	$P < .0114$
Mid Autumn--Late Autumn	2.13	$P > .05$*
Gulf of Maine		
Early Spring--Mid Spring	7.13	$P < .0076$
Early Spring--Late Spring	16.87	$P < .0001$
Late Spring--Summer	4.60	$P < .0318$
Summer--Mid Autumn	0.88	$P > .05$*
Mid Autumn--Late Autumn	1.61	$P > .05$*

Among Area Differences

	X^2	
Early Spring	0.71	$P > .05$*
Mid Spring	10.25	$P < .0059$
Late Spring	10.47	$P < .0053$
Summer	4.80	$P > .05$*
Mid Autumn	20.33	$P < .0001$
Late Autumn	16.62	$P < .0002$

*Differences are not significant.

Table V. Comparison of relative abundance of zooplankton components in the Gulf of Maine, Georges Bank, and Southern New England sub-areas of the coastal ecosystem, early spring through late autumn, 1977.

Area	Season	Median Vol cc/100 m^3	Copepoda	Chaetognatha	Cladocera	Amphipoda	Euphausiacea	Coelenterata	Thaliacea	Pelecypoda	Cirripedia	Appendicularia	Ostracoda	Polychaeta	Other
Gulf of Maine	Early Spring March-April	13.54	96.3				1.2								2.5
	Mid Spring April-May	32.64	99.8												0.2
	Late Spring May-June	59.95	99.6												0.4
	Summer July-August	48.64	97.5		1.1										1.4
	Fall Oct-November	54.64	99.0												1.0
	Late Fall Nov-December	42.31	98.6												1.4
Georges Bank	Early Spring	20.32	74.5	2.8			1.1				20.4				1.2
	Mid Spring	68.12	96.5												3.5
	Late Spring	126.97	94.2	2.2										1.0	2.6
	Summer	49.22	78.4	13.7	2.9	1.0		1.5							2.5
	Fall	40.40	95.1	1.3						1.7					1.9
	Late Fall	27.10	86.6	5.5						6.9					1.0
Southern New England	Early Spring	21.96	88.2								9.6				2.1
	Mid Spring	59.68	92.3	3.2				1.3							3.2
	Late Spring	81.55	88.4	6.3	3.0										2.3
	Summer	50.15	78.6	5.5	10.7	1.9			2.2						1.1
	Fall	23.58	79.3	1.9	12.4	1.9			2.2			1.0			1.3
	Late Fall	19.63	95.1	2.6									1.1		1.2

Table VI. Abundance, percentage composition, median/100 m^3 and percentage dominance of copepod species in the Gulf of Maine, Georges Bank, and Southern New England, early spring through late autumn, 1977.

Area	Season	*Calanus finmarchicus*	*Pseudocalanus minutus*	*Metridia lucens*	*Oithona* sp.	*Centropages typicus*	*Temora longicornis*	*Centropages hamatus*	*Acartia longiremis*	*Paracalanus parvus*	*Acartia tonsa*	*Temora turbinata*	*Temora stylifera*	*Labidocera aestiva*	*Calanus minor*	*Candacia armata*	C
Gulf of Maine	Early Spring	48.6/12018 72.00	27.1/767 4.00	8.6/511	13.6/730 8.00												2
	Mid Spring	85.0/45920 96.67	9.1/4607	5.5/2404													0
	Late Spring	75.2/54383 83.33	17.5/13057 3.33	6.9/4987													0
	Summer	79.9/58874 96.43	10.0/6112	4.2/2932		4.2/2419			1.3/589								0
	Fall	51.3/44401 70.83	11.4/6420 4.17	3.5/2713		29.3/13802 8.33				2.6/1205							1
	Late Fall	38.7/32262 40.00	14.6/7880	4.3/3132		35.5/26603 20.00				5.5/2605							1
Georges Bank	Early Spring	51.7/6414 50.00	38.7/5373 46.67	2.8/46	6.0/57												0
	Mid Spring	72.8/46422 95.65	24.6/18604 4.35	1.0/0													1
	Late Spring	60.5/90081 58.06	37.2/47283 35.48	1.6/365													0
	Summer	38.1/15518 33.33	29.3/12285 19.05			12.1/7364 4.76		18.5/5486 19.05									2
	Fall	2.5/1676	19.8/8804 15.00	2.0/395		50.1/38147 50.00		18.4/721 10.00		1.9/590							5
	Late Fall	4.3/1192 5.00	28.0/14798 15.00	1.7/358		57.0/19118 40.00		3.8/371		2.2/942				1.2/0			1
Southern New England	Early Spring	8.5/1772 13.79	75.1/30600 72.41	1.3/248	1.1/226	5.4/3895	6.2/0	1.3/0									2
	Mid Spring	38.8/21297 33.33.	51.1/54681 53.33	2.9/766		1.8/441	3.3/951										2
	Late Spring	37.2/58152 33.33	44.3/96508 33.33	2.3/9280		1.5/1335	11.7/274 13.33										3
	Summer	22.9/17274 33.33	13.3/4256		1.4/709	49.4/18765 36.11		2.4/0		1.2/0	5.0/0 2.78						1
	Fall	3.3/991	9.5/1531	1.2/68	1.1/68	66.9/28569 63.33				1.2/31	3.4/87	2.7/0	2.6/104		1.5/305	1.1/147	5
	Late Fall		25.5/4794			62.8/31144 77.78				2.6/1833		3.2/1381			1.2/0		5

Table VII. Kruskal-Wallis Chi-Square (χ^2) and probability values for among season, between season, and among area comparisons of copepod abundance levels--Southern New England, Georges Bank, and Gulf of Maine.

Pseudocalanus minutus

Among Season Differences

Southern New England	Georges Bank	Gulf of Maine
χ^2 88.55 P < .0001	χ^2 31.73 P < .0001	χ^2 42.92 P < .0001

Between Season Differences

	χ^2			
Southern New England				
Early Spring--Mid Spring	3.04	P	>	.0812
Early Spring--Late Spring	11.74	P	<	.0006
Late Spring--Summer	38.69	P	<	.0001
Summer--Mid Autumn	3.57	P	>	.0589*
Mid Autumn--Late Autumn	4.16	P	<	.0415
Georges Bank				
Early Spring--Mid Spring	8.45	P	<	.0036
Early Spring--Late Spring	24.06	P	<	.0001
Late Spring--Summer	8.85	P	<	.0029
Summer--Mid Autumn	0.57	P	>	.4494*
Mid Autumn--Late Autumn	1.76	P	>	.1850
Gulf of Maine				
Early Spring--Mid Spring	14.76	P	<	.0001
Early Spring--Late Spring	24.15	P	<	.0001
Late Spring--Summer	6.20	P	<	.0128
Summer--Mid Autumn	1.34	P	>	.2475*
Mid Autumn--Late Autumn	.51	P	>	.4754*

Among Area Differences

	χ^2			
Early Spring	43.71	P	<	.0001
Mid Spring	37.17	P	<	.0001
Late Spring	31.12	P	<	.0001
Summer	8.97	P	<	.0113
Mid Autumn	13.61	P	<	.0011
Late Autumn	4.80	P	>	.0907*

*Differences are not significant.

Table VII Continued.

Calanus finmarchicus

Among Season Differences

Southern New England	Georges Bank	Gulf of Maine
χ^2 70.02 P < .0001	χ^2 75.03 P < .0001	χ^2 62.3 P < .0001

Between Season Differences

	χ^2			
Southern New England				
Early Spring--Mid Spring	17.70	P	<	.0001
Early Spring--Late Spring	21.67	P	<	.0001
Late Spring--Summer	14.46	P	<	.0001
Summer--Mid Autumn	17.82	P	<	.0001
Mid Autumn--Late Autumn	5.22	P	<	.0224
Georges Bank				
Early Spring--Mid Spring	20.45	P	<	.0001
Early Spring--Late Spring	27.27	P	<	.0001
Late Spring--Summer	16.45	P	<	.0001
Summer--Mid Autumn	7.44	P	<	.0064
Mid Autumn--Late Autumn	0.06	P	>	.8091*
Gulf of Maine				
Early Spring--Mid Spring	36.01	P	<	.0001
Early Spring--Late Spring	36.41	P	<	.0001
Late Spring--Summer	0.03	P	>	.8641*
Summer--Mid Autumn	2.67	P	>	.1023*
Mid Autumn--Late Autumn	1.53	P	>	.2165*

Among Area Differences

	χ^2			
Early Spring	11.85	P	<	.0027
Mid Spring	5.92	P	>	.0517*
Late Spring	0.53	P	>	.5443*
Summer	28.20	P	<	.0001
Mid Autumn	41.73	P	<	.0001
Late Autumn	33.24	P	<	.0001

*Differences are not significant.

Table VII. Continued.

Centropages typicus

Among Season Differences

Southern New England	Georges Bank	Gulf of Maine
χ^2 68.3 P < .0001	χ^2 63.6 P < .0001	χ^2 55.0 P < .0001

Between Season Differences

	χ^2			
Southern New England				
Early Spring--Mid Spring	6.33	P	<	.0119
Early Spring--Late Spring	0.73	P	>	.3938
Late Spring--Summer	12.30	P	<	.0004
Summer--Mid Autumn	1.14	P	>	.2851*
Mid Autumn--Late Autumn	1.37	P	>	.2415*
Georges Bank				
Early Spring--Mid Spring	1.86	P	>	.1731*
Early Spring--Late Spring	7.70	P	<	.0055
Late Spring--Summer	9.13	P	<	.0025
Summer--Mid Autumn	21.49	P	<	.0001
Mid Autumn--Late Autumn	10.19	P	<	.0014
Gulf of Maine				
Occurrences too few to test for significance.				

Among Area Differences

	χ^2			
Early Spring	22.54	P	<	.0001
Mid Spring	8.31	P	<	.0157
Late Spring	10.81	P	<	.0045
Summer	16.23	P	<	.0003
Mid Autumn	10.01	P	<	.0067
Late Autumn	5.69	P	>	.0582*

*Differences are not significant.

Table VIII. A comparison of habitat variability, species diversity, and productivity between two shelf ecosystems of the same latitude.[1]

	Oregon	New York
Temperature range of the inshore mixed layer	8-14°C year^{-1}	4-24°C year^{-1}
Cumulative nitrate within the inshore mixed layer	2.2 g-atom NO_3 m^{-3} year^{-1}	1.3 g-atom NO_3 m^{-3} year^{-1}
Primary production of inshore waters	193 gC m^{-2} year^{-1}	150-200 gC m^{-2} year^{-1}
Number of inshore copepod species	26 within 18 km of the coast	29 within 25 km of the coast
Estuarine dependent fish species	44% of commercial catch year^{-1}	45% of commercial catch year^{-1}
Marine fish species on shelf and slope	∿ 219	∿ 200
Fish yield of the shelf ecosystem	10 tons km^{-2} year^{-1}	5-10 tons km^{-2} year^{-1}

---

[1] Walsh, John J., Terry E. Whitledge, L.A. Codispoti, Steven O. Howe, Creighton D. Wirick and Louis J. Castiglione. The biological response to transient forcings of the spring bloom within the New York Bight. Unpublished manuscript Brookhaven National Laboratory, Upton, N.Y. 66 pp. 1976.

FISHABLE BIOMASS OF GEORGES BANK, GULF OF MAINE AND SOUTHERN NEW ENGLAND

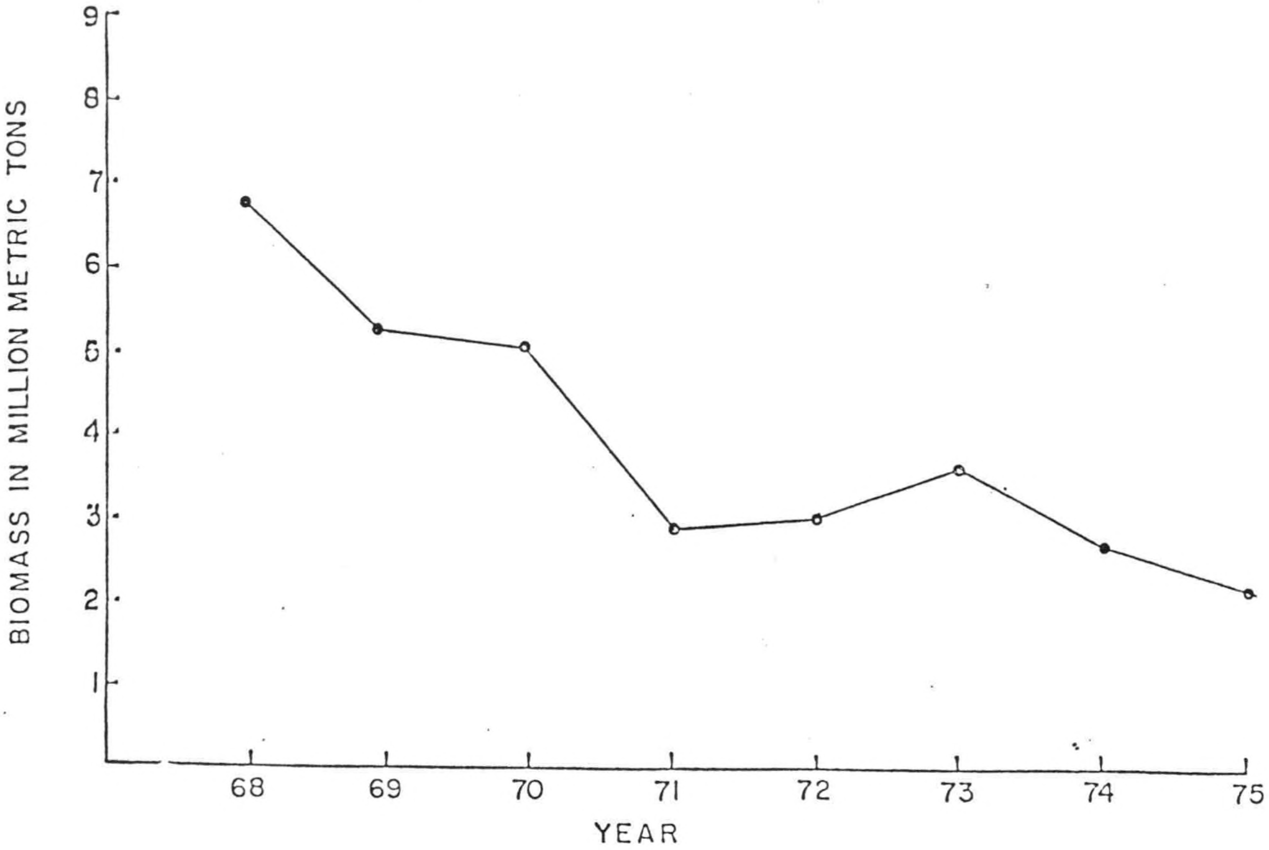


Figure 1. Decline in the fishable biomass of Georges Bank, Gulf of Maine and Southern New England 1968-1975. Between 1968-1969 and 1974-1975, the biomass decreased 65%. Adapted from Clark and Brown (1977).

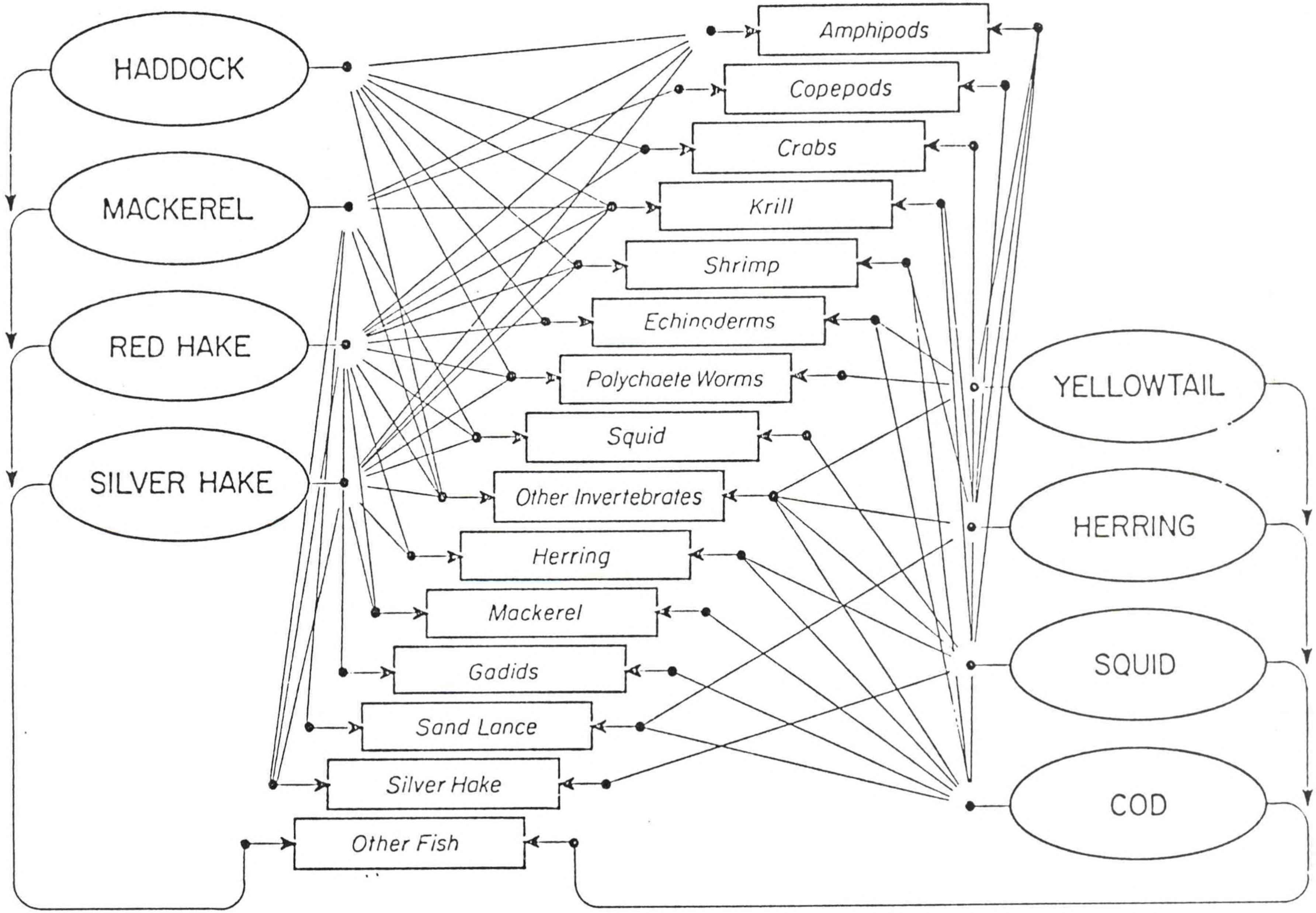
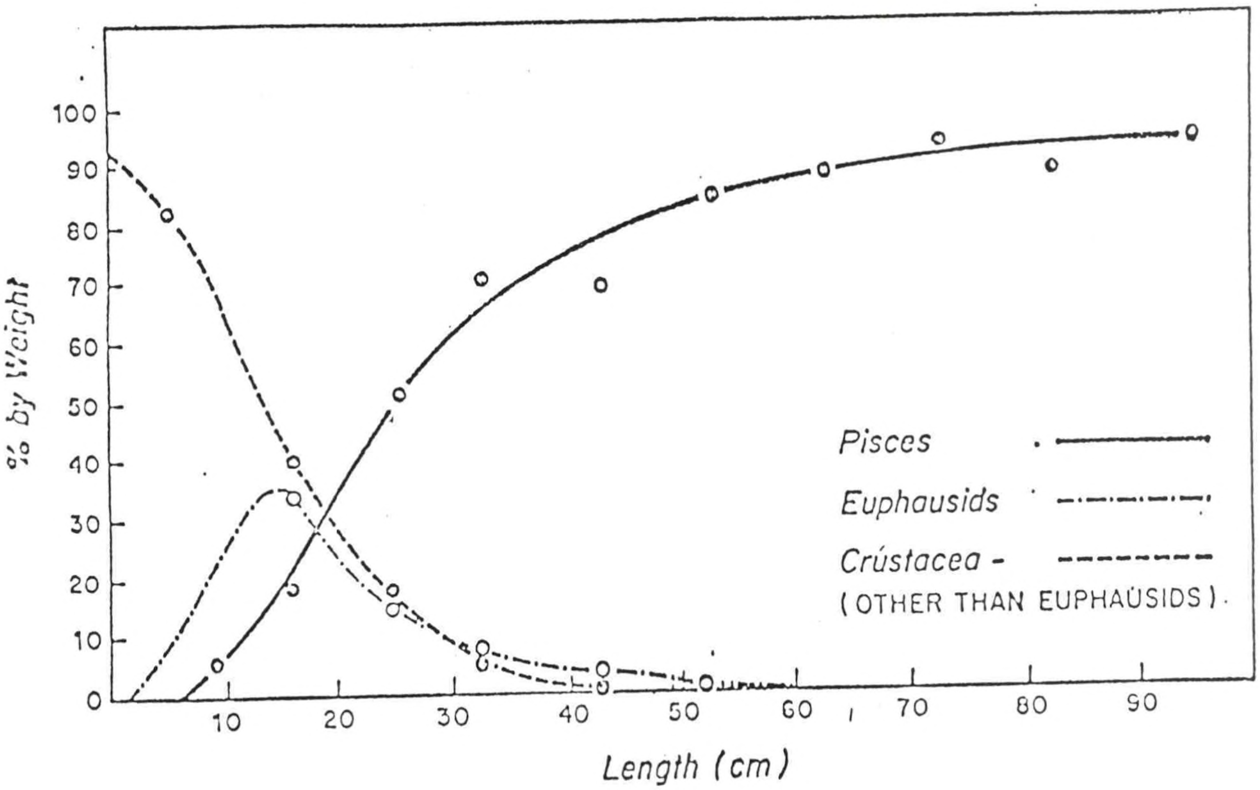

HADDOCK
MACKEREL
RED HAKE
SILVER HAKE
Amphipods
Copepods
Crabs
Krill
Shrimp
Echinoderms
Polychaete Worms
Squid
Other Invertebrates
Herring
Mackerel
Gadids
Sand Lance
Silver Hake
Other Fish
YELLOWTAIL
HERRING
SQUID
COD

Figure 2. Schematic presentation of predator-prey interactions for the more important species of fish and squid off the northeast coast of the U. S. Predator names are enclosed in ovals; prey are shown in rectangles. From Langton and Bowman (1977).



% by Weight
100
90
80
70
60
50
40
30
20
10
0
10
20
30
40
50
60
70
80
90
Length (cm)
Pisces
Euphausids
Crústacea -
(OTHER THAN EUPHAÚSIDS).

Figure 3. Change in the composition of the prey of cod in the eastern Atlantic. From Edwards (1976).

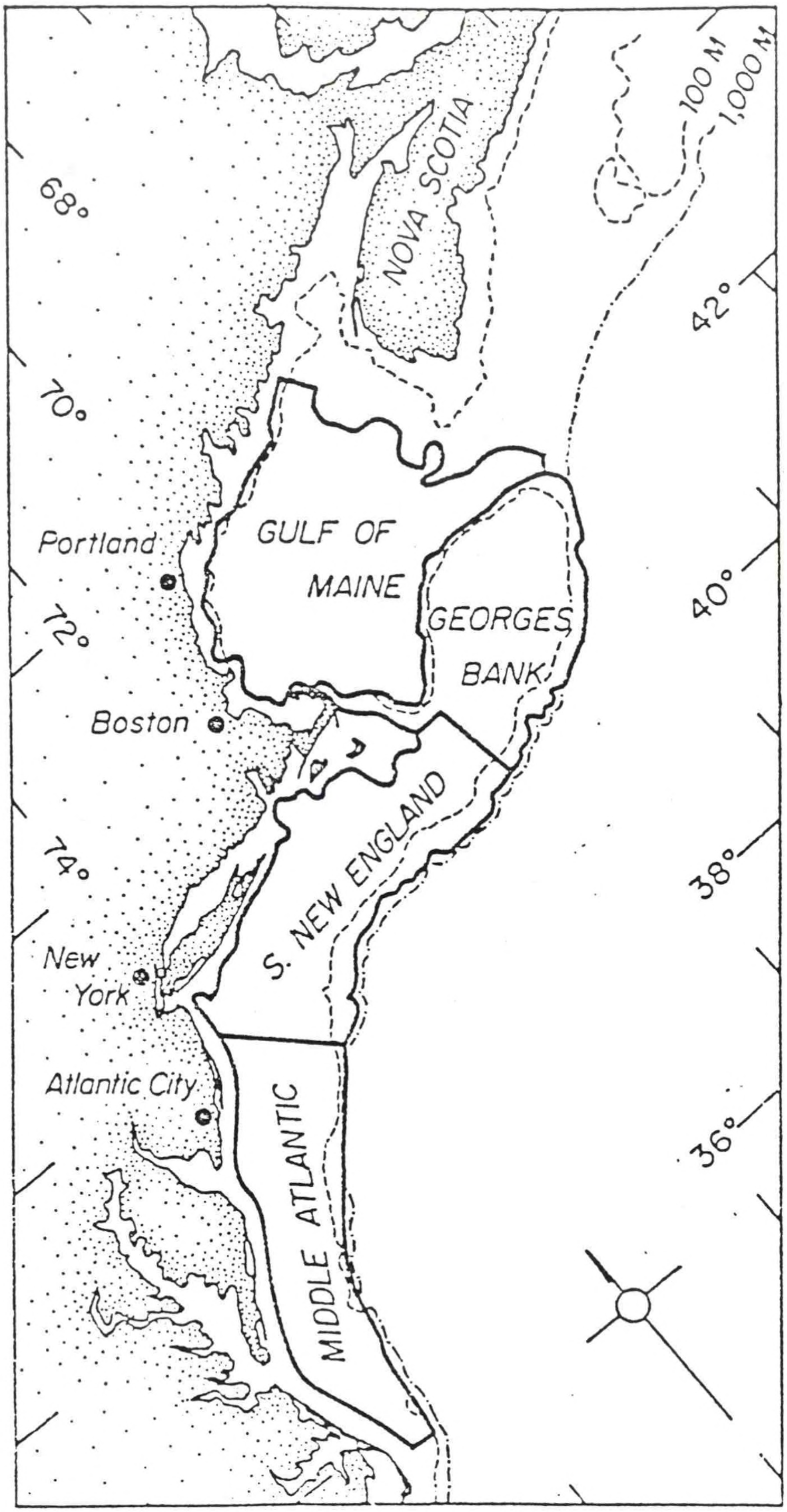

100 M
1,000 M
NOVA SCOTIA
68°
70°
72°
74°
42°
40°
38°
36°
Portland
Boston
New York
Atlantic City
GULF OF MAINE
GEORGES BANK
S. NEW ENGLAND
MIDDLE ATLANTIC

Figure 4a. The four geographic areas of the Northwest Atlantic surveyed from 1971 through 1977 during MARMAP operations of the Northeast Fisheries Center, Woods Hole, Massachusetts.

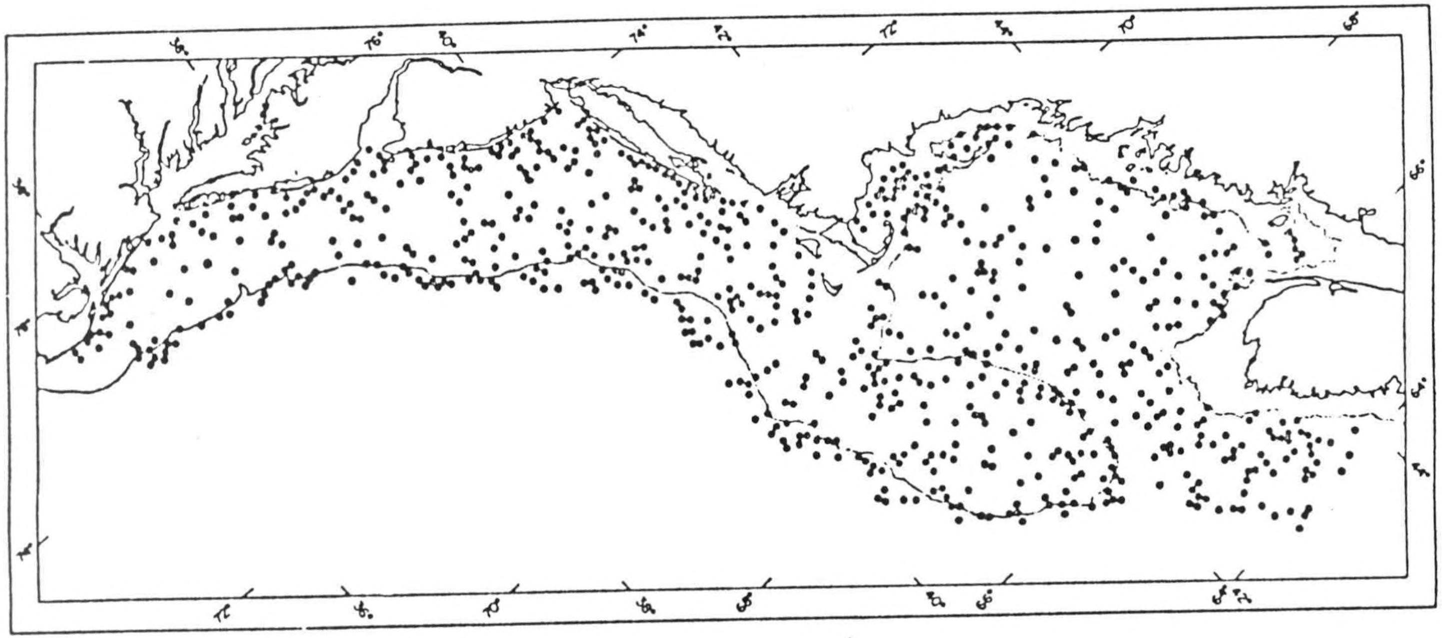
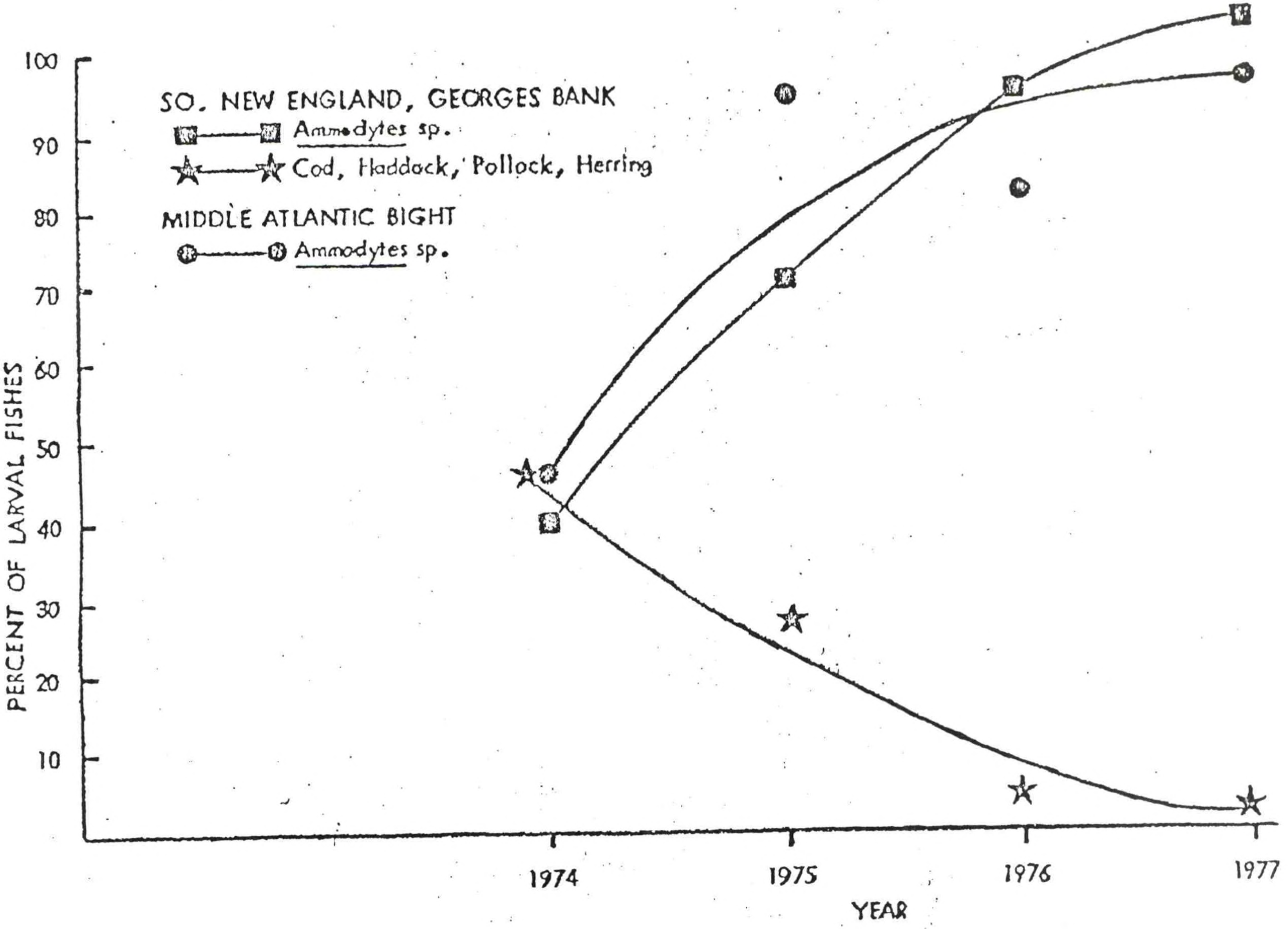


Figure 4b. MARMAP station locations sampled six times a year for ichthyoplankton, zooplankton, primary productivity, chlorophyll, nutrients, and hydrography.



100
90
80
70
60
50
40
30
20
10
PERCENT OF LARVAL FISHES
SO. NEW ENGLAND, GEORGES BANK
Ammodytes sp.
Cod, Haddock, Pollock, Herring
MIDDLE ATLANTIC BIGHT
Ammodytes sp.
1974
1975
1976
1977
YEAR

Figure 5. Changes in the percentage composition of <u>Ammodytes</u> spp. larvae in the Georges Bank Southern New England, and Mid-Atlantic Bight sub areas of the coastal ecosystem 1974-1977. Changes in the percentage composition are also given for cod, haddock, pollock, and herring for the Southern New England and Georges Bank sub areas. From Smith et al. (1978).

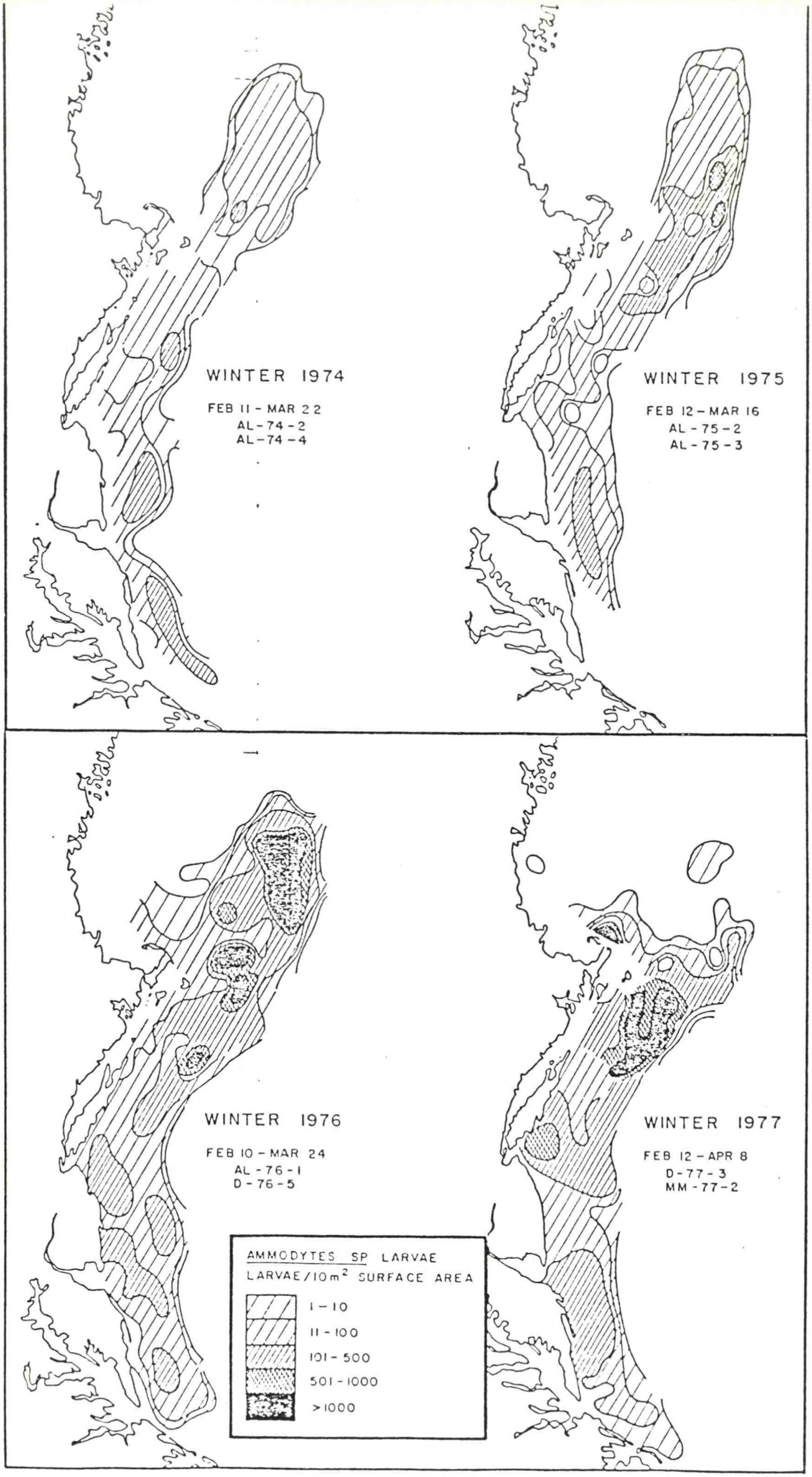

WINTER 1974
FEB 11 - MAR 22
AL-74-2
AL-74-4
WINTER 1975
FEB 12 - MAR 16
AL-75-2
AL-75-3
WINTER 1976
FEB 10 - MAR 24
AL-76-1
D-76-5
WINTER 1977
FEB 12 - APR 8
D-77-3
MM-77-2
AMMODYTES SP LARVAE
LARVAE/10m² SURFACE AREA
1 - 10
11 - 100
101 - 500
501 - 1000
>1000

Figure 6. Changes in the abundance of _Ammodytes_ spp. larvae in early spring in the MARMAP sampling area off the northeast U. S. coast 1974-1977. From Smith et al. (1978).

a

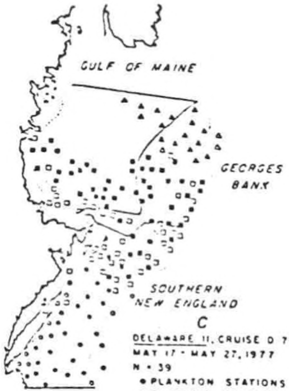
GOERLITZ, CRUISE 77-01
MAR 3 - APR 7, 1977
N = 106
● PLANKTON STATIONS
● PLANKTON SAMPLES ANALYSED

DELAWARE II, CRUISE D 77-03
MAR 19 - APR 8, 1977
N = 18
□ PLANKTON STATIONS
■ PLANKTON SAMPLES ANALYSED

b

ALBATROSS IV, CRUISE 77-02
APR 15 - MAY 20, 1977
N = 100
● PLANKTON STATIONS
● PLANKTON SAMPLES ANALYSED

DELAWARE II, CRUISE D, 77-05
MAY 3 - MAY 15, 1977
N = 34
□ PLANKTON STATIONS
■ PLANKTON SAMPLES ANALYSED

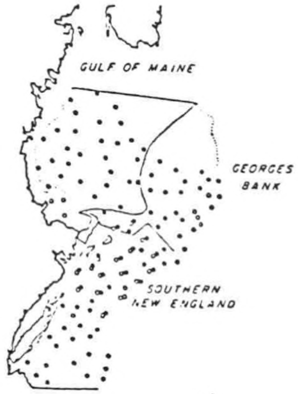


c

DELAWARE II, CRUISE D 77-05
MAY 17 - MAY 27, 1977
N = 39
● PLANKTON STATIONS
● PLANKTON SAMPLES ANALYSED

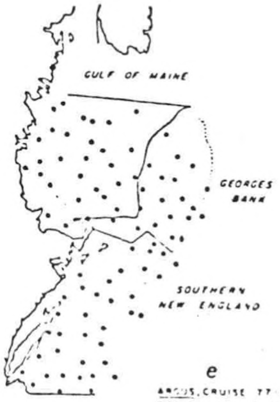
NOGLIKI, CRUISE 77-02
MAY 22 - JUNE 6, 1977
N = 93
□ PLANKTON STATIONS
■ PLANKTON SAMPLES ANALYSED

DELAWARE II, CRUISE 77-07
PART I JUNE 9 - JUNE 17, 1977
N = 19
△ PLANKTON STATIONS
▲ PLANKTON SAMPLES ANALYSED



d

YUBILEINIY, CRUISE 77-02
JULY 30 - SEPT 3, 1977
N = 122
● PLANKTON STATIONS
● PLANKTON SAMPLES ANALYSED



e

ARGUS, CRUISE 77-01
OCT 18 - NOV 12, 1977
N = 87
● PLANKTON STATIONS
● PLANKTON SAMPLES ANALYSED

f

KELEZ, CRUISE 77-11, 77-12
NOV 25 - DEC 13, 1977
N = 53
● PLANKTON STATIONS
● PLANKTON SAMPLES ANALYSED

MOUNT MITCHELL, CRUISE 77-11
NOV 2 - NOV 19, 1977
N = 30
□ PLANKTON STATIONS
■ PLANKTON SAMPLES ANALYSED

Figure 7. Sampling locations during the 1977 MARMAP surveys of the Gulf of Maine, Georges Bank, and Southern New England waters: (a) early spring; (b) mid-spring; (c) late spring; (d) summer; (e) mid-autumn; (f) late autumn.

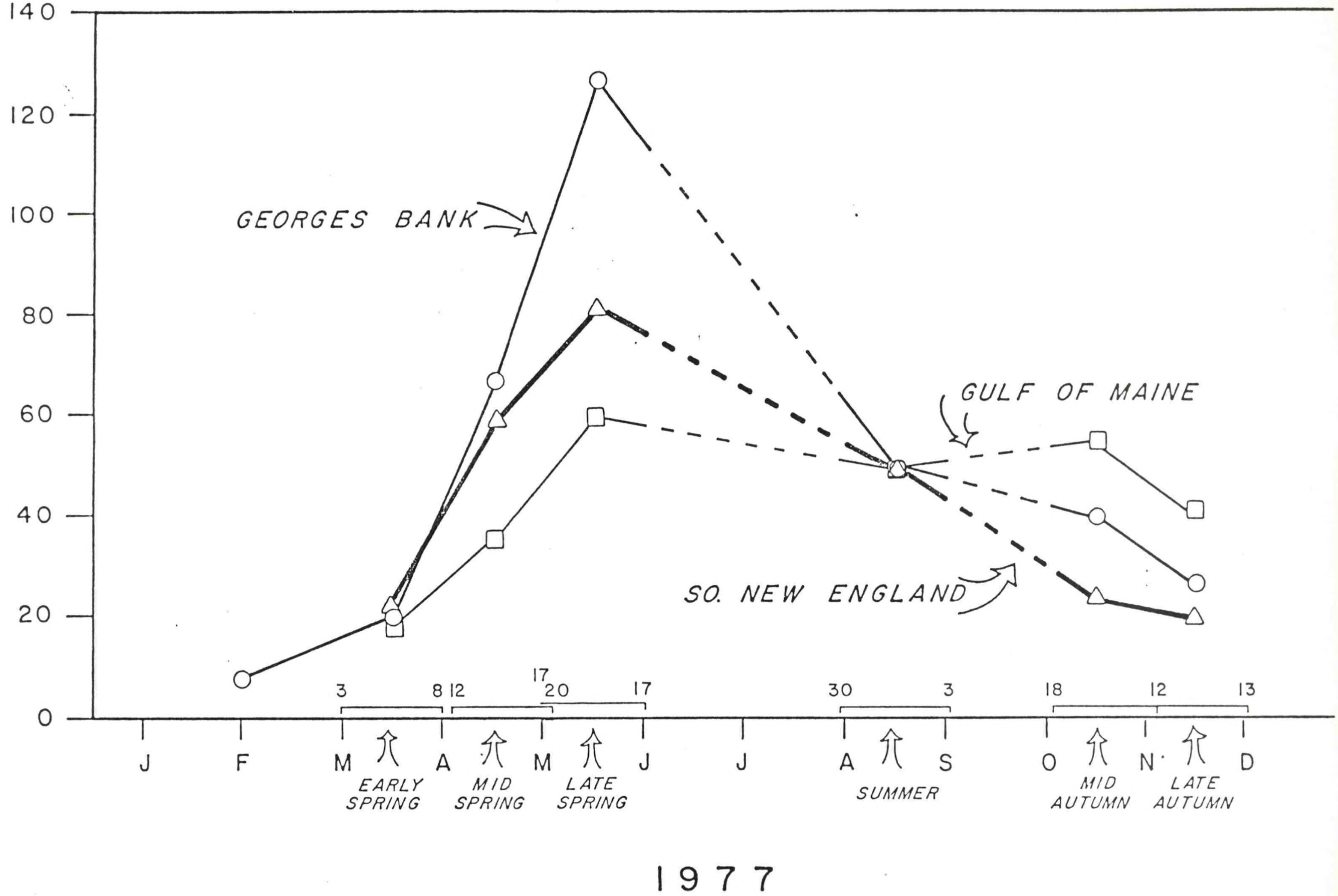
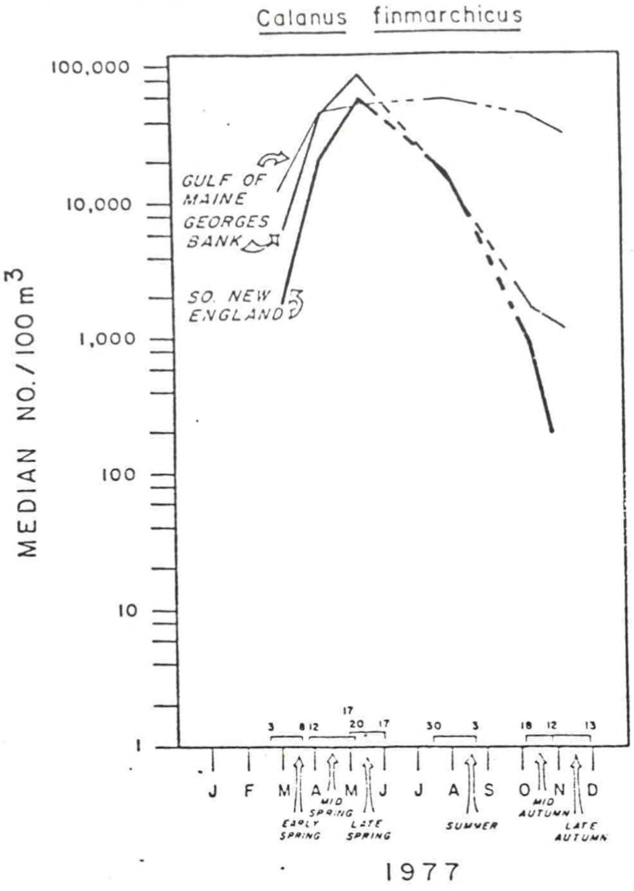
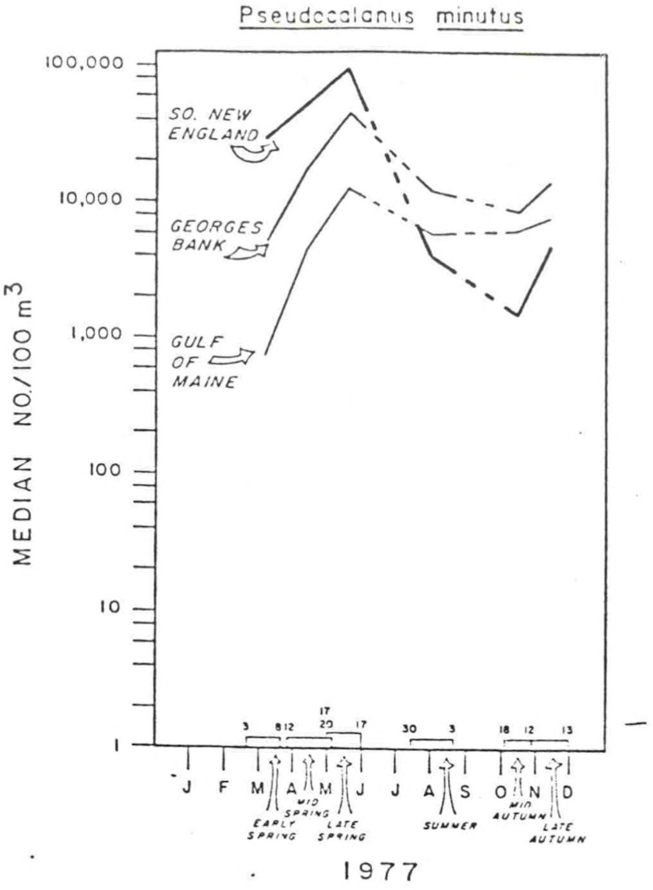

140
120
100
80
60
40
20
0
GEORGES BANK
GULF OF MAINE
SO. NEW ENGLAND
3
8
12
17
20
17
30
3
18
12
13
J
F
M
A
M
J
J
A
S
O
N
D
EARLY SPRING
MID SPRING
LATE SPRING
SUMMER
MID AUTUMN
LATE AUTUMN
1977

Figure 8. Changes in median zooplankton volumes in the Gulf of Maine, Georges Bank, and Southern New England, March-December, 1977; time periods covered during each of the six surveys are bracketed; mid-points of the survey periods are shown by arrows; dashed lines represent interpolated values for inter-survey periods.


Calanus finmarchicus
100,000
10,000
1,000
100
10
1
MEDIAN NO./100 m3
GULF OF MAINE
GEORGES BANK
SO. NEW ENGLAND
3 8 12 17 20 17 30 3 18 12 13
J F M A M J J A S O N D
EARLY SPRING
MID SPRING
LATE SPRING
SUMMER
MID AUTUMN
LATE AUTUMN
1977


Pseudocalanus minutus
100,000
10,000
1,000
100
10
1
MEDIAN NO./100 m3
SO. NEW ENGLAND
GEORGES BANK
GULF OF MAINE
3 8 12 17 20 17 30 3 18 12 13
J F M A M J J A S O N D
EARLY SPRING
MID SPRING
LATE SPRING
SUMMER
MID AUTUMN
LATE AUTUMN
1977

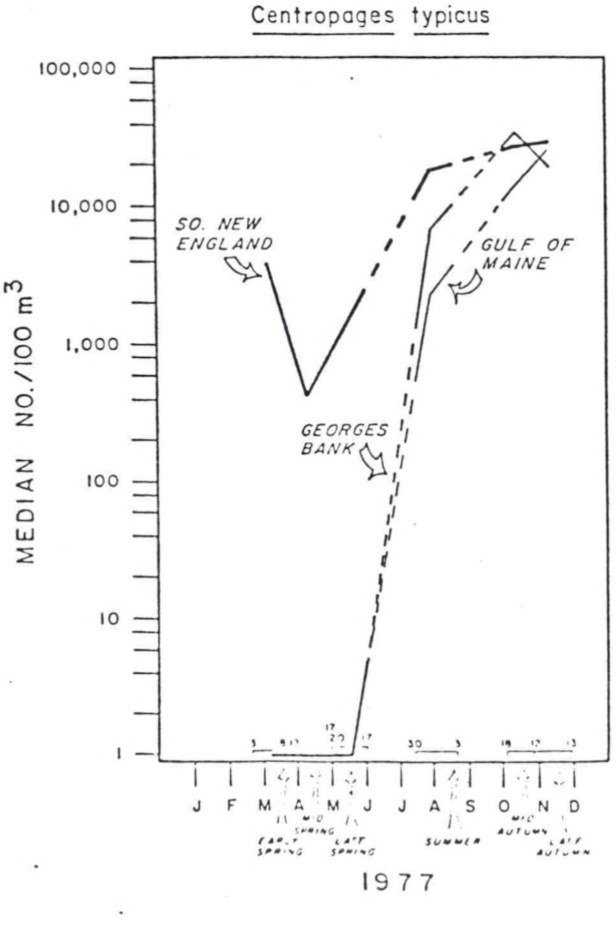
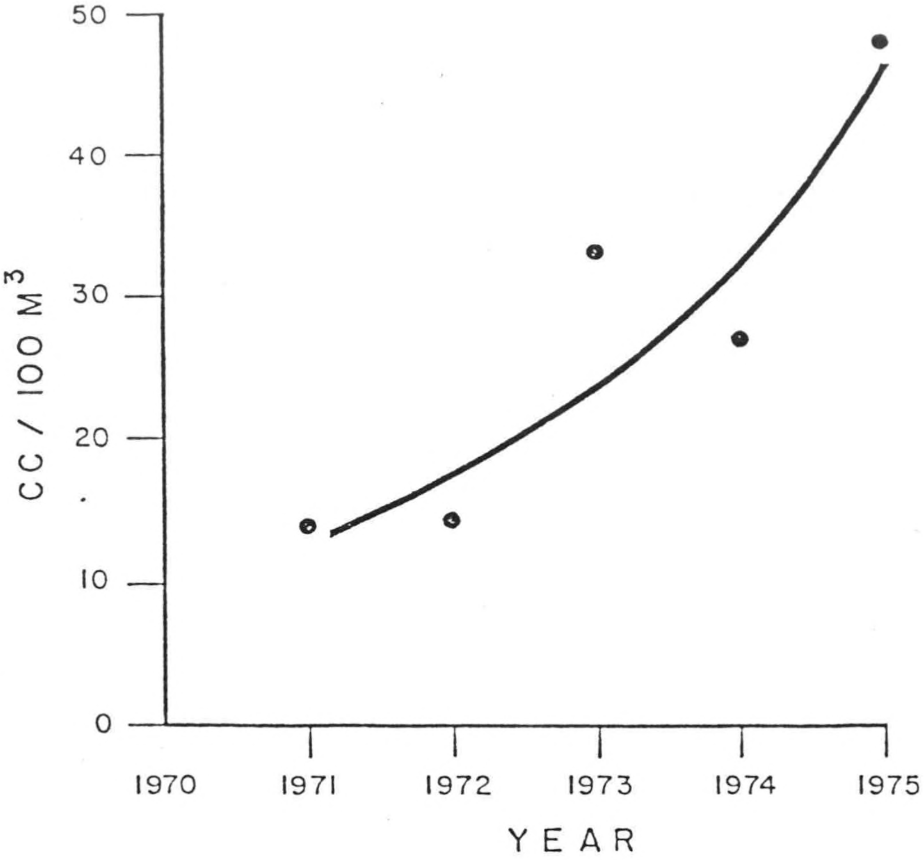

Centropages typicus
100,000
10,000
1,000
100
10
1
MEDIAN NO./100 m3
SO. NEW ENGLAND
GULF OF MAINE
GEORGES BANK
3 8 12 17 20 17 30 3 18 12 13
J F M A M J J A S O N D
EARLY SPRING
MID SPRING
LATE SPRING
SUMMER
MID AUTUMN
LATE AUTUMN
1977

Figure 9. Median seasonal abundance levels for the three dominant copepod species in Gulf of Maine, Georges Bank, and Southern New England waters: (a) *Calanus finmarchicus*; (b) *Pseudocalanus minutus*; (c) *Centropages typicus*. Time-periods covered by each of the survey periods are in brackets. Dashed lines represent interpolated values for inter-survey periods.



50
40
30
20
10
0
CC / 100 M^3
1970
1971
1972
1973
1974
1975
YEAR

Figure 10. Median zooplankton volumes, spring, Georges Bank, 1971-1975.

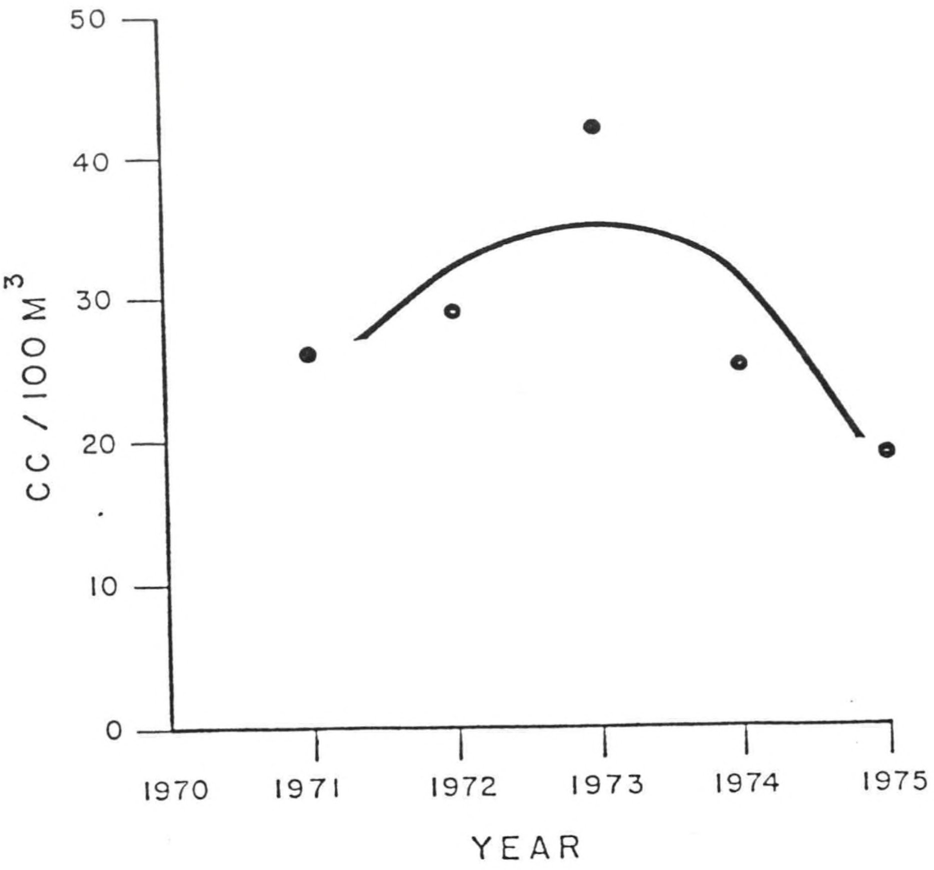

50
40
30
20
10
0
CC / 100 M^3
1970
1971
1972
1973
1974
1975
YEAR

Figure 11. Median zooplankton volumes, autumn, Georges Bank, 1971-1975.

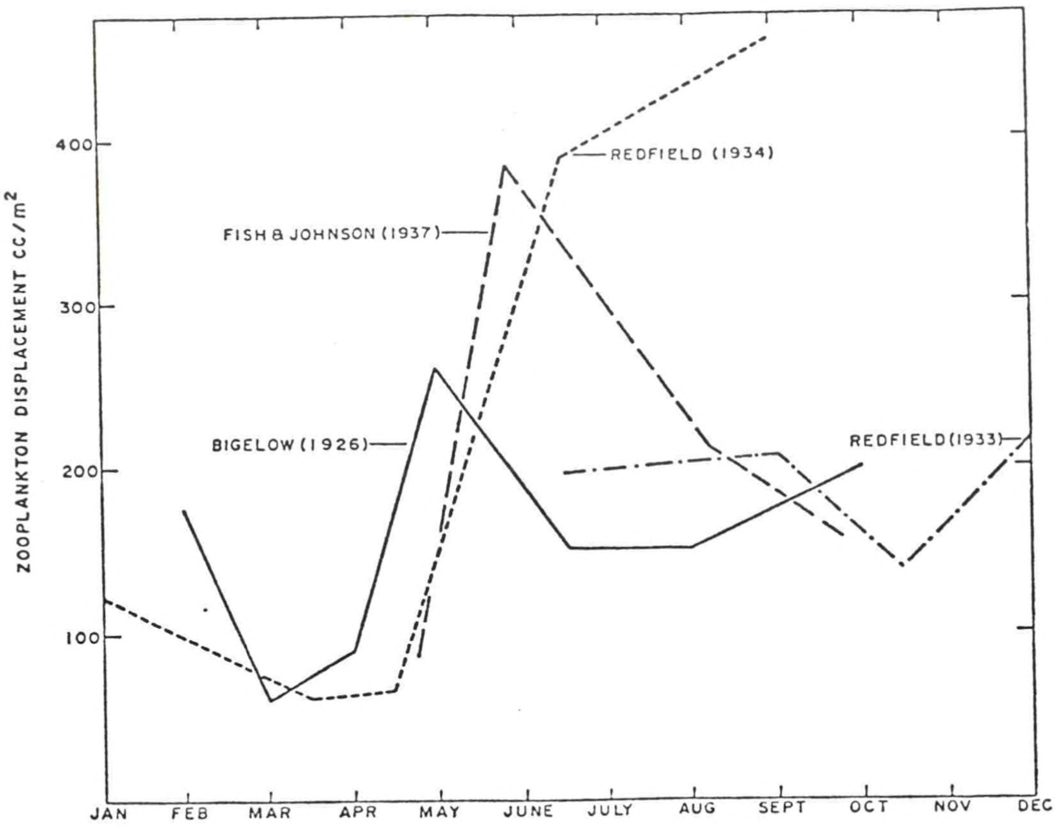

ZOOPLANKTON DISPLACEMENT cc/m²
400
300
200
100
JAN
FEB
MAR
APR
MAY
JUNE
JULY
AUG
SEPT
OCT
NOV
DEC
REDFIELD (1934)
FISH & JOHNSON (1937)
BIGELOW (1926)
REDFIELD (1933)

Figure 12. Seasonal changes in zooplankton displacement volume in the Gulf of Maine, Georges Bank area. From Cohen (1976).

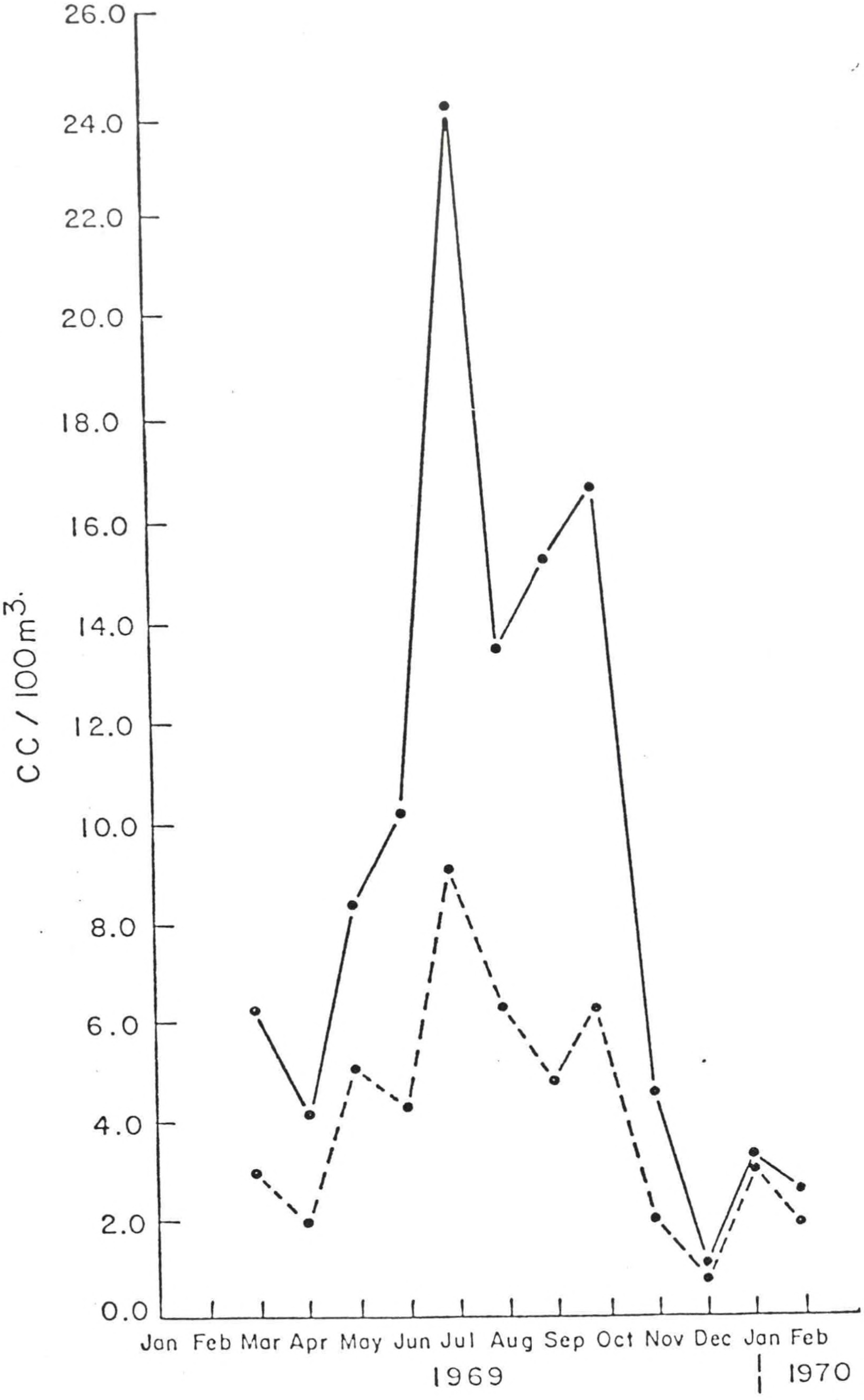
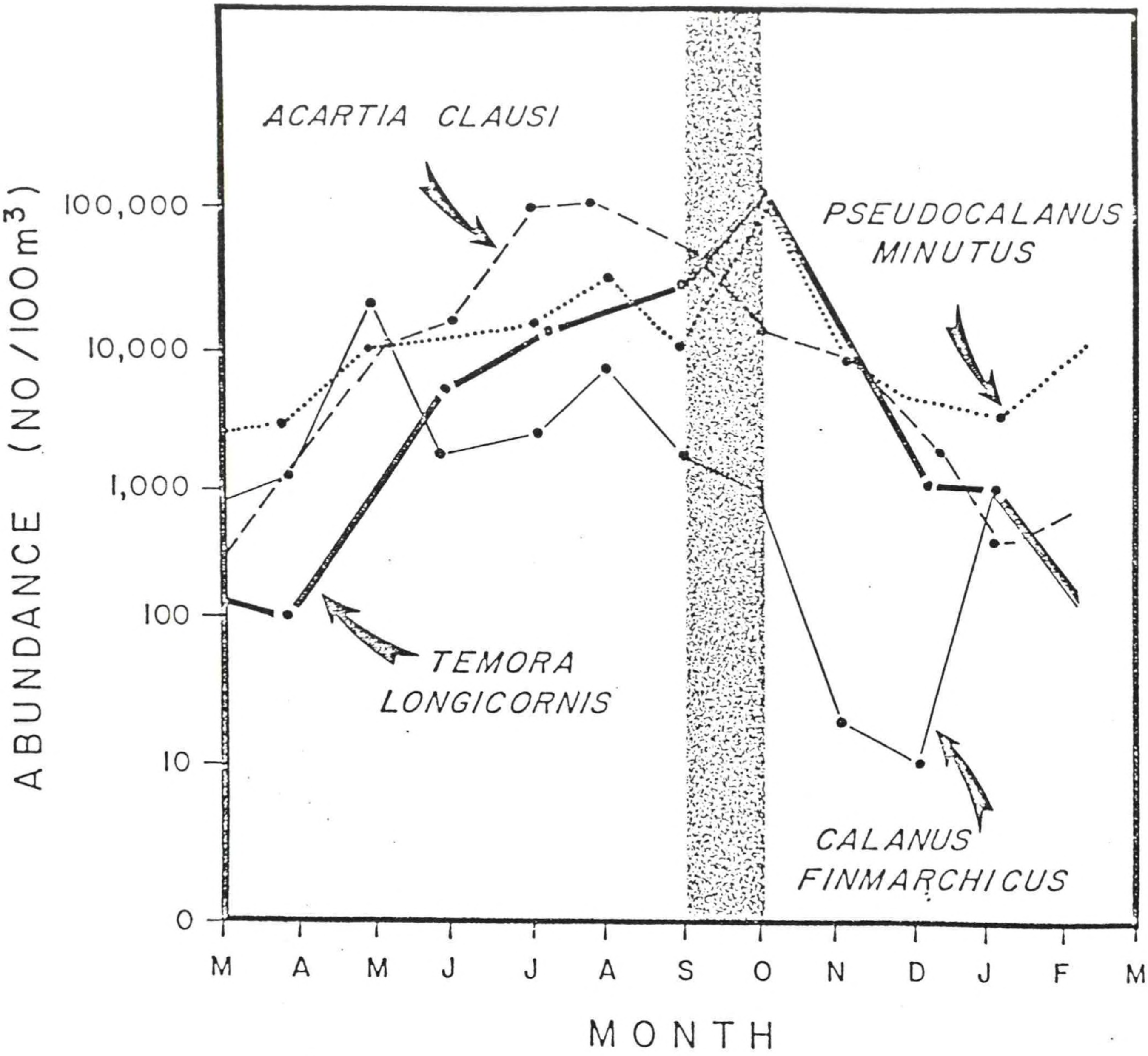
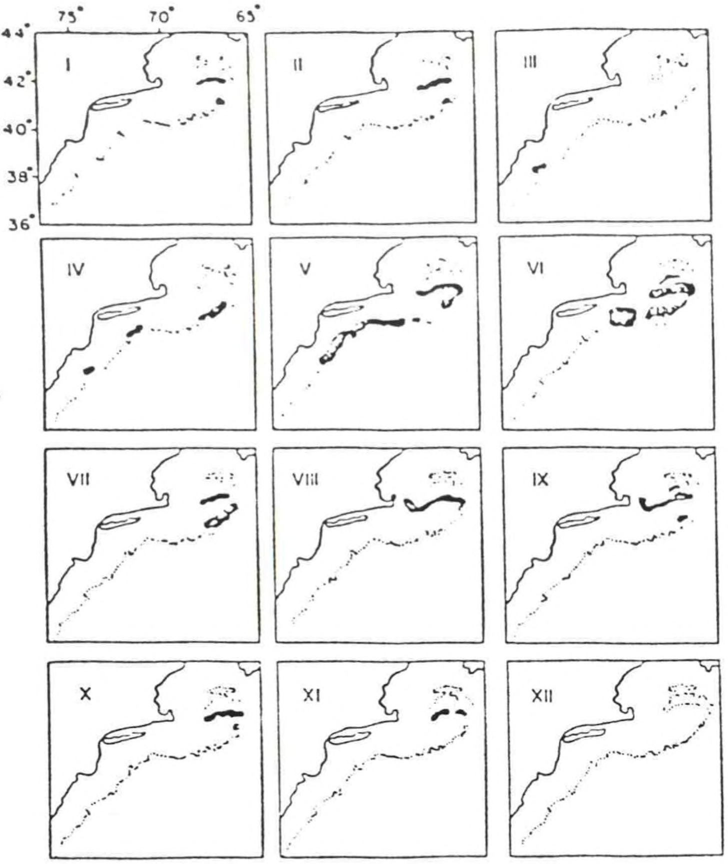

26.0
24.0
22.0
20.0
18.0
16.0
14.0
12.0
10.0
8.0
6.0
4.0
2.0
0.0
CC / 100m³.
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Jan
Feb
1969
1970

Figure 13. Monthly changes in zooplankton biomass in coastal waters of central Maine. Solid line depicts volumes of the 0.253-mm mesh bongo net; dashed-line is for the 0.366-mm mesh net. From Sherman et al. (1976).

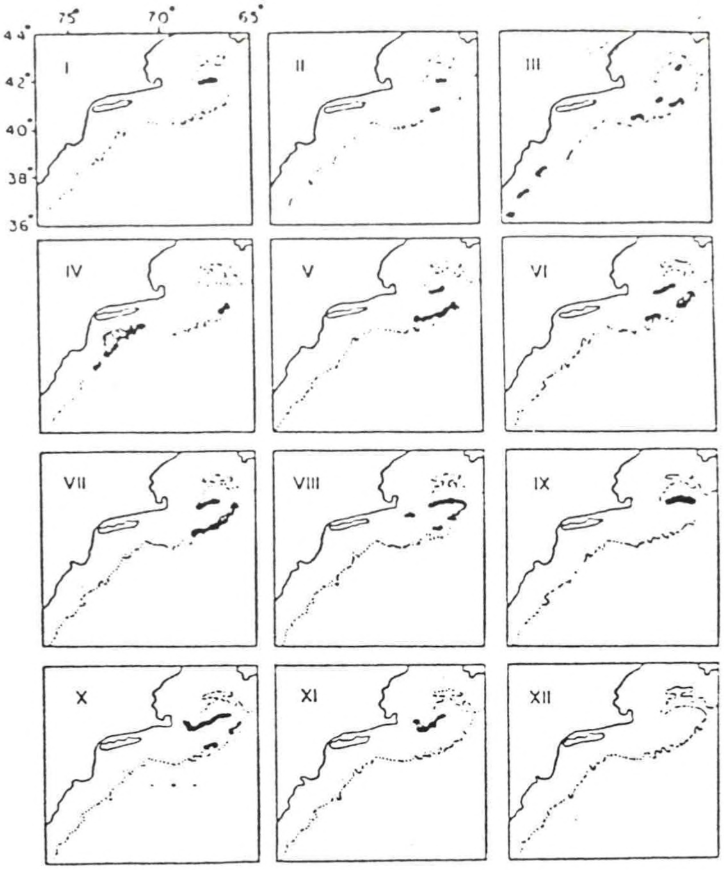


ACARTIA CLAUSI
PSEUDOCALANUS MINUTUS
TEMORA LONGICORNIS
CALANUS FINMARCHICUS
ABUNDANCE (NO/100m^3)
100,000
10,000
1,000
100
10
0
M
A
M
J
J
A
S
O
N
D
J
F
M
MONTH

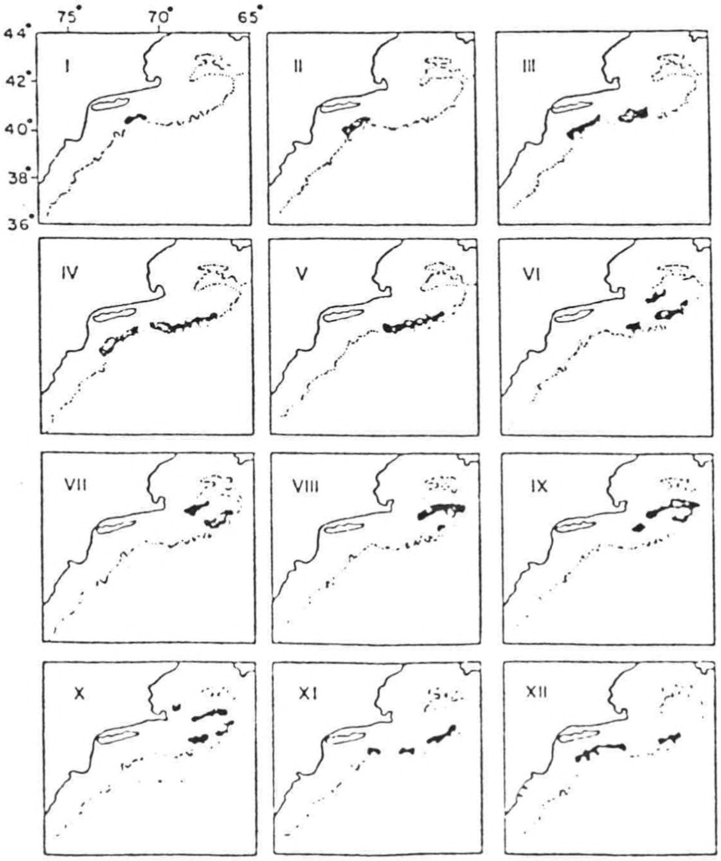
Figure 14. Monthly changes in the abundance of the dominant copepod species in coastal waters of central Maine, October 1968 through February 1970. The shaded area depicts the peak spawning period of herring along the coast of the Gulf of Maine. From Sherman et al. (1976).



1963

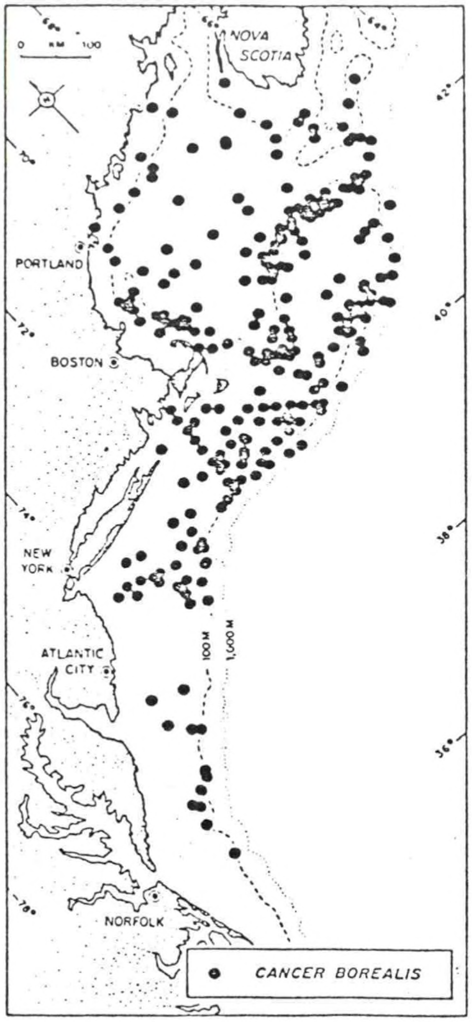


1964



1965

Figure 15. Annual recurring patterns of herring distributions in waters of Georges Bank and the Mid-Atlantic Bight. From Zinkevitch (1967).


0 KM 100
NOVA SCOTIA
PORTLAND
BOSTON
NEW YORK
ATLANTIC CITY
NORFOLK
100 M
1,000 M
42°
40°
38°
36°
72°
74°
76°
78°
● CANCER BOREALIS

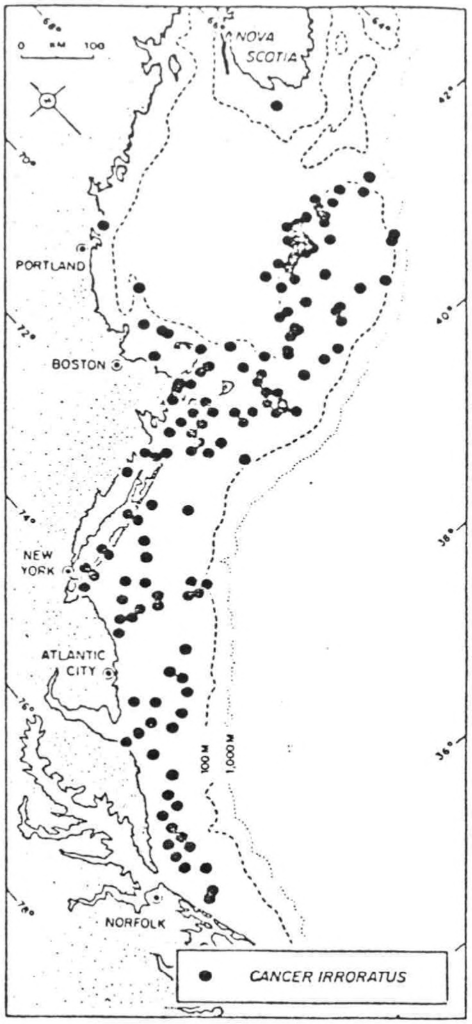
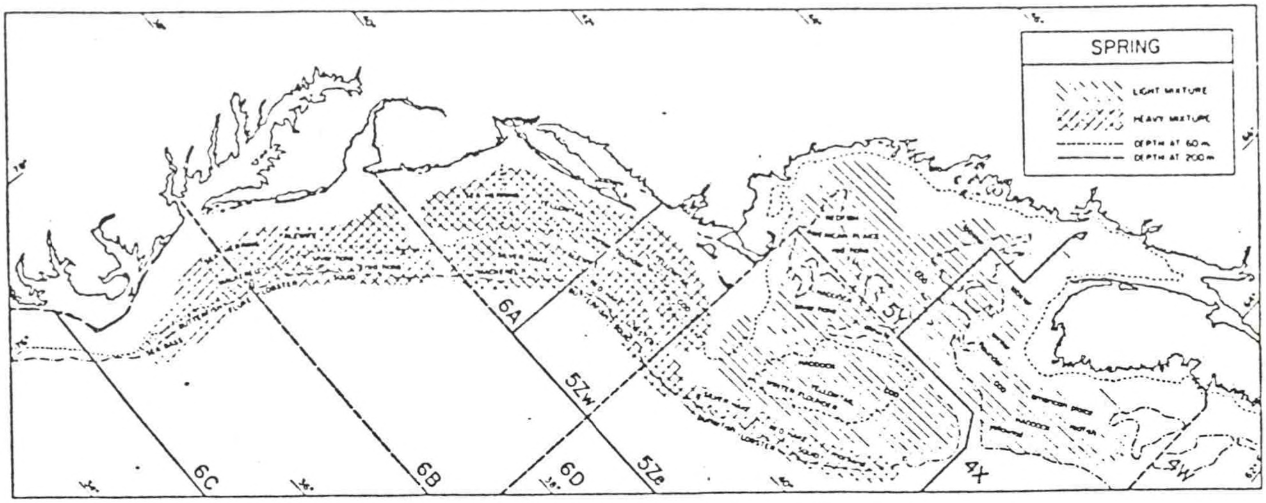

0 KM 100
NOVA SCOTIA
PORTLAND
BOSTON
NEW YORK
ATLANTIC CITY
NORFOLK
100 M
1,000 M
42°
40°
38°
36°
72°
74°
76°
78°
● CANCER IRRORATUS

Figure 16. Examples of distributions of macrobenthos, *Cancer borealis* and *C. irroratus* from the MARMAP sampling area off the northeast coast of the U. S. From Williams and Wigley (1977).


SPRING
LIGHT MIXTURE
HEAVY MIXTURE
DEPTH AT 60 m
DEPTH AT 200 m
6C
6B
6D
6A
5Zw
5Ze
5Y
4X
4W

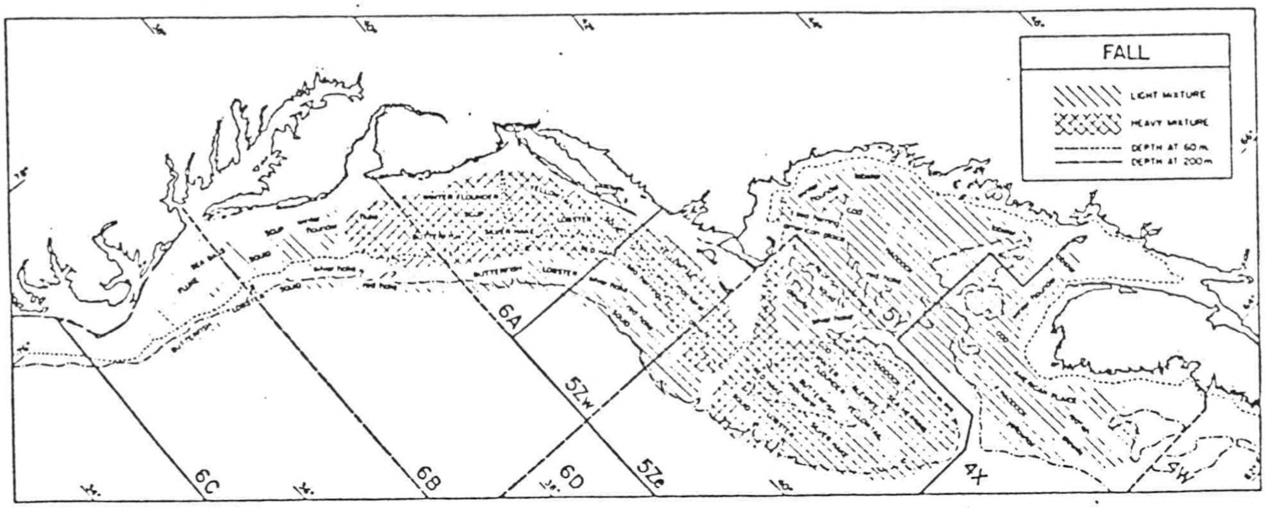
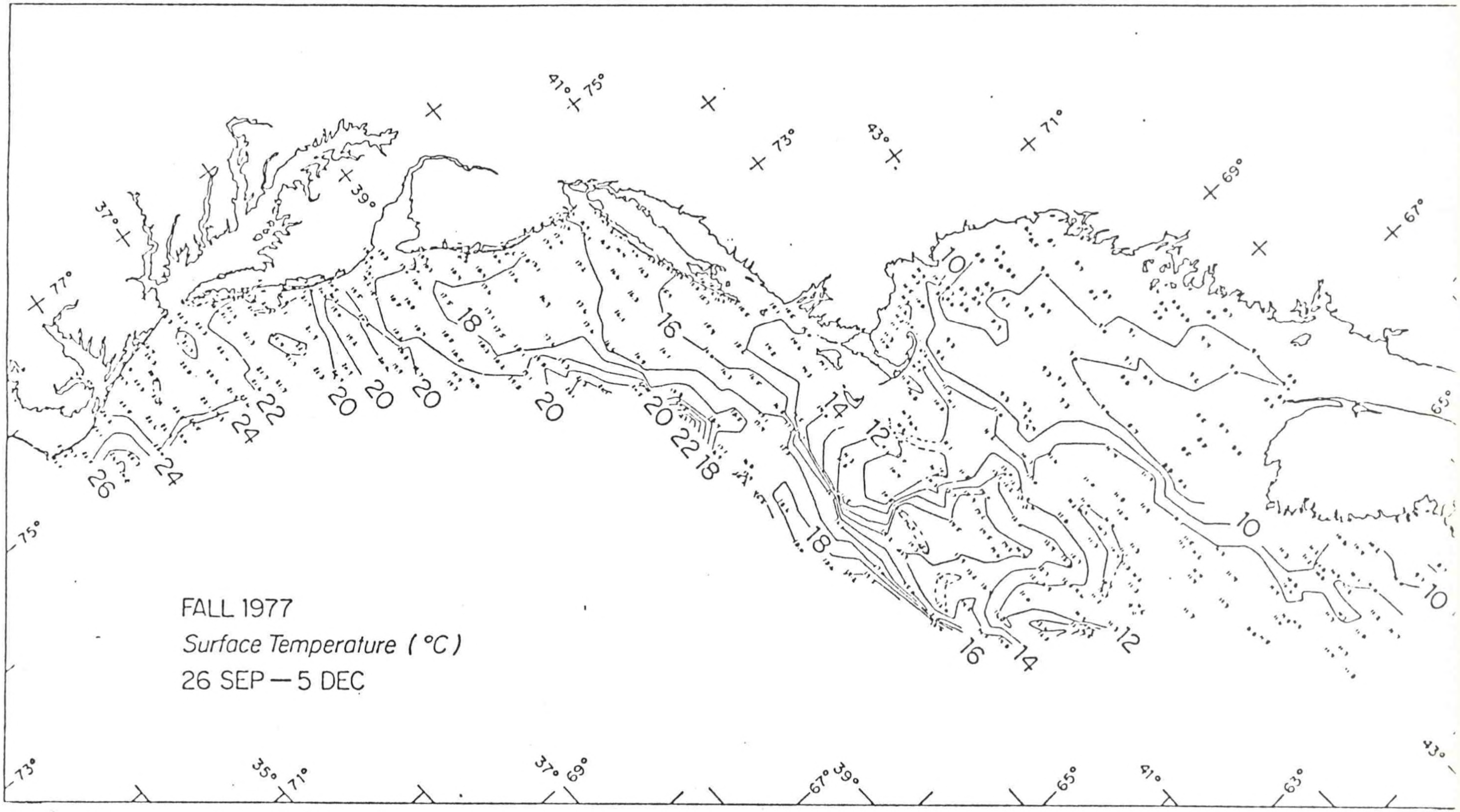

FALL
LIGHT MIXTURE
HEAVY MIXTURE
DEPTH AT 60 m
DEPTH AT 200 m
6C
6B
6D
6A
5Zw
5Ze
5Y
4X
4W

Figure 17. Generalized pattern of species mixture of fish in the MARMAP sampling area off the northeast U. S. From Grosslein and Bowman (1973).



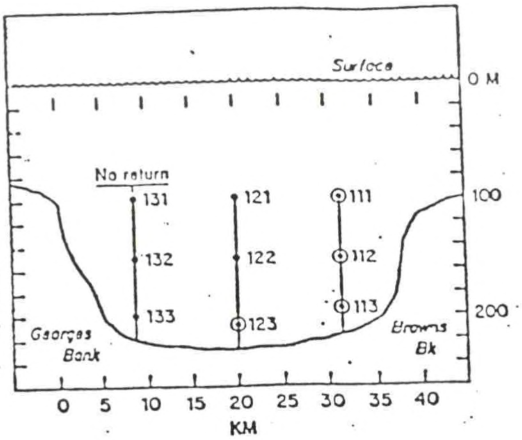
FALL 1977

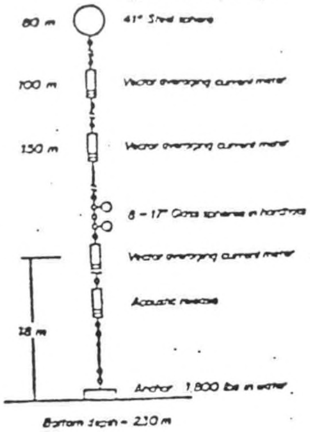
Surface Temperature (°C)

26 SEP — 5 DEC

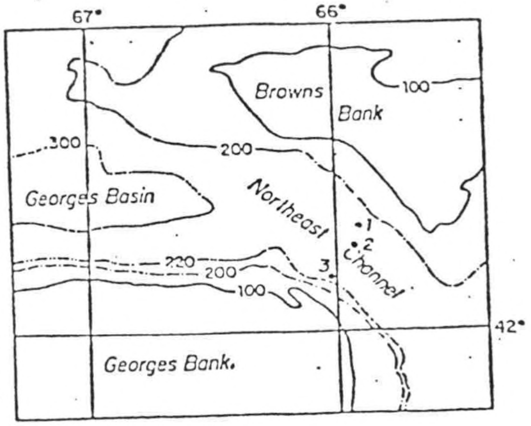
Figure 18. An example of the surface salinity and temperature charts prepared from the observations made on the MARMAP bottom surveys, Fall 1977. From Pawlowski et al. (1978).

Approximate
Positions
NORTHEAST
CHANNEL




NORTHEAST CHANNEL
ARRAY
Typical Mooring Design

Bathymetry
and
Mooring Positions
NORTHEAST
CHANNEL



7-month
Mean Currents
in the
NORTHEAST
CHANNEL

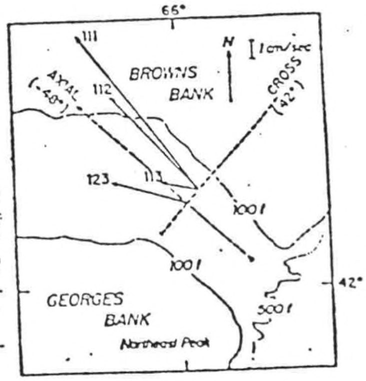


Figure 19. MARMAP bottom current monitoring experiment in the northeast channel of the Gulf of Maine. Lower left depicts general area of the experiment; upper right shows the typical current meter array; upper left shows the approximate positions of the array in the water column, and lower right indicates the mean directional flow and relative velocity of the currents, the numbers represent the current meter positions with respect to depth.

ESTIMATED PRODUCTION OF FISH BIOMASS MT / Km^2 / YR

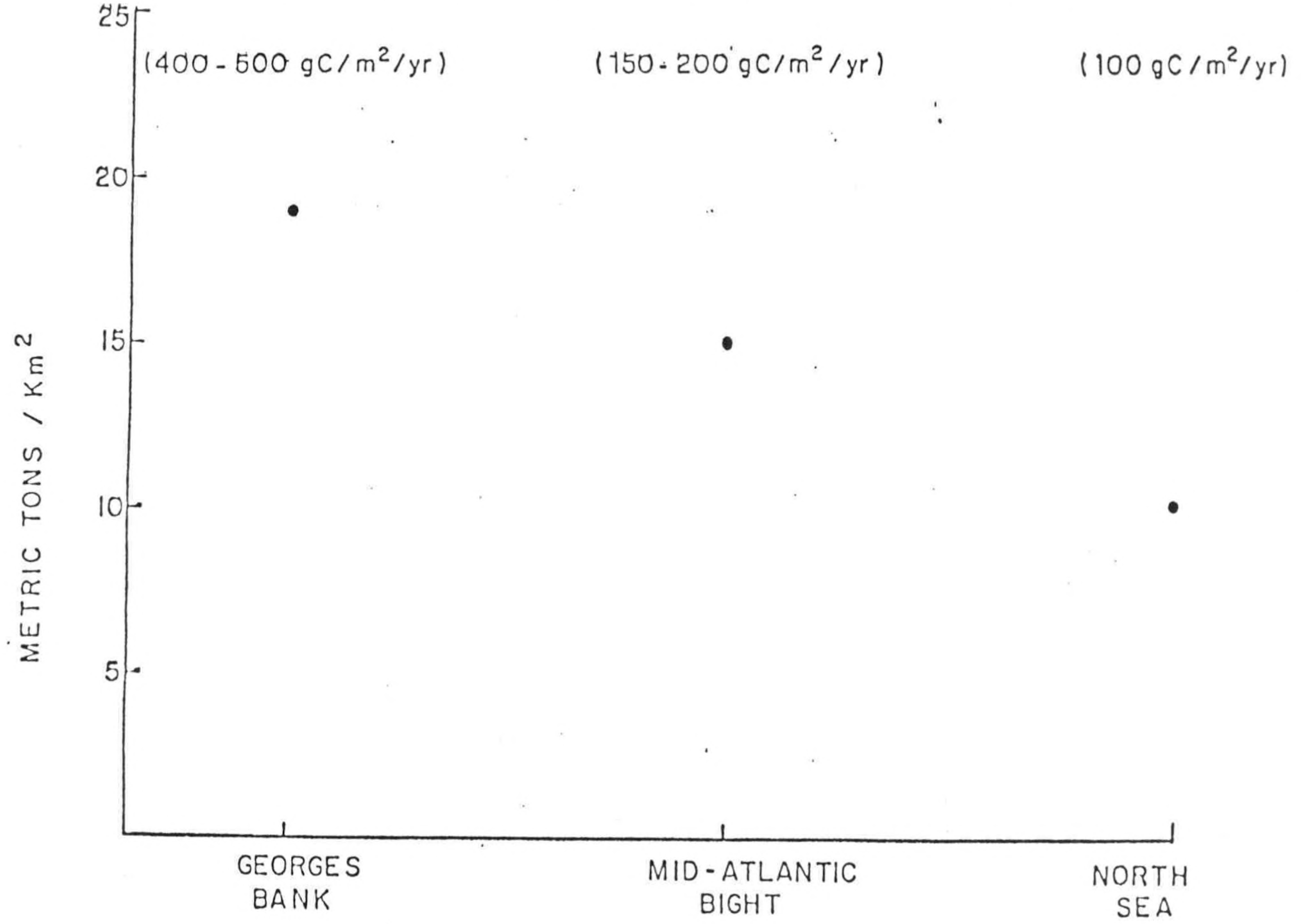
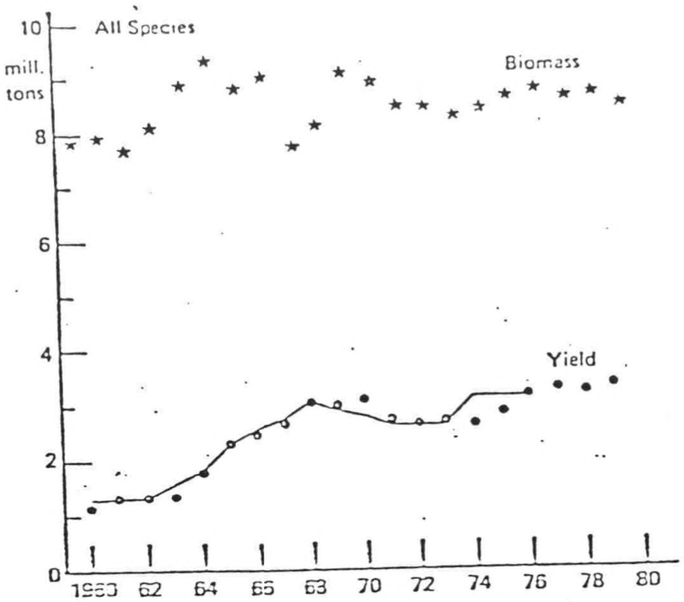
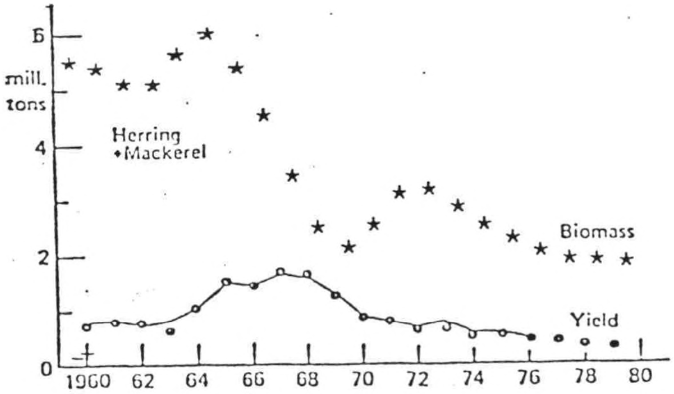


Figure 20. Estimated annual primary production of three areas--Georges Bank, Mid Atlantic Bight, and the North Sea--compared against estimated production of fish biomass.


All Species
mill. tons
Biomass
Yield
10
8
6
4
2
0
1960
62
64
66
68
70
72
74
76
78
80


mill. tons
Herring
+Mackerel
Biomass
Yield
6
4
2
0
1960
62
64
66
68
70
72
74
76
78
80

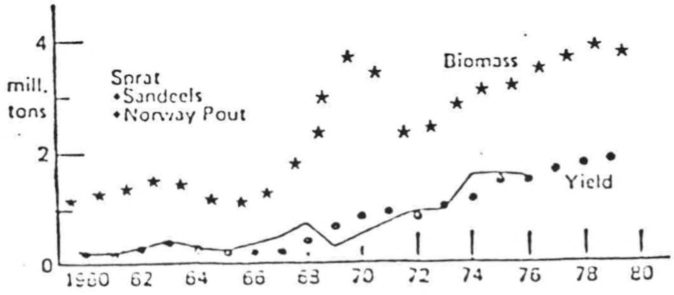

mill. tons
Sprat
+Sandeels
+Norway Pout
Biomass
Yield
4
2
0
1960
62
64
66
68
70
72
74
76
78
80

Figure 21. Estimated changes in the biomass of fishes in the North Sea 1960-1976 with model simulated projection to 1980. From Ursin (1977).

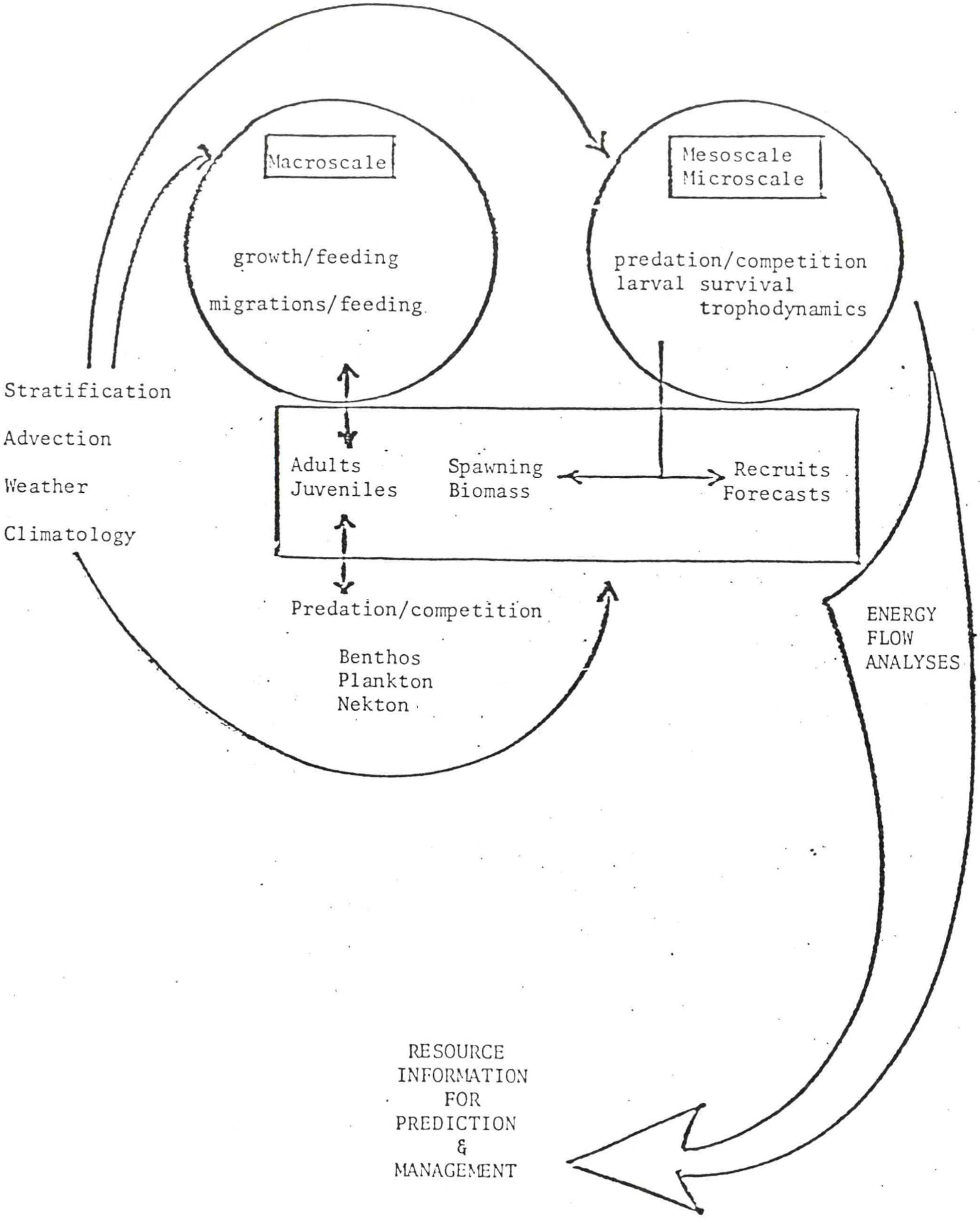

Macroscale
growth/feeding
migrations/feeding
Mesoscale
Microscale
predation/competition
larval survival
trophodynamics
Stratification
Advection
Weather
Climatology
Adults
Juveniles
Spawning
Biomass
Recruits
Forecasts
Predation/competition
Benthos
Plankton
Nekton
ENERGY
FLOW
ANALYSES
RESOURCE
INFORMATION
FOR
PREDICTION
&
MANAGEMENT

Figure 22. Schematic outline of the principal focus of the MARMAP ecosystem study of the Northeast Fisheries Center. The rectangle depicts the interactions under investigation to obtain a better understanding of the relationship between the size of a spawning biomass of fish and subsequent year-class recruitment. Studies are underway on the larval, juvenile, and adult fishes within the context of measuring energy flow through the system, and the effects of fishing, pollution and environmental changes on the flow. Macroscale surveys are made up to 6x/yr to monitor changes of fish, plankton, and hydrography. Mesoscale surveys are conducted from the onset of larval hatching up to juvenile development on target species. Herring has been the target species since 1971 in studies of recruitment processes off the northeast coast. Microscale studies of larval herring growth and predator-prey studies are planned for 1979.