Status Report on

Production Studies at the Northeast Fisheries Center

by

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INTRODUCTION

A major long-term objective of the Northeast Fisheries Center (NEFC) is to develop models which will: (1) predict natural fluctuations in fish and shellfish populations more than a year or two in advance, and (2) predict effects of various management strategies on community stability, species composition and production (including the effects of pollution). We are convinced that if such models are to yield real predictive capability they must ultimately include specific knowledge of the factors which actually control the critical life processes of reproduction, growth, and survival of organisms. In order to acquire such knowledge, field and laboratory studies must be designed to test hypotheses about controlling mechanisms. The enormous scale and complexity of the marine ecosystem precludes ever obtaining detailed information on controlling mechanisms for all the species and processes in the system. In fact, the ecosystem is so complex that for the foreseeable future it will be necessary to monitor the system continuously to learn how it varies in the large-scale holistic sense, at the same time we are conducting smaller scale studies to test hypotheses on the dynamics of its various components. Results of modeling studies must be compared with empirical observations on the behavior of the system for a long period of time in order to establish confidence.

Our basic research strategy may be described in terms of three phases corresponding to three time-space scales of events; namely macro-, meso-, and microscale. All three are essential to development of quantitative models.

In the area of field studies the macroscale is represented by the MARMAP program which monitors the large-scale annual and seasonal variations (2 to 6 times a year) in the distribution, standing crop, and population structure, of principal biological communities (phytoplankton, zooplankton, fish, benthos) from Cape Hatteras to Nova Scotia. The ICNAF larval herring program is an example of a mesoscale study. It provides monthly surveys of the Georges Bank and Nantucket Shoals area from September through February to monitor production (in numbers), growth, feeding, dispersal, and survival of sea herring larvae. The microscale is represented by a 4-week multi-ship study of a single patch of herring larvae and associated zooplankton on Georges Bank, scheduled for October 1978. Sampling will be sufficiently intensive to monitor horizontal and vertical movements, patchiness of plankton and feeding of larvae on a scale of meters and hours. Growth, survival, and dispersal of larvae in relation to circulation will be measured on a scale of days and kilometers. Such a study is necessary, for example, to test hypotheses about

the role of zooplankton abundance and micro-distribution on larval feeding and survival, and the role of circulation in dispersal of larvae around (and off) Georges Bank. The laboratory studies by Laurence on energetics and feeding behavior of larval fish are also microscale and are of critical importance to our development and testing of hypotheses and models linking larval fish survival to zooplankton dynamics. We also believe it will be necessary to conduct partially controlled in situ experiments at sea ("Big-Bag") to clarify some aspects of larval fish dynamics in a more natural environment. Other laboratory studies by Laurence and investigators elsewhere in the Center are looking at the physiology, genetics, and behavior of selected fish species under both (environmentally) stressed and unstressed conditions.

In the area of modeling we are, in a sense, also taking approaches varying from the macro- to microscale, and, as for the field studies, we feel that all three are necessary. First, we have constructed a preliminary static equilibrium energy budget for Georges Bank using available data to estimate production and biomass of biological components; this is macroscale in the sense that we are dealing strictly in terms of production-biomass ratios (P/B) of entire trophic levels or communities and we are attempting to estimate long-term mean values, on an annual (as opposed to a seasonal or shorter term) basis. The second step will be to construct an energy flow model utilizing information on the energetics of representative species and life stages at the individual organism level, relative to the entire life cycle (e.g., larval, juvenile, and adult stages of fish) - i.e., mesoscale. In this case food consumption is partitioned into growth, reproductive products, maintenance metabolism, and waste. Two approaches are being considered: (1) estimating consumption by application of digestion rates to average gut content, and (2) estimating consumption by summing its four components. Particular focus here will be given to modeling food web interactions involving fishes from larvae to adults.

A third stage is to model small parts or components of the system which may involve extremely short spans of time, e.g., first feeding of recently hatched larvae, i.e., microscale.

So far we have completed only a first approximation of the gross static energy budget for Georges Bank. This report outlines the sources of data and circulations for this energy budget which takes account of production of phytoplankton, zooplankton, benthos, and fish. We have compared empirical estimates of biomass and production of phytoplankton and fish with theoretical estimates derived from energy conversion factors reported in the literature. Estimates of zooplankton and benthos biomass have also been treated in this manner. The objective was to examine the conversion efficiencies to see if there were glaring inconsistencies between theoretical and empirical results. We compared Georges Bank to North Sea production in order to see if there are major differences in the level or partitioning of energy between the two areas. In the last section of this report we have briefly outlined our plans for the next stages of modeling the Georges Bank system.

PRIMARY PRODUCTION

Although a great deal of phytoplankton work was done on Georges Bank in the first half of the century some of the results are not quantitative because phytoplankton nets were used and these do not adequately sample the nanoplankton (Ryther and Yentsch, 1959). A more quantitative picture of the production cycle is provided by Riley (1941) but his estimates of primary production were made using the oxygen production technique on surface samples only. He extrapolated a value for the water column from the surface value. After the war there was a lapse in studying the biological oceanography of Georges Bank. It was not until the last few years that sufficient resources became available to the NEFC to begin significant quantitative studies of primary and secondary production on Georges Bank.

Methods

New emphasis was placed on plankton and additional funding became available in the early 1970's through the establishment of the Marine Monitoring, Assessment and Prediction Program (MARMAP) of the National Marine Fisheries Service (NMFS), and particularly in the northeast United States with the organization of the NEFC with headquarters at Woods Hole. About the same time the International Commission for the Northwest Atlantic Fisheries (ICNAF) began an intensive five-nation study of the early life history of sea herring in the Georges Bank-Gulf of Maine region. The major objective of the program was to identify factors controlling the success of herring year classes. The program has concentrated on the first six months of larval life, but has also involved studies of the herring egg beds. Intensive larval surveys have been conducted each autumn and winter since 1971 to measure larval production, dispersal, growth, feeding, and survival (Figure 1). Initially, the surveys consisted only of plankton hauls with bongos and minimum hydrographic observations. It was recognized that understanding dispersal and survival and growth of larvae would require a better knowledge of the physical and biological variables in the Gulf of Maine-Georges Bank region. Thus, beginning in 1975 the sampling area was restricted to the Georges Bank-Nantucket Shoals area (Figure 1) to allow more intensive and comprehensive sampling, including nutrients, chlorophyll and primary production in addition to the usual samples for ichthyoplankton, zooplankton, salinity, temperature, and dissolved oxygen.

Cruises were made on Georges Bank every month from September to December in 1975, and in February, April, and August 1976. During these cruises primary production was measured using the ^{14}C techinque developed by Steeman-Nielsen as modified by Strickland and Parsons (1968). Chlorophyll and nutrient samples (silicate, phosphate, and nitrate) were taken and processed according to standard oceanographic techniques for auto-analyzer (Strickland and Parsons, 1968).

Seasonal Cycle and Annual Production

The seasonal cycle obtained by the NEFC does not appear to fit the pattern proposed by Riley (1941) for Georges Bank. Instead of a spring bloom, the peak primary production occurs in late summer (Figure 2). Admittedly our seasonal coverage is sparse and may not accurately reflect the seasonal cycle. A phyptoplankton bloom may be over in a matter of days, and our cruises in the critical spring period consist of only one 3-week cruise in February, and a similar cruise in April. Nevertheless, we have estimated the annual primary production on a m^2 basis for Georges Bank. The primary production data for each station during each cruise was integrated over the water column, and the average value of $mgC/m^2/hr$ for each cruise was then converted to $mgC/m^2/day$ based on the length of daylight during each cruise. If we assume that the photosynthesis per unit radiation is constant throughout the day (Platt, 1971) our estimates will tend to be upper limits, since most of our experiments were done around noon, the time of maximum insolation. Integrating the curve of $mgC/m^2/day$ throughout the year yields a value of 533 $gC/m^2/yr$. This value is very highly compared to that of 200 $gC/m^2/yr$ for Massachusetts Bay, a shallow, highly productive area in the Gulf of Maine (Parker and Mulligan, in TRI-GOM PARK 1974). Lower values have also been reported from similar coastal environments by Steele (1974) in the North Sea (90 $gC/m^2/yr$), Ryther and Yentsch (1963) in the New York Bight (120 $gC/m^2/yr$), and Malone (1976) in the New York Bight apex (370 $gC/m^2/yr$).

Another estimate of the annual primary production can be obtained using the data from Colton et al. (1968). The seasonal cycle of primary production from these data is presented in Figure 2. In 1964-1965 the plot shows a spring bloom in March with a decrease through the remainder of the year to a low winter level. The case in 1965-1966 is somewhat different showing a peak in December, with a pronounced decrease in March and a small bloom in June. A plot of primary production versus chlorophyll a concentration from our cruises was constructed (Figure 3). A curve was fitted to these points with the equation $Y = 41.64X^{.25}$ with an $r^2 = 0.61$ (significant at 95% level) as was a straight line $Y = 0.31X+86.34$, $r^2 = 0.72$ (significant at 95% level). Although the straight line fits the data better in terms of r^2 we feel that the curve is more representative of the relationship of primary production to chlorophyll at low levels of chlorophyll (i.e., using the straight line when chlorophyll concentration equals zero, the primary production would still equal 86 $mgC/m^2/yr$). Applying the curve to the data of Colton et al. yields a value of 470 $gC/m^2/yr$ while using the straight line fit gives 450 $gC/m^2/yr$. These figures are in close agreement with the figure of 400 $gC/m^2/yr$ for Georges Bank derived by Yentsch (unpublished manuscript).

Yentsch estimated the primary production from the chlorophyll data of Colton et al. (1968) and the NEFC using the method of Ryther and Yentsch (1957) which is a comparison of the upper limits of phytosynthesis with chlorophyll in a light limited system. It appears that the overall primary production of particulate matter on Georges Bank is on the order of 400-500 $gC/m^2/yr$, making it one of the most productive areas in the ocean.

Partitioning and Conversion of Energy

In the New York Bight Apex the contribution of the nonoplankton (<22μ) was 59% of the annual phytoplankton production, while net plankton accounted for 41% (Malone, 1976). If a similar partitioning of the primary production is assumed for Georges Bank then the contribution of the nanoplankton would be approximately 275 $gC/m^2/yr$ while the net plankton would contribute about 200 $gC/m^2/yr$. The energy budget for Georges Bank (using an approach similar to that of Crisp (1975)) is presented in Figure 4.

Platt (1971) has done some work on the caloric equivalents of phytoplankton. He found that at the beginning of the spring bloom caloric values were 18.36 KCal/gC dropping to 14.9 KCal/gC as the bloom passed. The mean value found by Platt is 15.8 KCal/gC. Expressing the yearly primary production of Georges Bank in this way we get a range of 6652 to 9147 $KCal/m^2/yr$, with an average of 7110 $KCal/m^2/yr$.

The production of the nonoplankton would pass to higher trophic levels through a longer food chain than that of the net plankton (Parsons and Lebrasseur, 1970), with a subsequent decrease in the relative amount of food available to the higher trophic levels. For example, converting 3146 $KCal/m^2/yr$ to microzooplankton with an ecological efficiency of 32% (Steele, 1974) would yield 1007 $KCal/m^2/yr$ microzooplankton. If the ecological efficiency of the next step is 20% there would be 201 $KCal/m^2/yr$ of macrozooplankton available to predacious zooplankton and pelagic fish. The net plankton food chain would skip the microzooplankton step and the 200 $gC/m^2/yr$ would yield 64 $gC/m^2/yr$ macrozooplankton available to higher trophic levels. Even though the nanoplankton fix more carbon one can see from the food chain calculations that they will contribute less food to the higher trophic levels.

Another source of primary production products that ultimately may be available to higher trophic levels may come from dissolved organic carbon (D.O.C. excreted by photoplankton). Choi (1972) has shown that this averages about 30% of the particulate carbon fixed on the Scotian Shelf. If Georges Bank phytoplankton operate similarly to those of the Scotian Shelf approximately 2113 $KCal/m^2/yr$ enters the water column as D.O.C. If the D.O.C. reenters the food chain as bacteria with a conversion efficiency of 30% (Parsons and Sekai, 1970) this would amount to another 640 $KCal/m^2/yr$. This would, however, pass to higher trophic levels through the longer food chain outlined above and so only yield about 40 $KCal/m^2/yr$ to higher trophic levels.

It appears from a simple food chain calculation that the most important part of the primary producers is the net plankton even though they contribute a smaller percentage to the total primary production than the nanoplankton.

Discussion

The seasonal cycles of Riley (1941), Colton et al. (1968) and the present work are presented in Figure 2. Riley (1941) presents the classic

picture of temperate waters, a large primary bloom in the spring followed by a smaller bloom in the fall. The data from Colton et al.(1968) present a somewhat different picture. In 1964-1965 the pattern is similar to that of Riley's data with a peak in March although no secondary peak appeared. In 1965-1966, however, the peak occurred in December with a secondary peak in June, while the lowest values of the year were reached in March. The NEFC data present still another view, with the peak occurring in August. The variability between these three sets of data suggests several possibilities. The first is that on Georges Bank the production cycle is highly variable from year to year. This much variability in the primary productivity would have serious consequences for the herbivores; they would have to be extremely flexible in matching their food requirements, and, hence, time of reproduction and growth to the phytoplankton. The carnivores would then be faced with a similar problem. The second alternative is that because of the gross time scale of all three investigations compared to the time required for phytoplankton blooms to occur, coupled with the effects of patchiness over the Banks, none of the seasonal cycles accurately represent the sequence and scale of events. While the sampling that has been done by the NEFC is probably adequate to obtain a first approximation of the yearly primary production this is not adequate for an understanding of how the production is transformed into biomass of the higher trophic levels. As Lasker (1975) has shown, timing of the phytoplankton blooms plays a very important role in the transfer of energy to higher trophic levels.

ZOOPLANKTON

Methods

Major surveys of the zooplankton of the entire Gulf of Maine-Georges Bank area have been carried out by Bigelow (1926) and Fish and Johnson (1937). Since then there have been numerous investigations, though usually on a smaller geographic scale, of the zooplankton in the Gulf (Clarke, 1933, 1934; Clarke and Zinn, 1937; Redfield, 1939, 1941; Redfield and Beale, 1940; Clarke et al., 1943; Riley and Bumpus, 1947; Whitely, 1948; Colton et al., 1962; Mullen, 1963; Pavshtics, 1963; Pavshtics and Gogoleva, 1964; Sherman, 1966, 1968, 1970; Sherman and Perkins, 1971).

The early studies were for the most part qualitative in nature, e.g., the nets lacked flow meters, and the later studies were usually of a small-scale spatially and of short duration. Since a complete time series was lacking, the NEFC instituted a program of taking zooplankton samples during the spring and fall groundfish cruises starting in 1971 (a prototype MARMAP series). The sampling was intensified on the larval herring surveys and included 165μ, 255μ, 333μ, and 505μ mesh bongo nets. The samples are presently being sorted at the Polish Sorting Center in Szczecin, Poland, and the zooplankton biomass estimates are not yet available. For the moment we must rely on the data collected on the groundfish cruises.

Comparison of Empirical and Theoretical Production Estimates

The results from the groundfish surveys yield an average displacement volume for spring 1972-1975 of .48 cm^3/m^3 and for fall of .32 cm^3/m^3. These figures are close to the value reported by Lough (1975) for the fall of 1974 (.49 cm^3/m^3). The dry weights for the groundfish survey are .02 g/m^3 for both spring and fall. This works out to about 1 gm dry wgt/m^2 in both spring and fall. This is considerably lower than the average value of 6 gm wgt/m^2 reported for the North Sea (Steele, 1974). There are several possibilities why the value is so low. The samples measured are all from the 333μ net and so the small zooplankters such as Centropages and Pseudocalanus, which are very abundant on Georges Bank, as well as the early stages of large R forms, such as Calanus, were undersampled. The time of year during which the samples were taken, early spring and fall, might have been at times of low zooplankton abundance, Riley and Bumpus (1946) report a range of values from 2.8 to 38.1 gm dry wgt/m^2 with a mean value of 16.7 gm dry wgt/m^2. These figures were arrived at by assuming that 25% of the displacement volume was the dry weight of the zooplankton. The work by the NEFC (Bearse, unpublished data), based on actual measurements, shows that the dry weight is actually only about 6% of the displacement leading to a range of .62 to 9.16 gm dry wgt/m^2 with an average of 2.97 gm dry wgt/m^2 from the data of Riley and Bumpus (1946). Riley and Bumpus (1946) show that the times of the highest displacement volumes were in April, May, and June with the peak in May, the time of year not sampled by the NEFC. This leads one to suspect that the NEFC data underestimates the actual abundance.

Another way of approaching the problem would be to use the method of Sheldon et al. (1978). Using their method (assuming a ratio of predator to prey of 14), and using the pelagic fish biomass of 4.2 KCal/m^2 or 1.05 g dry wgt/m^2 one arrives at a standing stock of zooplankton of about 1 gm dry wgt/m^2, similar to the NEFC data. This is subject to two limitations: (1) the stocks of pelagics are severely depressed on Georges, and (2) the demersal species also feed on zooplankton. If we take the value of biomass for pelagics from 1964-1966 (before overfishing) of 29.2 KCal/m^2 or 7.2 g dry wgt/m^2 we get an estimate of zooplankton standing stock of about 7 gm dry wgt/m^2. This could well be an underestimate since it neglects feeding by the demersal species. If we work backwards with the P/B ratio of seven (Crisp, 1975) and the caloric conversion of 5.25 KCal/g dry wgt (Laurence, 1976), the standing stock of Calanus is about 4.3 g dry wgt/m^2. This is higher than the figure for total standing stock and almost as high as the average for all species for the North Sea. It appears that the NEFC estimates are low and the standing stock of zooplankton on Georges Bank is probably in the range of 12-24 g dry wgt/m^2.

Work has been done on the production of zooplankton on Georges Bank by Green et al. (1977), who have estimated that the production of Calanus is 79.46 mg C/m^2/day for a period of 100 days from March to June using the method of Winberg et al. (1971). This is a total production of 7.946 mg C/m^2/100 days. If we assume an equal amount of production in July and August and no production during November to February the total is 15.892 gC/m^2/yr or 158.92

KCal/m^2/yr (1 gC = 10 KCal Crisp, 1975). This is about 20% of the theoretical value from the energy budget which does not seem unreasonable because this is a minimum estimate and for only one species.

Partitioning and Conversion of Energy

Based on a theoretical food web (Figure 3) going from nanoplankton to microzooplankton to macrozooplankton with another branch going from net phytoplankton to macrozooplankton and assuming an ecological efficiency of 32% for herbivores and 20% for omnivores (Steele, 1974) we get a macrozooplankton production of 871 KCal/m^2/yr. If we then assume that there are about 5.25 KCal/g dry wgt (Laurence, 1976) we get about 165 g dry wgt/m^2/yr production. The production to biomass ratio is about 7 in the natural environment for Calanus (Crisp, 1975). If we further assume that this is representative of all the zooplankton on Georges Bank, we arrive at a standing stock estimate of about 24 g dry wgt/m^2, which is very close to that of Riley and Bumpus (1946). This would, of course, be reduced with a more complicated food web where predation by zooplankton carnivores is taken into account. At present we have no data on the numbers of carnivores and their food habits. Working solely from phytoplankton production, the number may be somewhat inflated because of the conversion from phytoplankton production in gC/m^2/yr to KCal/m^2/yr. The conversion chosen from Platt (1971) was about 16 KCal/gC. This was determined during a bloom period and so would tend to be a maximum value.

Discussion

There are several assumptions made that greatly oversimplify the processes in the ocean and there is also a large discrepancy between NEFC data and the older data of Riley and Bumpus (1946) as well as the between the NEFC data and the calculations based on the work of Green et al. (1977) and Sheldon et al. (1977). More research is needed in the areas of secondary production and zooplankton biomass to clear up these inconsistencies.

BENTHOS

There has been a great deal of work on the benthic fauna of the Georges Bank-Gulf of Maine area carried out at the NEFC (Wigley and McIntyre, 1964; Wigley and Emery, 1968; Wigley and Theroux, 1970). Most of this work has been directed towards macro- and megabenthic species although some was on the meiobenthos.

Methods

We began our estimate by reviewing the literature for the dominant or trophically important benthic species or taxonomic groups on Georges Bank (Wigley, 1968; Bowman, et al., 1976; Wigley, unpublished data). We found approximately 80 species that fit the above definition for one reason or another. The literature on these or related species was reviewed for any data on estimated productivity; very little was found, mostly for commercially valuable species, e.g., sea scallop, but not enough to estimate total benthic

productivity for Georges Bank.

An alternate method was attempted based on the use of production-biomass (P/B) ratios. This could be done because average benthic biomass data for Georges Bank was available (Wigley, 1961). This estimated average biomass was first converted into KCal. The conversions (Table 1), based on apparent modal values reported by Brawn et al. (1968), Cummins and Wuycheck (1971), and Thayer et al. (1973), were applied to Wigley's data which was separated into five groups: crustacea, mollusca, echinodermata, annelida, and miscellaneous (mostly coelenterates and ascidiacea). The result was an estimated average biomass of 77 $KCal/m^2$.

A variety of annual P/B estimates is available in the literature for benthic invertebrates. They range from 0.2 for Barents Sea benthos (Zenkevitch, 1956) to 5.0 for ampelescid amphipods (Sanders, 1956). The most frequently occurring P/B estimate for temperate benthic macrofauna appears to be about 1.5 (Raymont, 1963; Moiseev, 1969; Zenkevitch, 1956). Although Sanders (1956) estimated the P/B for Long Island Sound to be between 2-5, considering the dominance of relatively low production mollusks and echinoderms on George Bank we used 1.5, even though this could possibly be an overestimate. Applying the P/B ratio of 1.5 to the 77 $KCal/m^2$ biomass average resulted in an estimated benthic production of 117 $KCal/m^2/yr^{-1}$.

Wigley is currently working on new biomass data for Georges Bank (unpublished data) which may increase the estimated average biomass by 65% to around 240 gms wet wgt/m^2. This would increase the estimated production to about 192 $KCal/m^2/yr$.

Production Estimates

The value of 192 $KCal/m^2/yr$ is the value that is used in the construction of the energy budget although there is a wide range of possible values.

The benthic data is subject to many assumptions and the values for the two areas (North Sea and Georges Bank) could be different. For example, the average wet weight of the benthos on Georges Bank is 240 g/m^2 (Wigley, unpublished data) and using Crisp's conversion (Table 5, Figure 2, Crisp, 1975) of .2 x wet wgt = $KCal/m^2$ we get 48 $KCal/m^2$. Converting using the P/B of 1.5 we get a production estimate of 72 $KCal/m^2/yr$. However, if we use Crisp's value of P/B = 3, we get 144 $KCal/m^2/yr$. Furthermore, if we use the higher value of .5x wet wgt = $KCal/m^2/yr$ (Table 5, Crisp, 1975) we get .5 x 24 gm wet wgt = 120 $KCal/m^2$ x 3.0 = 360 $KCal/m^2/yr$. The macrobenthic production ranges from 72 to 360 $KCal/m^2/yr$. This has some interesting consequences for our food chain calculations. If 4319 $KCal/m^2/yr$ is available to the benthos and 360 $KCal/m^2/yr$ is produced we get a maximum growth efficiency of 7%, which is half the 15% assumed by Crisp (1975). One reason this is so low is that all of the 4319 $KCal/m^2/yr$ were assumed to be available to the macrobenthos which is not the case.

Crisp used a value of 13% available to the meio- and microfauna. Applying this to our value of 4319 yields 561 KCal/m^2/yr to the meio- and microfauna, and gives a maximum calculated growth efficiency of 360/3758 = 10%. Using our value of 192 KCal/m^2/yr this works out to 5%. This seems rather low and might be because: (1) some of the material reaching the benthos is refractory and/or (2) there is a great deal exported from the system. In Crisp (1975) the growth efficiency is 60/400 = 15%. His production figure of 6 KCal/m^2/yr was arrived at by assuming P/B ratio of 3.0, however, if we use our P/B ratio of 1.5 his growth efficiency drops to 30/400 = 7.5%. In Figure 5 we have increased the yield to the benthos to 762 KCal/m^2/yr and using a growth efficiency of 15% we would expect a production of about 115 KCal/m^2/yr. This is twice as high as the value derived by Crisp (1975) from a benthic biomass of 20 KCal/m^2. If Crisp (1975) had used the conversion of .5 x wet wgt = KCal/m^2 he would have gotten a biomass of 50 KCal x P/B = 3 = 150 KCal/m^2/yr. These figures show that a lot more work is necessary on benthic production before any definite values can be placed on it. However, at this time we can say that the benthic production is higher on Georges Bank (probable range 72-360 KCal/m^2/yr) than in the North Sea (probable range 60-115 KCal/m^2/yr).

FISH

The principal focus of the Woods Hole Laboratory and more recently the NEFC has traditionally been to develop a scientific basis for fishery management, first under the International Commission for the Northwest Atlantic Fisheries (ICNAF) and now under extended jurisdiction. For this reason our data on fish biomass and production are among the best information we possess.

Methods

Initially, the exploitable nekton community was divided into stock units as managed under ICNAF. Further division of the "other finfish" categories by species, and classification of all species by size groupings or feeding habits is needed. As this data becomes available, especially on feeding habits, it will be incorporated into the energy budget. Preliminary estimates of Georges Bank nekton production is shown in Table 3. Exploitable nekton means animals of sufficient size to contribute to commercial catch, usually at least 15 cm in length. The stock size estimates in metric tons are based on the relative abundance in bottom trawl surveys and weighting factors as reported by Clark and Brown (1977), or as estimated in resource assessments based on commercial catch data (Tables 4 and 5). Biomass estimates for Georges Bank were calculated by multiplying the stock biomass by the ratio of the area of Georges Bank to the stock area and relative abundance on Georges Bank, based on autumn surveys, to the relative abundance over the entire stock area. Some bias is introduced where the autumn spatial distribution of the stock does not reflect the average distribution for the year (weighted for seasonality in production). In the case of herring and mackerel, biomass was assigned to Georges Bank according to Anthony (personal communication). The production to biomass ratios (P/B) of a population (Table 5) equals total instantaneous

mortality at equilibrium where the contribution of recruitment to production (in weight) is insignificant. Therefore, natural and fishing mortality were estimated. These rates are subject to the most uncertainty for squid, other finfish, redfish, and red hake. Production in wet weight was converted to $KCal/m^2$ using the conversion of 1 KCal/g wet wgt, and 51.45×10^9 m^2 as the area of Georges Bank.

Production Estimates

The production estimates for the various commercially important species on Georges Bank are presented in Table 7. The total production has declined since 1964-1966 from about 27 $KCal/m^2/yr$ to approximately 19 $KCal/m^2/yr$ in 1973-1975. The production of pelagic species (mackerel, herring, and squid only) has declined from about 9 to 7 $KCal/m^2/yr$ while the drop in demersal species was from 18 to 12 $KCal/m^2/yr$ (see bottom of Table 7). In the pelagic category, herring declined drastically over this period but this decline was partially compensated for by substantial increases in mackerel and *Illex*. It should be noted that hakes (silver and red) are not classified as pelagic although they are vulnerable to pelagic gear, and silver hake feed extensively on euphausiids. Also the "other finfish" category contains some species which are usually considered pelagic.

Discussion

These estimates are subject to certain biases. Since the stocks were generally declining during the period considered, production was probably overestimated. Also substantial production (in terms of the fishery results from recruitment that reflects growth of fish not included in the biomass estimates. That is, estimates exclude the biomass of animals younger or smaller than indicated in the tables under the column "age or size range of population estimate" (Table 5). Thus, production of the exploitable biomass is overestimated, but this bias may be more than compensated by the underestimation of production by pre-recruits. At this time we think that the estimates for mackerel, herring, silver hake, and haddock are the most reliable, while the estimates for both squid species and other finfish are the most doubtful.

ENERGY BUDGETS - GEORGES BANK VS NORTH SEA

The construction of an energy budget for Georges Bank was chosen as the best method for organizing the data on the various trophic levels collected by the NEFC. In addition, information from the literature for similar species was utilized as necessary to complete the budget. The construction of the Georges Bank energy budget was modeled after those of Steele (1974) and Crisp (1975) for the North Sea.

The energy flow for the North Sea is compared with that on Georges Bank in Figures 4 and 5. Note that Georges Bank is much more productive at all levels in the food web, and that the fish values for Georges Bank represent the most recent period (1973-75).

Primary Production

The yearly primary production on Georges Bank is in the range of 400-500 $gC/m^2/yr$. This range was arrived at by direct measurements using ^{14}C techniques by the NEFC as well as calculations based on the chlorophyll data of Colton et al. (1968), by Yentsch (unpublished manuscript) and Cohen and Wright (in preparation). The accepted value for the North Sea is about 100 $gC/m^2/yr$. It appears that Georges Bank has a level of primary production four to five times that of the North Sea. The greater productivity of Georges Bank is due primarily to its shallowness. Wind and tidal mixing bring nutrients up from the sediments on the bank as well as advecting nutrient-rich deep water from the Gulf of Maine and the slope onto the bank.

Zooplankton Production

The zooplankton production based on a theoretical food chain calculation (Figure 4) is 871 $KCal/m^2/yr$. This agrees with the figure of 730 $KCal/m^2/yr$ derived from Riley's (1947) work by Tranter (1976). The zooplankton production in the North Sea is 178 $KCal/m^2/yr$ by a similar food chain calculation, 175 $KCal/m^2/yr$ by a calculation based on production to biomass ratios (Crisp, 1975) or 220 $KCal/m^2/yr$ based on a modified P/B ratio (Figure 5). It appears that the zooplankton production on Georges Bank is around 800 $KCal/m^2/yr$ while in the North Sea it is approximately 200 $KCal/m^2/yr$. At the level of secondary production, Georges Bank seems to be four times greater.

Benthic Production

Benthic production on Georges Bank ranges from 72 to 360 $KCal/m^2/yr$ compared to 60 to 115 $KCal/m^2/yr$ in the North Sea. Since the benthos is dependent on the energy input from the water column it is not surprising that the benthos is more productive on Georges Bank. Also it is probable that filter feeders on Georges Bank consume live phytoplankton because of the strong vertical mixing and the shallowness of the bank. These ranges are subject to many errors and furthermore do not take into account the meio- and microfauna. It will be necessary to carry out more studies of benthic production to reduce the uncertainty around these values.

Fish Production

The current estimated production of fish is higher on Georges Bank than for the North Sea (19 $KCal/m^2/yr$ versus 10.5 $KCal/m^2/yr$). This is what one might expect based on the higher production at the lower trophic levels. However, the difference is entirely due to the much higher production of demersal fish on Georges Bank since production of pelagics appears to be about the same in both areas. The production of pelagic fish in the North Sea is 8 $KCal/m^2/yr$, as compared with7 $KCal/m^2/yr$ on Georges Bank. At present stocks of herring are at an extremely low level of abundance on Georges Bank, and a more valid comparison might be to use the production estimate for the earlier period. In 1964-1966 the production of pelagics on Georges Bank was 9.2

KCal/m^2/yr (only 15% greater than in the North Sea). From the much higher figures of secondary production on Georges Bank one would expect a much higher pelagic fish production. There are several possibilities why the value is relatively low: (1) it does not include all the species which belong in the pelagic category and/or (2) some of the plankton may be lost to pelagics on Georges Bank because they are carried off the bank (Redfield, 1939), and 3) we have underestimated the amount of production actually generated on Georges Bank for pelagic species such as mackerel, sand launce, and perhaps Illex. The demersal fish production on Georges Bank is about five times higher than that in the North Sea (12.4 vs 2.5 KCal/m^2/yr), but part of the demersal production for Georges Bank belongs in the pelagic category. It is clear that when we consider the production for the entire shelf region from Cape Hatteras to Nova Scotia, including the Gulf of Maine, the level of fish production will drop more in line with that of the North Sea. However, we do not yet have comparable data for the areas adjacent to Georges Bank. Finally, it should be noted that we are talking about production on a per m^2 basis; the actual total yield of the North Sea is of course greater than Georges Bank because the area is significantly greater.

Discussion

The construction of the energy budget was intended as a device to organize our data and that in the literature into a form that might make the relationships of the various trophic levels clearer. It has provided as many questions as answers and pointed out several key areas where we lack sufficient data. Most notably our knowledge of the benthos is incomplete. We have only a slight idea as to the production of the macrobenthos and are almost wholly ignorant of the biomass and production of the meio- and microfauna. Our knowledge of zooplankton dynamics is also limited to only one study on the production of zooplankton, and only in the past few months has the basis for complete seasonal coverage of the zooplankton been implemented (MARMAP cruises). One of the big surprises to arise out of the energy budget exercise was finding out just how much primary production there was on Georges Bank. Previous estimates had been in the range of 200 to 300 gC/m^2/yr. We have revised the estimate upwards to 400 to 500 gC/m^2/yr and a picture is emerging of a seasonal cycle different from the classical spring-bloom/fall-bloom cycle (Riley, 1941, 1946). We now think that after an initial increase in the spring, production remains at high levels throughout the summer and into the fall. This is probably due to a continuous supply of nutrient rich water available from the Gulf of Maine and the slope water that is advected onto Georges Bank by tidal mixing. The shallowness of Georges Bank coupled with wind and tidal mixing also allows a constant supply of regenerated nutrients form the benthos to reach phytoplankton in the photic zone.

In addition to serving as a framework for organizing our data we are using the energy budget to look at comparisons between Georges Bank and the North Sea. This will help identify gross errors in either theoretical or empirical results, or possibly real differences in the levels or flows of energy between the two areas. These differences may give clues as to the characteristics of the systems which exert controlling influences.

FUTURE STUDIES

Gross Energy Budget

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 previously mentioned; 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. Here 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. 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. The energy pathways between "trophic categories" will be examined through analysis of food habits, and the total consumption of each "trophic category" will be compared with the production estimates of its prey groups. By a "trophic category" we mean simply a group of organisms within a trophic level classified by size and feeding characteristics, e.g., adult pelagic fishes feeding solely on zooplankton, or adult demersal fish feeding largely on benthic forms. Basically, an iterative approach will be used, where we shall compare independent estimates of critical rates and quantities and then try to narrow the range of discrepancies by adjusting model parameters where gross imbalances are revealed.

We do have a very comprehensive and quantitative data base on mean gut contents of fishes in our area. However, one of the major hurdles relative to direct estimation of food consumption is the fact that we do not have accurate estimates of digestion rates for more than a few fish species. Here too

iterative approaches will be required.

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. Right now we are just beginning to search for an analytical approach to this problem.

Larval Fish Dynamics

A major focus for the NEFC will continue to be on larval fish studies. We plan to continue macro-, meso-, and microscale studies in the field and the experimental lab work. This year we will concentrate on developing a generalized model of larval survival incorporating information from both field and lab studies; Laurence and Lough from NEFC will be working with Jan Beyer from Denmark. The larval patch study in October will provide the first chance to test some aspects of this model with a field experiment on sea herring. Also our studies on larval fish will be complemented by primary and secondary production studies by Jim Thomas at the Sandy Hook Laboratory and John Walsh, et al. of the Brookhaven National Laboratory.

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Table 1. Cruises and samples obtained for phytoplankton investigation by the NEFC.

Date	Cruise	Number of stations	Total Number of Samples					Primary production	Notes
			Phosphate	Silicate	Nitrate	Chloro-phyll	*In vivo* fluorescence		
8-18 July 1975	Albatross IV 75-07	75	211	211	211	315	None	None	Data report available.
23 Sept.-30 Oct. 1975	Delaware II 75-15	27	248	248	248	168	None	None	Data report available.
24 Sept.-10 Oct. 1975	Belogorsk 75-2	90	617	617	617	205	None	None	Data report available.
15-31 Oct. 1975	Belogorsk 75-3	94	628	628	628	241	None	None	Data report available.
31 Oct.- 16 Nov. 1975	Anton Dohrn 75-187	100	523	523	623	330	None	None	Data report available.
2-19 Dec. 1975	Albatross IV 75-14	83	491	491	491	195	✓	9 stations	Data report and analysis available.
9-25 Feb. 1976	Albatross IV 76-01	49	304	304	304	255	✓	5 stations	Data report and analysis available.
9 Apr.-4 May 1976	Wieczno 76-01	143	292	292	292	164	✓	7 stations	Data report and preliminary analysis available.
11-21 May 1976	Albatross IV 76-03	100	722	722	722	604	✓	8 stations	Data report and preliminary analysis available.
15 May 1976	U.S.C.G. 005	18	87	87	87	None	None	None	Data report available.
25-26 May 1976	U.S.C.G. 006	18	87	87	87	None	None	None	Data report available.
28 July-16 Aug. 1976	Albatross IV 76-05	133	682	682	682	1009	None	22 stations	Data report and preliminary analysis available.
1-18 Oct. 1976	Anandale 76-01	80	153	153	153	153	None	None	Nutrients to be run at Sandy Hook after 9 Jan. 1978.
13 Oct.-4 Nov. 1976	Wieczno 76-03	112	755	755	755	300	None	10 Stations	Nutrients to be run at Sandy Hook after 9 Jan. 1978.
14 Nov.-1 Dec. 1976	Anton Dohrn 76-02	137	1250	1250	1250	900	None	27 Stations	Nutrients to be run at Sandy Hook after 9 Jan. 1978.
26 Nov.-12 Dec. 1976	Researcher FRG 11-76	110	590	590	590	590	None	None	Nutrients to be run at Sandy Hook after 9 Jan. 1978. Chlorophylls at Sandy Hook.

Table 2. Conversion of Wigley's (1961) wet wgt data into KCal.

Taxonomic group	$\overline{X}$ Wet wgt (gms/m^2)	KCal/gm/wet wgt	KCal/m^2
Crustacea	8.2	1.10 (1.0-1.3)*	9.0
Mollusca	64.6	.50 (.37-.80)	32.3
Echinodermata	48.4	.43 (.1-.6)	20.8
Annelida	9.2	.70 (.5-1.0)	6.4
Miscellaneous	26.2	.35 (.05-.4)	9.2
Total	156.6		77.0

*range of estimated values

Table 3. Preliminary Estimates of Georges Bank Nekton Production

Michael Sissenwine March 28, 1977

Species Group	Stock Strata	Stock Area Nautical Miles	[1]Stock size estimates (MT) 1964-1966	1973-1975
Cod 5Z	5-25	25,115	132,823	135,616
Haddock 5Ze	13-25	15,300	336,046	45,212
Redfish 5	5-30, 36-40	43,007	55,810	60,022
Silver hake 5Ze	13-25	15,300	349,239	245,002
Red hake 5Ze	13-25	15,300	59,650	24,967
Pollock 5+6	1-30, 36-40	48,355	72,109	56,097
Yellowtail fl. 5Ze	13-25	15,300	45,911	15,831
Other fl. 5+6	1-30, 36-40	48,355	58,152	34,162
Herring 5Z+6	1-25	30,463	1,677,833	126,259
Mackerel 3-6	1-30, 36-40	48,355	314,364	945,125
Other finfish 5+6	1-30, 36-40	48,355	595,010	383,008
Illex 5+6	1-30, 36-40	48,355	19,210	147,906
Loligo 5+6	1-30, 36-40	48,355	17,955	174,189

[1]Based on retransformed stratified mean catches per tow from Fall Bottom Trawl Survey and weighting coefficients from Clark and Brown, 1977; to be published Fish. Bull.

Table 4. Stock estimates for Georges Bank based on bottom trawl survey and commercial catch data.

Species Group	Direct Stock Estimates (MT) 1963-1965	1972-1974	Area Ratio, AR (Georges Bank area/Stock area)
Cod			0.609
Haddock	222,667	66,667	
Redfish			0.356
Silver hake	532,470	397,776	
Red hake	56,872	42,053	
Pollock			0.316
Yellowtail flounder	32,510	20,422	
Other flounder			0.316
Herring	1,347,667	470,000	0.502
Mackerel	508,000	735,000	0.316
Other finfish			0.316
Illex			0.316
Loligo			0.316

Source - Haddock - Hennemuth, 1969, Res. Doc. 69/90
Clark, 1975, Res. Doc. 75/48

Herring - ICNAF, Summ. Doc. 75/19

Mackerel - Anderson et al., Res. Doc. 76/XII/132

Silver hake - Anderson, Working Paper 76/IV/93

Red hake - Anderson, Res. Doc. 74/19 and personal communication

Yellowtail - Parrack, 1977, unpublished

Table 5. Population estimates for Georges Bank. See text for details.

Species Group	[1]Survey Density Ratio, DR 1963-1965	1972-1974	[2]Georges Bank Pop. Est. (MT) 1964-1966	1973-1975
Cod	1.46	1.55	118,100	128,014
Haddock			222,667	66,667
Redfish	0.06	0.13	1,192	2,778
Silver hake			532,470	397,776
Red hake			56,872	42,053
Pollock	0.64	0.35	14,583	6,204
Yellowtail			35,510	20,422
Other flounder			16,354	12,522
Herring			[3]1,426,158	107,320
Mackerel			[4]76,200	110,250
Other finfish	0.47	0.98	88,370	118,609
Illex	2.00	1.93	12,140	90,205
Loligo	0.58	0.26	3,291	14,311
Total			2,603,907	1,117,131

[1]Mean catch per tow on G.B./Mean catch per tow for stock area

[2]Pop. Est. for G.B. = DR · AR · Pop. Est. for stock

[3]85% of 5Z-6 herring stock assumed on Georges Bank
Personal communication, V. Anthony

[4]15% of 3-6 mackerel stock assumed on Georges Bank
Personal communication, V. Anthony

Table 6. Estimates of natural mortality, fishing mortality, and production to biomass ratios. See text for details.

Species groups	Age or Size Range in pop. est.	Natural mortality	Fishing Mortality 1964-1966	Fishing Mortality 1973-1975	P/B = Z 1964-1966	P/B = Z 1973-1975
Cod	2-3+ (commercial)	0.2	0.33[1]	0.30[2]	0.53	0.50
Haddock	"	0.2	0.70[3]	0.24[1]	0.90	0.44
Redfish	6+ (commercial)	0.1-0.2	0.40[4]	0.40[4]	0.50	0.50
Silver hake	1+	0.4	0.44[5]	0.58[5]	0.88	0.98
Red hake	2+ (commercial)	0.4	0.64[1,6]	0.39[1]	1.04	0.79
Pollock	3-4+ (commercial)	0.2	0.50[7]	0.50[7]	0.70	0.70
Yellowtail	2+ (commercial)	0.2	1.04[8]	1.38[8]	1.24	1.58
Other flounder	20 cm+ (commercial)	0.2	0.70[4]	0.90[4]	0.90	1.10
Herring	3+	0.2	0.19[9]	0.47[9]	0.30	0.67
Mackerel	1+	0.3	0.04[10]	0.73[10]	0.34	1.03
Other finfish	20 cm+ (commercial)	0.2	0.40[4]	0.40[4]	0.60	0.60
Illex	6 months +	1.2	0.0[1]	0.2[1,11]	1.20	1.40
Loligo	6 months +	1.56	0.0[1]	0.3[1,11]	1.56	1.86

[1] Based on catch to stock size ratio

[2] Penttila and Gifford, Res. Doc. 75/46

[3] Clark, Res. Doc. 76/VI/35, Table 5

[4] Clark and Brown, 1977, Fish. Bull.

[5] Anderson, Working Paper, 76/IV/65

[6] Catch data from Anderson, 76/IV/65, Working Paper

[7] Clark et al., Res. Doc. 76/VI/47

[8] Parrack, 1977, unpublished

[9] Summ. Doc. 75/19

[10] Anderson et al. 76/XII/132

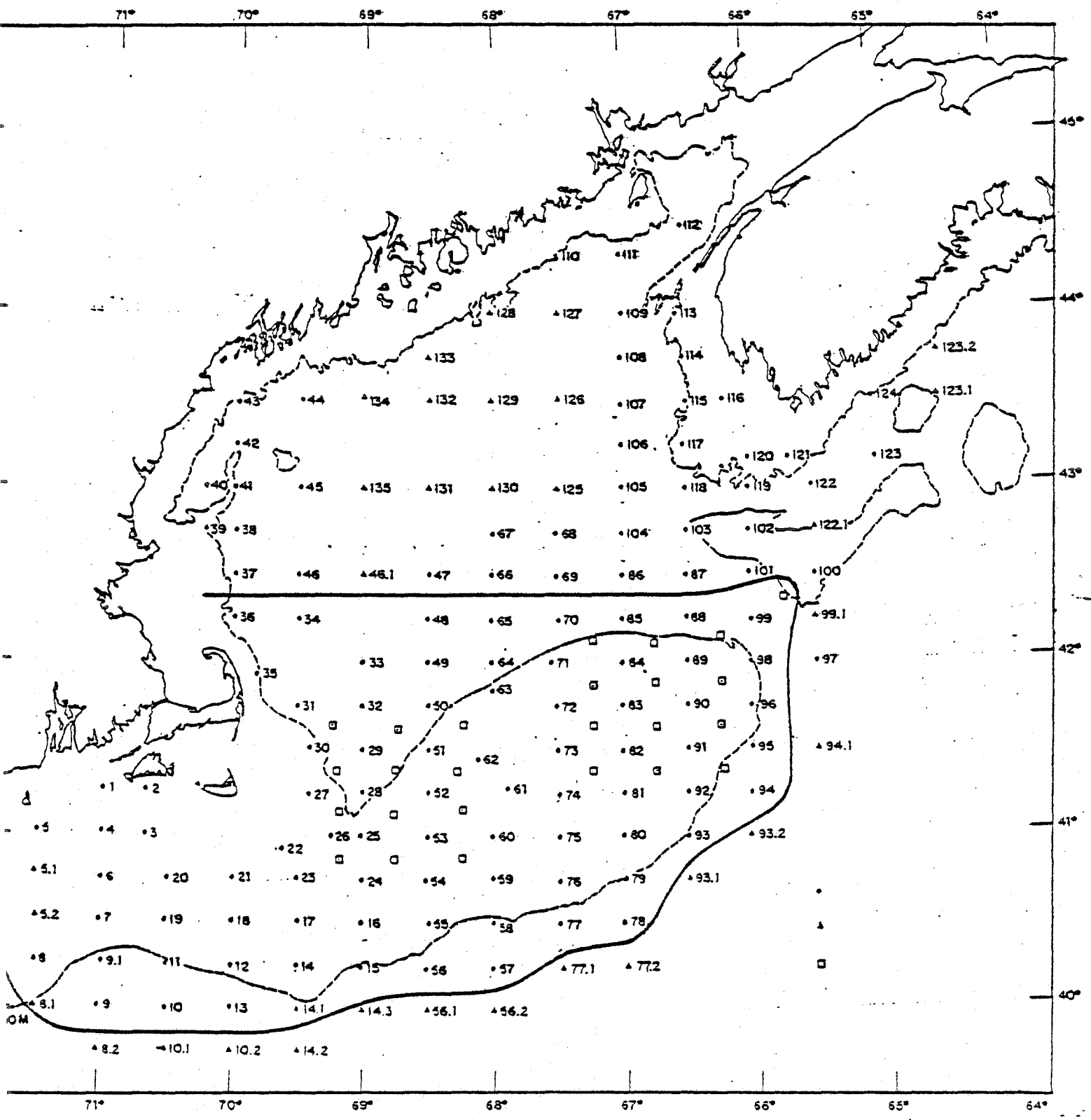
[11] See 1975 Redbook page 54 for catch summary

Table 7. Production of various species of fish and squid for Georges Bank.

Species groups	[1]Production (in 10^6 KCal.) 1964-1966	1973-1975	[2]Prod. (KCal.)/m^2 1964-1966	1973-1975
Cod	62,593	64,007	1.22	1.24
Haddock	200,400	39,333	3.90	0.58
Redfish	596	1,389	0.02	0.02
Silver hake	468,573	389,820	9.10	7.58
Red hake	59,147	33,222	1.14	0.64
Pollock	10,208	4,343	0.20	0.08
Yellowtail	44,032	32,267	0.86	0.62
Other flounder	14,718	13,774	0.28	0.26
Herring	427,847	71,904	8.32	1.40
Mackerel	25,908	113,557	0.50	2.20
Other finfish	53,092	71,165	1.04	1.38
Illex	14,568	126,289	0.28	2.46
Loligo	5,134	26,618	0.10	0.52
		Total	26.96	18.98

[1]1.0 KCal. per gram wet wgt, Crisp 1976, Table 2.
[2]Based on $51.45 \times 10^9 m^2$ area of Georges Bank

Pelagic (herring, mackerel, squid)	9.20	6.58
Demersal (all other species)	17.76	12.40



gure 1. Area covered by the larval herring survey. Stations within dark lines are the standard stations. Those outside are sampled on selected cruises.

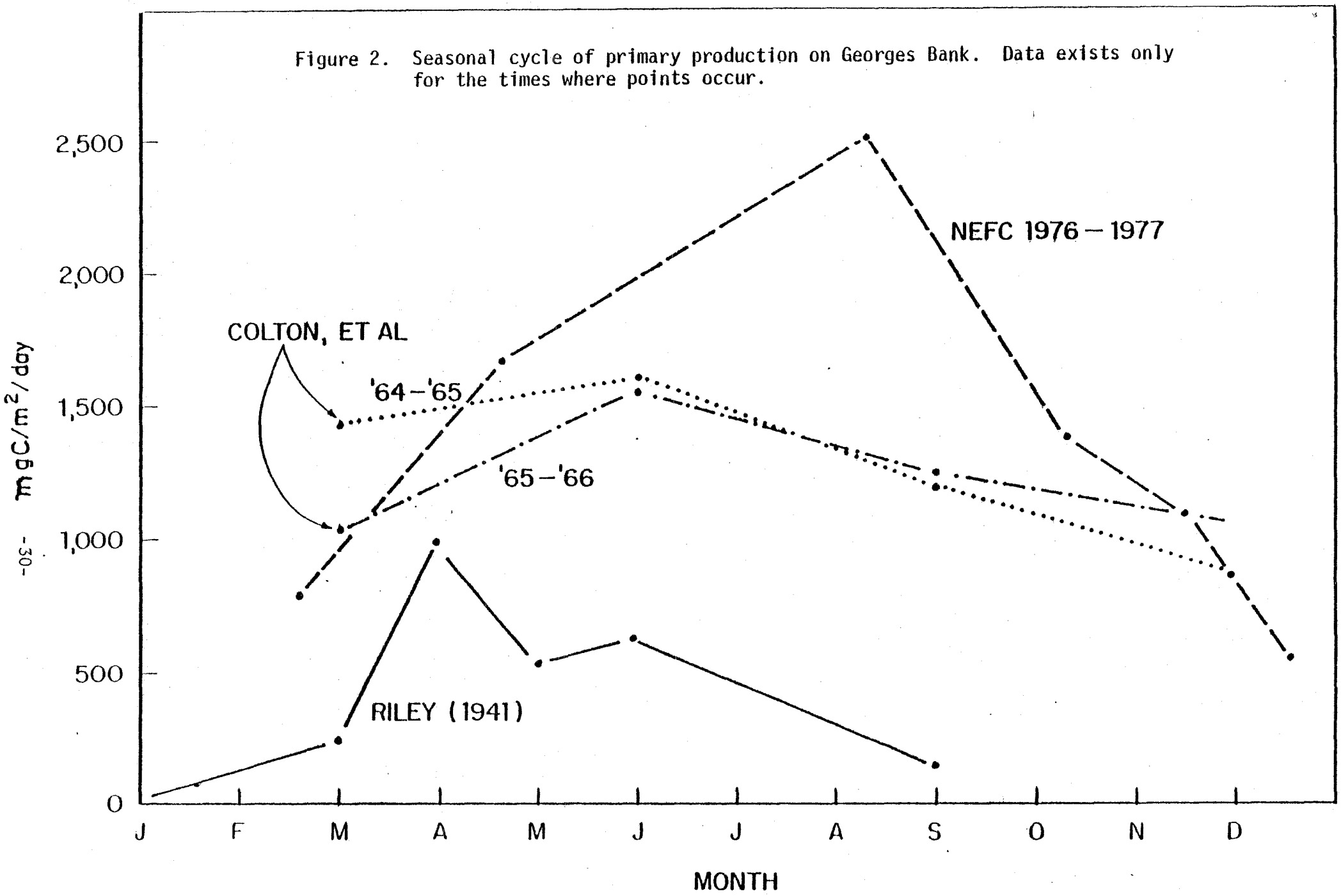
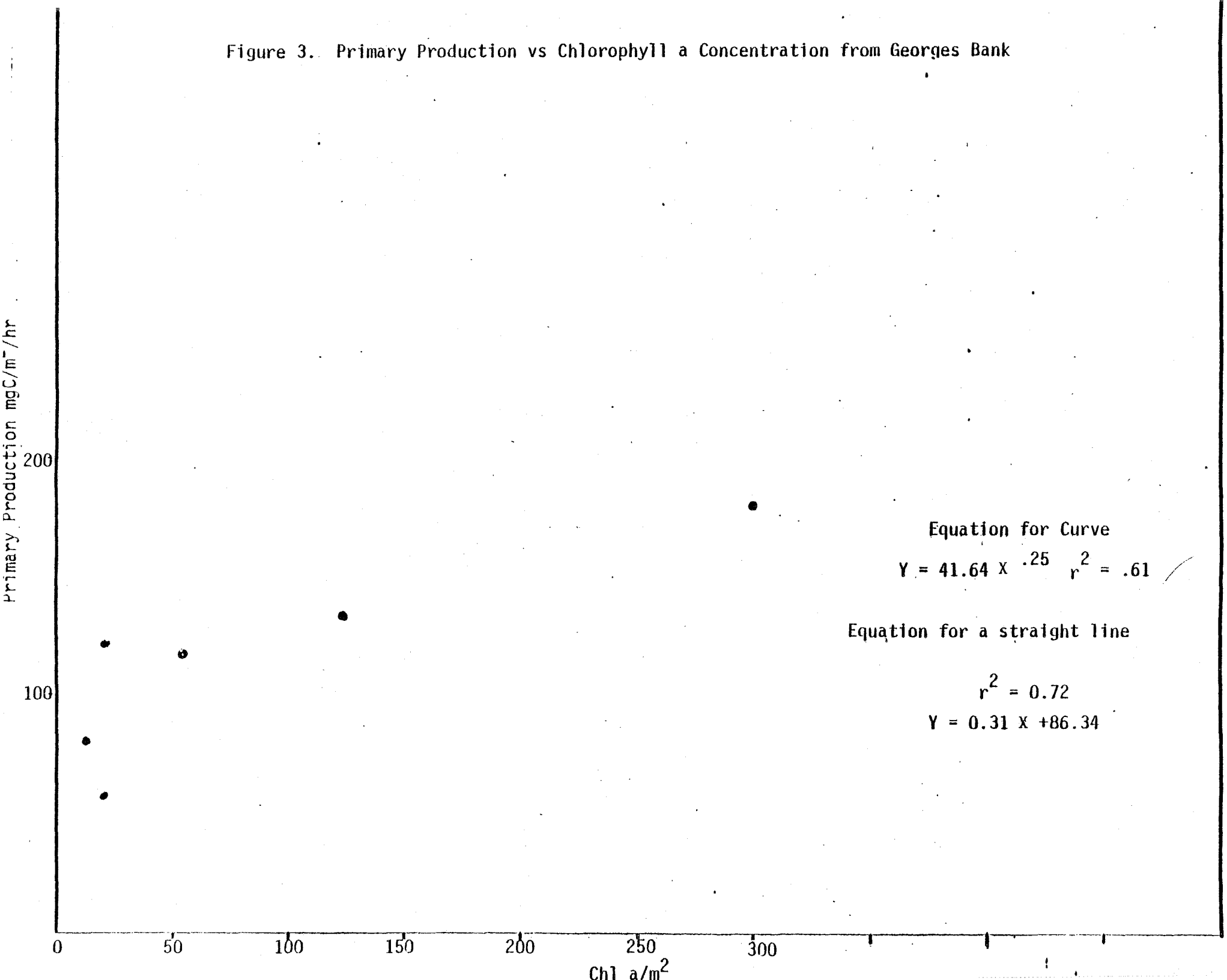


Figure 2. Seasonal cycle of primary production on Georges Bank. Data exists only for the times where points occur.

Figure 3. Primary Production vs Chlorophyll a Concentration from Georges Bank



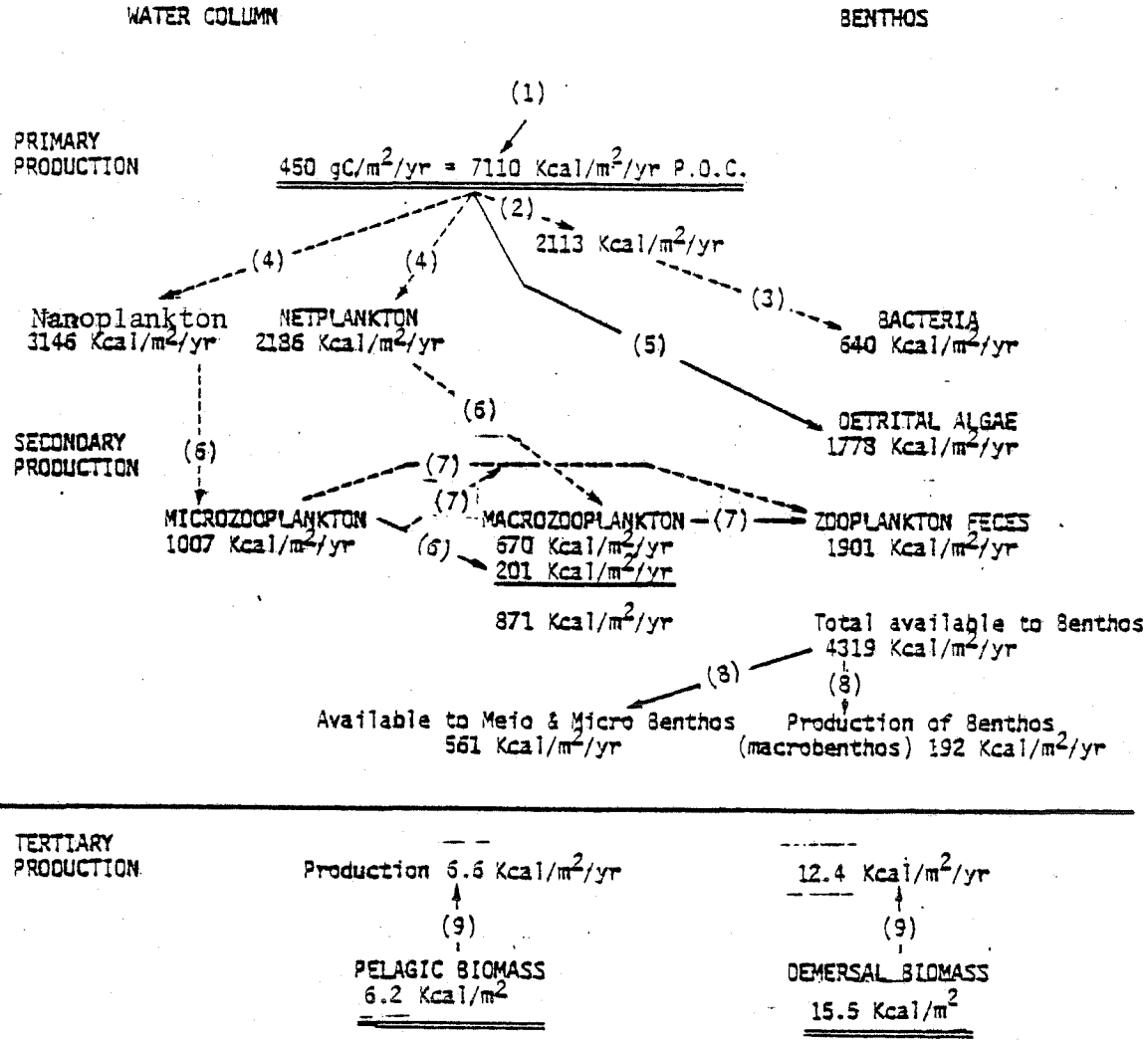


Figure 4. Energy budget for Georges Bank. Modified from Crisp (Figure 2, 1975). In the above figure engery flow between trophic levels is linked by arrows, but the direction of the arrow represents the logical derivation of the values given, not the direction of energy flow, which is always from top to bottom of the page. The double underlined values are based on observations, the continuous interconnecting 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 ^{14}C measurements. Kcal/gC based on a factor of 15.8 (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 bacterial or bacteria which are attached to particles and enter benthos (Parsons and Sekai 1970).

(4) Estimate of nano and net plankton production based on Malone's (1976), observations that in N.Y. Bight 59%; 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, squid, and mackerel; demersal includes all other finfish and squid.

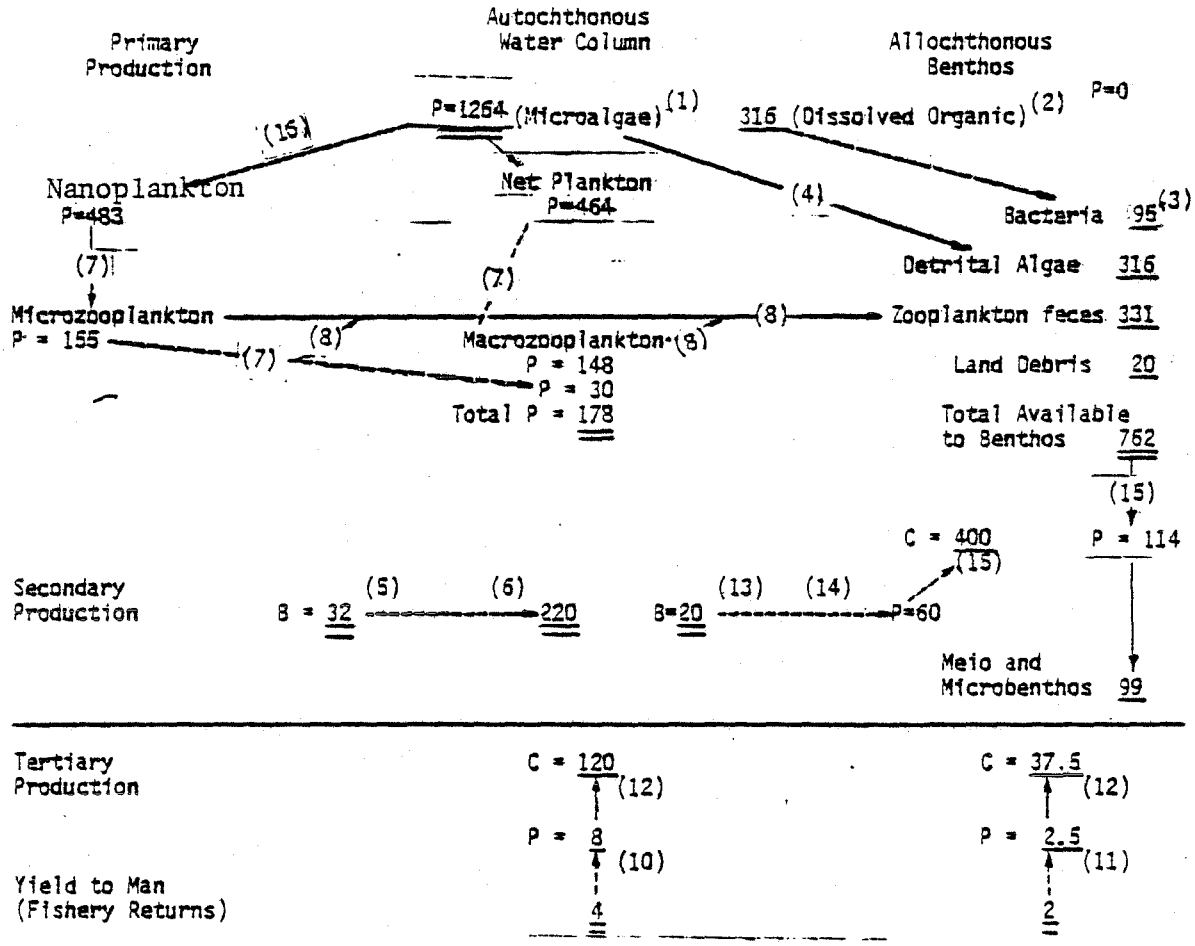


Figure 5. Energy budget for the North Sea.. Modified from Crisp (Figure 2, 1975). In the above figure energy flow between trophic levels is linked by arrows, but the direction of the arrow represents the logical derivation of the values given, not the direction of energy flow, which is always from top to bottom of the page. The double underlined values are based on observations, the continuous interconnecting 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) Production values based on Steemen Nielson (1958), Steele (1956), Steele and Baird (1961). Conversion of 15.8 Kcal/gc Platt (1971).
(2) Assumption that 20% of primary production is released as dissolved organic matter (Parsons and Seki, 1971).
(3) Assumption that 30% of dissolved photosynthetic material incorporated in benthic bacteria, or in bacteria which are attached to particles and enter the benthos.
(4) Assumption that 75% of microalgae eaten by herbivores.
(5) 5.25X dry weight values Laurance (1976) of zooplankton from Adams, quoted by Steele (1974).
(6) Production/biomass (P/B) ratio assumed to be 7 for Calanus in natural environment.
(7) P/C or growth efficiency assumed at 30% for hervivores, 20% for omnivores. (Steele 1974) longer food chain for nanoplankton based on Parsons and Lebrassuer (1970)
(8) Assimilation efficiency assumed 70%, feces 30% of consumption. (Table 3).
(9) Pure assumption, inserted for completeness.
(10) Pelagic fishing mortality assumed 50% of total.
(11) Demersal fishing mortality assumed 80% of total.
(12) Growth efficiency of fish population P/C taken as 1/15 (Mann, 1965).
(13) Benthic biomass taken as 100 gm^{-2}=20 kcal m^{-2}, average figure from Soviet work (Table 5).
(14) P/B for benthic invertebrates taken as 3.0 (Table 7).
(15) Growth efficiency assumed to be 15%.
(16) Estimate that 51% is nanoplankton, 49% is netplankton (Malone, 1976).