An Energy Budget of Georges Bank

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by

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Abstract

An energy budget of Georges Bank is described based on original data and a review of the published literature. Primary productivity of Georges Bank is extremely high (450 $gC \cdot m^{-2} \cdot yr^{-1}$ or 2.97×10^7 $J \cdot m^{-2} \cdot yr^{-1}$), apparently reflecting the rapid regeneration of nutrients on the bank unimpeded by a thermocline and the advection of nutrients from deeper waters on both sides of the bank. Zooplankton production based on biomass and a P/B ratio of 7 is estimated as 1.46×10^6 $J \cdot m^{-2} \cdot yr^{-1}$ (350 KCal $m^{-2} yr^{-1}$). Macrobenthos production is estimated at $7.53 \times 10^5 \cdot J \cdot m^{-2} \cdot yr^{-1}$ (180 KCal $m^{-2} yr^{-1}$) based on density estimates and production to biomass ratios. Exploited finfish and squid production ranged from 7.20 to 5.31×10^4 $J \cdot m^{-2} \cdot yr^{-1}$ (17.2 to 12.7 $KCal \cdot m^{-2} \cdot yr^{-1}$) between the period 1964-1966 and 1973-1975.

Georges Bank appears to be more productive per unit area at all trophic levels than the North Sea which is a much larger area. The difference in productivity is greater at lower trophic levels than for finfish and squid, possibly as a result of advection off Georges Bank.

Key Words: Energy budget, Georges Bank, food web, organic productivity.

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Introduction

Georges Bank has long been a major fishing ground of North American fishermen and during the 1960s and early 1970s was the site of an intensive multispecies distant water fishery. Landings peaked in 1972 at 625,000 tons, probably in excess of long-term sustainable levels. A gross static energy budget of Georges Bank was constructed to provide an estimate of total production potential and to clarify interrelationships among trophic levels. The energy budget is only one phase of the Northeast Fisheries Center's (NEFC) study of the Georges Bank ecosystem and is intended to provide a better scientific base for the exploitation and management of the multispecies fishery of the region.

The energy budget is based on results describing abundance and productivity at all trophic levels from both the published literature and original data of the NEFC. An energy budget may indicate inconsistencies in calculated productivity between trophic levels and identify critical pathways of energy flow. The energy budget for Georges Bank is compared to that of another major fishing area, the North Sea.

Primary Productivity

Although a great deal of phytoplankton research was conducted on Georges Bank in the first half of the century, results generally were not quantitative because phytoplankton nets were used thereby undersampling nanoplankton (Yentsch and Ryther 1959). A more quantitative description of the seasonal production cycle based on the oxygen production technique was provided by Riley (1941). His estimates of primary production are based on the light bottle - dark bottle technique. He used a surface

sample and extrapolated the production of the entire water column based on the general features of the vertical production curve. His results show a maximum value in April of .95 $gC \cdot m^{-2} \cdot day^{-1}$ followed by a decrease in May (.54 $gC \cdot m^{-2} \cdot day^{-1}$) and a rise to .63 $gC \cdot m^{-2} \cdot day^{-1}$ in June. There are no data for the rest of the summer; the next measurement, in September, was .14 $gC \cdot m^{-2} \cdot day^{-1}$.

During 1975-1976 six cruises were conducted on Georges Bank and surrounding waters by United States (NEFC) and other countries of the International Commission for the Northwest Atlantic Fisheries (ICNAF). Five additional cruises were conducted cooperatively by NEFC and the USSR during 1977-1978.

In 1975 and 1976 water samples were taken at 0, 10, 20, 50, 75, and 100 meters for salinity, temperature, dissolved oxygen, chlorophyll, and nitrate, using PVC Niskin bottles. In addition, there were from 4 to 27 stations per cruise at which primary productivity was determined using the ^{14}C method. All analyses were carried out using standard oceanographic techniques (Strickland and Parsons 1968). Primary productivity measurements were made at 100%, 50% 25%, 10%, and 1% light penetration depths. The appropriate light levels were obtained using neutral density filters in an on-deck simulated <u>in situ</u> incubator. The actual sampling depths for the different light levels were determined either by Secchi disc or by direct measurements using a Lambda submarine photometer. Incubations lasted approximately 4 hours starting in the morning and running until afternoon (Cohen and Wright 1979). During 1977-1978 the light depths were slightly different and the ^{14}C data includes extracellular release of dissolved organic carbon

(D.O.C.) and so are about 20% higher than the earlier samples which did not measure D.O.C. (Thomas et al. 1978, O'Reilly and Thomas 1979, O'Reilly and Busch 1979). Therefore the 1975-1976 data probably underestimate the actual production on Georges Bank.

The primary productivity data for each station during each cruise was integrated over the depth of the photic zone. The average value of $gC \cdot m^{-2} \cdot hr^{-1}$ for each cruise was then converted to $gC \cdot m^{-2} \cdot day^{-1}$ based on the average day length during that cruise. The resulting cycle of primary productivity is shown in Figure 1. It differs from the spring bloom pattern proposed earlier for Georges Bank (Riley 1941). Our data show an increase in the spring to a high level of productivity (ca 2 $gC \cdot m^{-2} \cdot day^{-1}$) which is maintained throughout the summer and into the late fall with a decline to low winter values in November-December. There is considerable variability associated with the estimates (the standard deviation is approximately half the mean values shown) because of the relatively few observations and the patchiness of phytoplankton blooms. However, the results show a consistent seasonal pattern over the four years of sampling. The differences between Riley's (1941) results and ours may be due to several possibilities. There may have been actual long-term changes in the production regime of phytoplankton on Georges Bank. However, it is more likely that the differences are due to the techniques used. Riley (1941) used the light bottle - dark bottle technique to estimate net productivity on surface samples and extrapolated to the entire water column. The more recent data used ^{14}C methods which give an estimate between net and gross production (Parsons et al. 1977).

Fig. 1 near here

Integrating our values over the year yields annual production 400-500 $gC \cdot m^{-2} \cdot yr^{-1}$, including extracellular release of D.O.C. (Cohen and Wright 1979). Analysis of NEFC chlorophyll data supports this high level of productivity (Cohen et al. 1978). This means that Georges Bank has one of the highest primary productivity levels in the ocean. Some other coastal marine estimates of annual primary productivity are (all in $gC \cdot m^{-2} \cdot yr^{-1}$): Long Island Sound, 250 (Parsons et al. 1977); Florida mangrove swamp, 600 (Odum 1971); North Sea, 90 (Steele 1974).

The high productivity of Georges Bank may be related to its unique topography and hydrography. Georges Bank is a partially closed system with respect to the surrounding waters. The mean circulation on top of Georges Bank is clockwise throughout the year (Butman et al. 1980) but there is considerable variability in the flow. Hopkins and Garfield (in press) have estimated that the residence time of water on the bank is two months during the winter and five months the rest of the year. Therefore a significant amount of nutrient regeneration is implied to support a high level of primary production. The shallow area on top of the bank is well mixed even during the summer, allowing nutrients regenerated in the water column and sediment to be available to the phytoplankton, unimpeded by a thermocline. Calculations based on data from 1977 (Thomas et al. 1978) show a nitrogen demand[2] range, based on the daily primary productivity,

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[2]The nitrogen demand was calculated using a ratio of C:N of 106:16; this is known as the Redfield ratio and it is thought to be generally applicable in the marine environment and organisms although deviations do occur (Red field 1934).

of .1-7 μg-at $N \cdot l^{-1} \cdot day^{-1}$ (mean of 2.0 μg-at $N \cdot l^{-1} \cdot day^{-1}$) in March-April and .5-1.65 μg-at $N \cdot l^{-1} \cdot day^{-1}$ (mean of 1.0 μg-at $N \cdot l^{-1} \cdot day^{-1}$) in July. After adjusting for the different seasonal depths of the photic zone, the nitorgen demand on a m^2 basis was about equal during March-April and July. At least half of the required nitrogen appears to be recycled and most of the remainder is believed to be derived from adjacent water masses. The regeneration rates of nitrogen in the water column (calculated from respiration data using an RQ=1, Thomas et al. 1978) can supply about 50% of the necessary nitrogen (range .13-3.96 μg-at $N \cdot l^{-1} \cdot day^{-1}$, mean of .93 μg-at $N \cdot l^{-1} \cdot day^{-1}$) in March-April and 70% in July (range .30-.98 μg-at $N \cdot l^{-1} \cdot day^{-1}$, mean of .70 μg-at $N \cdot l^{-1} \cdot day^{-1}$). The benthos contributes about 7% of the total nitrogen regenerated in March-April and 3% in July (Thomas et al. 1978). The amount of nitrogen entering through rainfall has been neglected and there are no nitrogen-fixing blue-green algae on Georges Bank.

The other principal mechanism that is probably at work year-round is advection of nutrients from the deeper waters on both sides of the banks as indicated in Figure 2. Vertical distributions and temperature and dissolved nitrate concentration along 68°W longitude (Figure 2), from a cruise in November 1975, illustrate some persistent features of the hydrography of Georges Bank: 1) the water on the shallow top of the bank is well mixed, by both winds and tidal action; 2) there is a region of strong gradients on the south side of the bank, representing the transition to Slope Water conditions; 3) another frontal region exists along the northern edge of the bank, usually with weaker gradients into the waters of the Gulf of Maine; 4) nitrate, which is representative of all dissolved nutrients, is low--sometimes undetectable--on top of the bank. It increases

Fig. 2 near here

both north and south with highest values in the deeper water. Chlorophyll distribution (not shown) is in sharp contrast to that of nutrients. The highest values of chlorophyll are found over the central portion of the bank, with very low values in the Gulf of Maine and particularly in the Slope Water. The nutrient-bearing water found throughout the year at depths of 150 m or more on both sides of Georges Bank is of oceanic origin. It is relatively warm but saline Slope Water, which flows intermittently through the Northeast Channel (sill depth 230 m) into the Gulf of Maine where it underlies the colder and fresher shelf waters (Ramp and Wright 1979). It is estimated that the amount of nitrogen which enters the Gulf of Maine through the Northeast Channel represents about 40% of the total amount needed for primary production on Georges Bank (Ramp et al. 1980). However, Ramp et al. (1980) emphasize that the flow field inside the Gulf of Maine is not yet understood and that the nutrients entering through Northeast Channel cannot all be used to support primary production on Georges Bank.

Georges Bank has a high level of primary productivity throughout the summer because of the steady supply of nutrients. The rate of primary productivity drops with decreased light levels in winter, when the critical depth (Riley 1942, Sverdrup 1953) is much shallower than the depth of the mixed layer which extends to the bottom. Phytoplankton then spend a large proportion of their time below the critical depth, and productivity is at a minimum. In spring, as the insolation increases, the critical depth deepens in relation to the mixed depth and a time is reached when photosynthesis in the water column exceeds respiration - thus the spring bloom commences. Following this, summer conditions are again reached.

Primary productivity excreted by the phytoplankton as dissolved organic carbon (D.O.C.) averages about 17% of the total primary productivity or about 77 $gC \cdot m^{-2} \cdot yr^{-1}$ (Thomas et al. 1978; O'Reilly and Busch 1979). This is about half of the value reported by Choi (1972) for the Scotian Shelf. The particulate organic carbon (D.O.C.) is comprised of 63% nanoplankton (235 $gC\ m^{-2} yr^{-1}$)and 37% net phytoplankton (138 $gC\ m^{-2} yr^{-1}$) (Thomas et al 1978, O'Reilly and Busch 1979).

Platt (1971) has estimated the caloric equivalents of phytoplankton. He found that at the beginning of the spring bloom, the caloric equivalent was 7.68×10^4 $J \cdot gC^{-1}$ (18.36 $KCal \cdot gC^{-1}$) dropping to 6.23×10^4 $J \cdot gC^{-1}$ (14.9 $KCal \cdot gC^{-1}$) as the bloom passed. The mean value reported by Platt is 6.61×10^4 $J \cdot gC^{-1}$ (15.8 $KCal \cdot gC^{-1}$). Expressing the yearly primary production of Georges Bank in caloric equivalents gives 2.47×10^7 $J \cdot m^{-2} \cdot yr^{-1}$ (5901 $KCal \cdot m^{-2} \cdot yr^{-1}$) as particulate production and D.O.C. of 5.06×10^6 $J \cdot m^{-2} \cdot yr^{-1}$ (1209 $KCal \cdot m^{-2} \cdot yr^{-1}$) (as indicated in Figure 3).

Fig. 3 near here

Zooplankton

Major surveys of the zooplankton of the entire Gulf of Maine - Georges Bank area were carried out by Bigelow (1926) and Fish and Johnson (1937). Since then there have been numerous investigations of zooplankton, though usually on a smaller geographic scale (Clarke 1933, 1934; Clarke and Zinn 1937; Redfield 1939; Redfield and Beale 1940, 1941; Clarke et al. 1943; Riley and Bumpus 1947; Whiteley 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. The later studies were usually of a small scale spatially and of short duration.

In 1971 NEFC began routine sampling of zooplankton with 333 μ bongos during spring and autumn bottom trawl cruises. Since 1976, plankton sampling by NEFC has been conducted on separate cruises and some smaller mesh nets, including 165 μ and 255 μ nets, were used in addition to 333 μ nets for zooplankton. However, data from the smaller mesh nets are not yet available. Intensive zooplankton sampling was also done from 1971 to 1978 on the ICNAF larval herring program covering the period from September to February; these data are also not yet available.

The mean density of zooplankton during 1972-1975 bottom trawl surveys was 0.02 g dry wgt$\cdot m^{-3}$ for both spring and fall. Assuming an average depth of 50 m, the equivalent density of zooplankton is estimated as about 1 g dry wgt$\cdot m^{-2}$. Similar calculations for the 1977 and 1978 plankton surveys which covered the period from March to November almost monthly, yielded average annual estimates of .037 and .025 g dry wgt$\cdot m^{-3}$ (corresponding to 1.85 and 1.25 g dry wgt$\cdot m^{-2}$) extrapolating from the early spring and late fall values to account for December through February (J. Kane, NEFC, Narragansett, Rhode Island, personal communication). These are considerably lower than the average value of 6 g dry wgt$\cdot m^{-2}$ reported for the North Sea (Steele 1974). The NEFC samples are all from the 333 μ net and so even copepodite stages (1-3) of relatively small zooplankters such as Centropages and Pseudocalanus, which are very abundant on Georges Bank, were undersampled.

Riley and Bumpus (1946) report a range of values from 2.8 to 38.1 gm dry wgt$\cdot m^{-2}$ with a mean value of 16.7 gm dry wgt$\cdot m^{-2}$. However, their values probably are too high since they used a wet volume to dry weight conversion of 25%; more recent estimates have given values averaging about 10% (Kane 1979). Assuming that 2 g dry wgt$\cdot m^{-2}$ is a minimum estimate of total zooplankton based on NEFC samples and that 15 g dry wgt$\cdot m^{-2}$ is a maximum based on the highest values reported by Riley and Bumpus (1946) revised according to Kane's (1979) displacement volume to dry weight conversion, we estimated the range in zooplankton production as 3.10×10^5-2.31×10^6 $J \cdot m^{-2} \cdot yr^{-1}$ (74-551 $KCal \cdot m^{-2} \cdot yr^{-1}$) based on a P/B ration of 7 (Crisp 1975) and a conversion factor of 2.20×10^4 $J \cdot g^{-1}$ dry wgt^{-1}(5.25 $KCal \cdot g^{-1}$ dry wgt) (Laurence 1976). Crisp (1975) used a P/B ratio of 7 for Calanus, applied to all zooplankton; we have made the same assumption. If omnivores have a 20% growth efficiency and herbivores have a 32% growth efficiency (Steele 1974) and both have an assimilation efficiency of 70% (Crisp 1975), then between 5 and 55% of the primary production must be consumed by zooplankton. For example, conservative estimates of production and consumption, if all zooplankton are herbivores, are 3.07×10^5 $J \cdot m^{-2} \cdot yr^{-1}$ or 73.5 $KCal \cdot m^{-2} \cdot yr^{-1}$ (2 g dry wgt$\cdot m^{-2}$x 2.20×10^4 J/g dry wgt x 7) and 1.37×10^6 $J \cdot m^{-2} \cdot yr^{-1}$ or 328.0 $KCal \cdot m^{-2} \cdot yr^{-1}$($3.07 \times 10^5$ $J \cdot m^{-2} \cdot yr^{-1}$/(0.32x0.7)), respectively. Consumption is then about 5% of primary productivity (1.37×10^6 $J \cdot m^{-2} \cdot yr^{-1}$/2.97x.07 $J \cdot m^{-2} \cdot yr^{-1}$). Similar calculations were done assuming all zooplankton are omnivores to obtain the upper limit. The figures agree well with the range of experimental observations made in the New York Bight and on Georges Bank by Walsh et al. (1978) and Dagg (personal communication). Based on the preceding discussion, a

mean zooplankton production rate of 1.46×10^6 $J \cdot m^{-2} \cdot yr^{-1}$ (350 $KCal \cdot m^{-2} \cdot yr^{-1}$) (well within the range of available estimates) was assumed (Figure 3).

Benthos

There has been a great deal of research on the benthic fauna of the Georges Bank - Gulf of Maine area carried out at the NEFC (Wigley 1961; Wigley and McIntyre 1964; Wigley and Emery 1968; Wigley and Theroux 1970). Most studies have been directed towards macro- and megabenthic species although some included the meiobenthos.

The literature was reviewed in order to determine dominant or trophically important benthic species of taxonomic groups on Georges Bank (Wigley 1968; Bowman et al. 1976; Wigley, personal communication). We found approximately 80 species that fit the above definition for one reason or another. The literature on these or related species was examined for any data on estimated productivity; a little was found for commercially valuable species, e.g., sea scallop, but not enough to estimate total benthic productivity on Georges Bank.

An alternate method was attempted based on the use of production to biomass (P/B) ratios. The most recent estimate of benthic macrofaunal biomass on Georges Bank is 240 g wet $wgt \cdot m^{-2}$ (Wigley, personal communication). This estimated average biomass was converted into $J \cdot m^{-2}$ using conversions in the literature for various groups of benthic invertebrates (Brawn et al. 1968; Cummins and Wuycheck 1971; and Thayer et al. 1973). The result was about 5.02×10^5 $J \cdot m^{-2} \cdot yr^{-1}$ (120 $KCal \cdot m^{-2} \cdot yr^{-1}$). P/B ratios from the literature were then used to calculate the yearly productivity from the biomass data.

A variety of annual P/B estimates is available in the literature for benthic invertebrates. Values range from 0.2 for Barents Sea benthos (Zenkevitch 1956) to 5.0 for ampeliscid 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 Georges Bank we used 1.5. This P/B ratio results in an estimate of macrobenthic productivity of 7.53×10^5 $J \cdot m^{-2} \cdot yr^{-1}$ (180 $KCal \cdot m^{-2} \cdot yr^{-1}$).

A similar procedure was used to estimate meiofaunal productivity on Georges Bank. Wigley and McIntyre (1964) sampled a transect of stations south of Martha's Vineyard, approximately 50 nautical miles west of the southwestern border of Georges Bank. Considering only the eight stations that were less than 200 m in depth (40-179 m), the average total macrofaunal biomass was 250 $g \cdot m^{-2}$ almost identical to a recent estimate for Georges Bank (240 $g \cdot m^{-2}$, Wigley, personal communication). Although the macrofaunal standing stocks are similar for these two areas we cannot be certain of the similarity in meiofaunal biomass or productivity; however, we have no choice but to use the available data. The meiofaunal biomass at these same eight stations ranged from 1.7 to 4.6 $g \cdot m^{-2}$ wet wgt and averaged 2.5 $g \cdot m^{-2}$ (Wigley and McIntyre 1964). Using Crisp's (1975) conversion of 2 g wet wgt per KCal, which is probably a minimum value for meiofauna, we get 5.23×10^3 $J \cdot m^{-2}$ (1.25 $KCal \cdot m^{-2}$), or a range of 3.56×10^3 to 9.62×10^3 $J \cdot m^{-2}$ (0.85 to 2.3 $KCal \cdot m^{-2}$). Meiofauna biomass estimates for some other areas are as follows: Western Baltic 1.05×10^4 $J \cdot m^{-2}$ (2.5 $KCal \cdot m^{-2}$)

(Arntz 1978); Helgoland Bay, 4.18×10^2 to 4.18×10^3 $J \cdot m^{-2}$ (0.1 to 1.0 $KCal \cdot m^{-2}$) (Gerlach 1971); and the North Sea, 1.55×10^4 $J \cdot m^{-2}$ (3.7 $KCal \cdot m^{-2}$) (McIntyre 1978). Meiofaunal biomass estimate for Georges Bank may be somewhat low. When compared on a total macro- to meiofauna biomass ratio basis, the 100:1 ratio for the Wigley and McIntyre (1964) data is greater than most other macro/meio ratios for other continental shelf areas of the temperate North Atlantic, e.g. 35:1 in Helgoland Bight (Gerlach 1971), 50:1 in Western Baltic (Arntz 1978), 40:1 in North Sea (McIntyre 1961, cited by Wigley and McIntyre 1964), and 90:1 in the English Channel (Mare 1942, cited by Wigley and McIntyre 1964). The high ratio is primarily due to one station with a high biomass of large infauna; the other seven stations had ratios ranging from 12:1 (inshore) to 120:1 (mid-shelf) with a mean of 40-45:1 (Wigley and McIntyre 1964). It is apparent that there is a great deal of room for error in adjusting our meiofaunal biomass, we have therefore accepted the estimate of 5.23×10^3 $J \cdot m^{-2}$ (1.25 $KCal \cdot m^{-2}$) with the caveat that it may be low.

Using the estimate of meiofauna biomass of 5.23×10^3 $J \cdot m^{-2}$ (1.25 $KCal \cdot m^{-2}$) we estimated annual production for Georges Bank by applying P/B ratios developed by Arntz (1978) for the Western Baltic. In the Western Baltic the estimates of the macrofaunal biomass (5.2×10^5 $J \cdot m^{-2}$, 132 $KCal \cdot m^{-2}$) and productivity (2.09×10^5 to 5.86×10^5 $J \cdot m^{-2} \cdot yr^{-1}$, $KCal \cdot m^{-2} \cdot yr^{-1}$ 50-140 $KCal \cdot m^{-2} \cdot yr^{-1}$) lie between Crisp's (1975) estimate for the North Sea and our estimate for Georges Bank, although as aforementioned, the meiofaunal biomass (1.05×10^4 $J \cdot m^{-2}$, 2.5 $KCal \cdot m^{-2}$) is twice the estimate we are using

for Georges Bank. The meiofaunal P/B ratios Arntz calculated ranged between 5:1 and 12:1. These ratios, applied to our Georges Bank meiofaunal biomass estimate, yield a range of annual production of 2.62×10^4 to 6.28×10^4 $J \cdot m^{-2} \cdot yr^{-1}$ (6.25 to 15 $KCal \cdot m^{-2} \cdot yr^{-1}$). This estimated range of annual meiofaunal production is less than values reported elsewhere in the North Atlantic, e.g. Steele (1974) reports 8.37×10^4 $J \cdot m^{-2} \cdot yr^{-1}$ (20 $KCal \cdot m^{-2} \cdot yr^{-1}$) in the North Sea and Elmgren (1976) reports 1.09×10^5 $J \cdot m^{-2} \cdot yr^{-1}$(26 $KCal \cdot m^{-2} \cdot yr^{-1}$) in the Baltic. Considering, however, that our Georges Bank biomass estimate is minimal, the actual production is probably very similar, i.e. around 8.37x10 $J \cdot m^{-2} \cdot yr^{-1}$ (20 $KCal \cdot m^{-2} \cdot yr^{-1}$). Based on these calculations the meiofauna appear to contribute only about 10% of the total benthic productivity on Georges Bank. This is much less than the reported relative contribution of the meiofauna elsewhere in the North Atlantic, e.g. Steele (1974) reports a value of 40% in the North Sea and Elmgren (1976) estimates one of 49% in the Baltic. This may reflect the fact that macrobenthos on Georges Bank can feed directly on living phytoplankton due to strong vertical mixing and shallow depths, resulting in a relatively higher proportion of macrobenthic production than found in the North Sea.

Although in general the meiofaunal benthic production may contribute less than 50% of macrofaunal production in temperate waters, the meiofauna has a much higher metabolism and rate of food consumption. Gerlach (1971) estimated the meiofaunal metabolism and food consumption to be five times the macrofaunal metabolism and food consumption in Helgoland Bay, for example.

Fish

The finfish and squid biomass, production rate and consumption rate for Georges Bank were estimated based on research vessel bottom trawl surveys and results of virtual population analysis, production to biomass ratios (P/B) and consumption to biomass ratios (C/B), respectively. The method of calculation is summarized below; further details are given by Grosslein et al. (1980).

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. Herring less than age 2 are not caught on Georges Bank. The 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 portion of mackerel consumption and production can be attributed to Georges Bank.

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

$$\alpha C = G + S + Q \tag{1}$$

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 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, using stock size estimates in numbers at age calculated by virtual population analysis (VPA). Estimates of G were based on observed growth rates of the species considered. Q is estimated as a power function of weight. The assimilation coefficient, α, was assumed equal to 0.8. S was estimated for each age and species based on a review of the literature and unpublished NEFC data on fecundity, percent maturity, and age and sex ratios. The geometric means (over all years considered) of P/B and C/B ratios for each species based on the annual virtual population estimates and Equation (1) are given in Table 1.

From the P/B and C/B ratios calculated for these six species 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 (1979).

The mean biomass of the six species considered above (herring, mackerel, cod, haddock, silver hake, and yellowtail flounder) during each period was based on virtual population analysis. Biomass estimators 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 per unit area of Georges Bank alone. 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. This procedure assumes identical fishing power of the standard survey trawl in all areas.

Production and consumption of pollock, other flounder, and other finfish were calculated by applying the geometric mean P/B and C/B ratios for all six species considered in Table 1 (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. 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. The calculated production, consumption, and biomass by species group per unit area of Georges Bank are given in Table 2. Results from the later period are included in Figure 3.

Both consumption and average biomass declined by about 42% between 1964-1966 and 1973-1975, but production declined by only 26%. The smaller 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.

Energy Budgets - Georges Bank vs North Sea

The Georges Bank energy budget was modeled after those of Steele (1974) and Crisp (1975) for the North Sea. The energy flow and relative productivity of the North Sea is compared with that on Georges Bank in Figures 3 and 4, where all values are shown in $J \cdot m^{-2} \cdot yr^{-1}$. It should be noted that Georges Bank appears to be more productive per unit area than the North Sea at all trophic levels. However, it is important to keep in mind that the North Sea is a much larger area than Georges Bank (570,000 km^2 vs 52,579 km^2) with greater heterogeneity, containing both shallow and relatively deep areas, and with a well developed thermocline in summer. The two areas are not strictly comparable oceanographically but do provide

Fig. 4 near here

a useful comparison since both are temperate shelf areas, heavily exploited with similar fish species, and have what appear to be generally similar trophic structures.

Primary Production

The annual primary production in the North Sea is considered to be on the order of 100 $gC \cdot m^{-2} \cdot yr^{-1}$ (Steele 1974; Crisp 1975) as compared with an estimated 400-500 $gC \cdot m^{-2} \cdot yr^{-1}$ on Georges Bank. Thus it appears that Georges Bank has a level of primary production about four to five times that of the North Sea on an annual basis. Recent studies in the southern bight area of the North Sea by Mommaerts (cited in Polk 1978), indicate production as high as 220 to 370 $gC \cdot m^{-2} \cdot yr^{-1}$. Since this study was in a shallow (<15 m) coastal region we have used the estimate based on earlier studies pending further investigation.

For comparison with Georges Bank we modified Crisp's energy budget for the North Sea by using the same conversion of 6.61×10^4 $J \cdot gC^{-1}$(15.8 $KCal \cdot gC^{-1}$) instead of 4.18×10^4 $J \cdot gC^{-1}$(10 $KCal \cdot gC^{-1}$) to calculate total energy produced by phytoplankton; this conversion results in a 58% increase in absolute primary production values over those used by Crisp. Thus the total primary production of the North Sea was estimated to be 6.61×10^6 $J \cdot m^{-2} \cdot yr^{-1}$(1580 $KCal \cdot m^{-2} \cdot yr^{-1}$), of which 5.49×10^6 J (1311 KCal) or 83% was available in particular form to herbivores (Figure 4).

Comparable figures for Georges Bank were total primary production of 2.97×10^7 $J \cdot m^{-2} \cdot yr^{-1}$ (7110 $KCal \cdot m^{-2} \cdot yr^{-1}$) of which 2.47×10^7 J (5901 KCal) or 83% was assumed to be available to herbivores and omnivores (Figure 3). The greater production on Georges Bank is probably due primarily to its shallowness. Wind and tidal mixing recycle nutrients in the water column

and 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. However, this advection implies transport of water off the bank, and some of the production probably is lost in this manner.

Zooplankton Production

Crisp (1975) estimated zooplankton production in the North Sea in two ways: 1) assuming 75% of particulate phytoplankton consumed by zooplankton with a growth efficiency of 30%, and 2) a direct estimate using zooplankton biomass and assuming a P/B rationof 7; these estimates were 7.53×10^5 and 7.32×10^5 $J.m^{-2}.yr^{-1}$ (180 and 175 $KCal.m^{-2}.yr^{-1}$), respectively. For comparison with Georges Bank we have recalculated zooplankton production for the North Sea but with somewhat modified assumptions. We assumed that 75% of particulate carbon is consumed by zooplankton with nanoplankton consumed by microzooplankton (32% growth efficiency) which are consumed by macrozooplankton (20% growth efficiency) and net phytoplankton consumed directly by macrozooplankton (32% growth efficiency). This trophic structure is based on the work of Parsons and Lebrasseur (1970). This probably overestimated macrozooplankton production as it assumed that 100% of microzooplankton are consumed. The resulting production is only 6.53×10^5 $J.m^{-2}.yr^{-1}$ (156 $KCal.m^{-2}.yr^{-1}$) even though the estimated initial amount of particulate carbon available was 58% higher than that used by Crisp (Figure 4). Our second estimate for the North Sea was 9.66×10^5 $J.m^{-2}.yr^{-1}$ (231 $KCal.m^{-2}.yr^{1}$) derived from the same zooplankton biomass and P/B ratio used by Crisp (1975) but substituting the conversion of 2.20×10^4 J.gC (5.25 $KCal.gC^{-1}$) for that of 1.67×10^4 $J.gC^{-1}$ (4 $KCal.gC^{-1}$) used in the

Crisp formulation, see Figure 4. The average of our two estimates (149 $KCal \cdot m^{-2} \cdot yr^{-1}$) for the North Sea is only slightly higher than Crisp's values but our estimate of the proportion of particulate carbon converted to zooplankton production is somewhat lower than Crisp's values, 15% versus 22%.

The zooplankton production for Georges Bank is 1.46×10^6 $J \cdot m^{-2} \cdot yr^{-1}$ (350 $KCal \cdot m^{-2} \cdot yr^{-1}$) which is about two times as large. This is half the ratio observed for the primary production (Figure 3). Better measures of zooplankton biomass on Georges Bank will be required before we can evaluate the zooplankton production estimates further. The results of calculations on the amount of phytoplankton consumed, discussed earlier in the paper, agree well with the experimental data (Walsh et al. 1978; Dagg, personal communication). This low value is not consistent with the values of 100% used by Steele (1974) and of 75% used by Crisp (1975). This disparity implies either a major difference between the North Sea and Georges Bank in the extent of zooplankton consumption or that the data or assumptions for one or the other location (or both) are incorrect. Assuming that the data for both areas are correct, a great deal more energy per unit area will be available to the benthos on Georges Bank than in the North Sea, since not only is the magnitude of primary productivity greater on Georges Bank but the fraction directly available to the benthos is also greater. Of course, some of the primary and secondary production is advected off the bank.

Benthic Production

We estimate total benthic production in the North Sea as 4.18×10^5 $J \cdot m^{-2} \cdot yr^{-1}$ (100 $KCal \cdot m^{-2} \cdot yr^{-1}$) as compared to 8.37×10^5 $J \cdot m^{-2} \cdot yr^{-1}$ (200 $KCal \cdot m^{-2} \cdot yr^{-1}$) for Georges Bank. Our North Sea estimate is based on Crisp's (1975) estimate of macrobenthos production of 2.51×10^5 $J \cdot m^{-2} \cdot yr^{-1}$ (60 $KCal \cdot m^{-2} \cdot yr^{-1}$) and Steele's (1974) conclusion that macrobenthos production is 60% of the total (ignoring microbenthos). This implies meiobenthos production of 1.67×10^5 $J \cdot m^{-2} \cdot yr^{-1}$ (40 $KCal \cdot m^{-2} \cdot yr^{-1}$) or twice that reported by Steele (1974). Using the direct estimates of North Sea meiofauna biomass of 3.7 $KCal \cdot m^{-2}$ by McIntyre (1978) and assuming a P/B ratio of 8.5, the midpoint of the range reported by Arntz (1978), meiobenthos production may be estimated directly as 1.20×10^5 $J \cdot m^{-2} \cdot yr^{-1}$ (31 $KCal \cdot m^{-2} \cdot yr^{-1}$). Meiobenthos production of 8.37×10^4 to 1.26×10^5 $J \cdot m^{-2} \cdot yr^{-1}$ (20-30 $KCal \cdot m^{-2} \cdot yr^{-1}$) for the North Sea appears consistent with Crisp's calculations; he estimated that 1.67×10^6 J (400 KCal) were consumed by macrobenthos leaving only 2.51×10^5 J (60 KCal) or 13% of available energy for meio- and microbenthos. A P/C ratio of about 0.4 or 0.5 which seems reasonable for the smaller benthic organisms would be sufficient to yield 8.37×10^4 to 1.26×10^5 $J \cdot m^{-2} \cdot yr^{-1}$ (20-30 $KCal \cdot m^{-2} \cdot yr^{-1}$). A P/C ratio of 0.7 would be required to yield 1.67×10^5 $J \cdot m^{-2} \cdot yr^{-1}$ (40 $KCal \cdot m^{-2} \cdot yr^{-1}$), the additional amount needed to provide a total benthic production of 4.18×10^5 $J \cdot m^{-2} \cdot yr^{-1}$ (100 $KCal \cdot m^{-2} \cdot yr^{-1}$) using Crisp's estimate of energy available to benthos.

If the total energy actually available to the benthos in the North Sea is as much higher as indicated by our estimates in the comparison with those of Crisp (3.28×10^6 vs 1.93×10^6 J) (783 vs 460 KCal - see Figure 4) then total benthic production in the North Sea could be substantially higher

higher than 4.18×10^5 $J \cdot m^{-2} \cdot yr^{-1}$ (100 $KCal \cdot m^{-2} \cdot yr^{-1}$). For example, if 1.67×10^6 J (400 KCal) are consumed by macrobenthos as estimated by Crisp then nearly half or 1.60×10^6 J (383 KCal) would be left for meio- and microbenthos of which much more than 15% could be converted into production. Assuming, however, that the benthic production estimates reported for the North Sea are approximately correct, this would imply that our absolute estimate of energy available to the benthos is too high - perhaps because the phytoplankton caloric conversion of 6.61×10^4 $J \cdot gC^{-1}$ (15.8 $KCal \cdot gC^{-1}$) is too high.

A more significant difference between the two areas is the apparent lower level of benthic production per m^2 on Georges Bank relative to total energy per m^2 in the system. Total benthic production on Georges is $8.37 \times 10^5 / 2.97 \times 10^7$ (200/7110) = 2.8% of the total energy available from phytoplankton as compared with $4.18 \times 10^5 / 6.61 \times 10^6$ (100/1580) = 6.3% for the North Sea, based on our calculations and shown in Figures 3 and 4. If we assume a 4.18×10^4 $J \cdot gC^{-1}$ (10 $KCal \cdot gC^{-1}$) conversion for phytoplankton production the comparable calculations would be $8.37 \times 10^5 / 1.88 \times 10^7$ (200/4500) = 4.4% and $4.18 \times 10^5 / 4.18 \times 10^6$ (100/1000) = 10% for Georges Bank and the North Sea, respectively. Either way the benthic production on Georges Bank appears to be low compared with the North Sea by more than a factor of 2. As noted earlier it is possible that production of the meio- and microbenthos is underestimated for Georges Bank.

If we assume that Steele's 60/40 ratio of macro- to meiofauna production applies to Georges Bank then total benthic production on Georges would be 1.26×10^6 $J \cdot m^{-2} \cdot yr^{-1}$ (300 $KCal \cdot m^{-2} \cdot yr^{-1}$), an increase of 50%. This would

reduce the discrepancy to somewhat less than a factor of 2 but the total benthic production on Georges would still be low relative to the North Sea. One possible explanation is advective loss of plankton production from Georges Bank. Over half the total carbon would have to be lost in this way to bring the benthic production/total production ratio into line with the North Sea, using the benthic production estimate of 8.37×10^5 $J \cdot m^{-2} \cdot yr^{-1}$ (200 $KCal \cdot m^{-2} \cdot yr^{-1}$) for Georges Bank, and about 1/3 the total would have to be lost if we use 1.26×10^6 $J \cdot m^{-2} \cdot yr^{-1}$ (300 $KCal \cdot m^{-2} \cdot yr^{-1}$). Another possible explanation might be that a greater proportion of energy on Georges Bank is tied up in large relatively slow-growing mollusks and echinoderms. On the other hand, it is also possible that filter feeders on Georges Bank consume live phytoplankton to a greater extent because of the strong vertical mixing and the shallowness of the bank.

Estimates of benthic productivity are subject to many errors and neither the Georges Bank nor the North Sea estimates adequately take into account the microfauna. More detailed studies of the benthic productivity in the two regions, and a better understanding of circulation on Georges Bank, will be required to evaluate these possibilities.

Fish Production

Crisp (1975) estimated the production of North Sea pelagic and demersal fish species as 3.3×10^4 $J \cdot m^{-2} \cdot yr^{-1}$ (8.0 $KCal \cdot m^{-2} \cdot yr^{-1}$) and 1.05×10^4 $J \cdot m^{-2} \cdot yr^{-1}$ (2.5 $KCal \cdot m^{-2} \cdot yr^{-1}$), respectively. These estimates are based on fishery production (by assuming exploitation rates). Georges Bank production of pelagics (herring, mackerel, and squid) was 2.59×10^4 and 2.38×10^4 $J \cdot m^{-2} \cdot yr^{-1}$ (6.2 and 5.7 $KCal \cdot m^{-2} \cdot yr^{-1}$) during periods of high and low biomass, respectively. The corresponding values for demersals were 4.60×10^4 and 2.93×10^4 $J \cdot m^{-2} \cdot yr^{-1}$

(11.0 and 7.0 $KCal \cdot m^{-2} \cdot yr^{-1}$). Thus, the pelagic production of the two areas is similar, but the demersal production of Georges Bank is substantially higher than the North Sea.

Both the total difference and the relative difference between demersal and pelagic components of fish production between the two regions pose questions analagous to those for the benthic production. Total fish production (per m^2) on Georges Bank was less than twice that in the North Sea although primary production appears more than four times as great on Georges Bank. The pelagic fish production estimates for Georges Bank were actually less than those for the North Sea, whereas demersal fish production on Georges Bank appeared to be 3-4 times that of the North Sea. It is quite possible that the P/B ratio used for squid was too low and this would have increased the pelagic production estimate somewhat for Georges Bank, but probably not enough to change the picture drastically. Mackerel production on Georges Bank was also probably underestimated by partitioning total production of the stock according to the size of Georges Bank relative to the total area inhabited by the stock. Another likely source of error could be unaccounted production of small pelagic species or species such as sand lance on Georges Bank. Finally, we have not yet accounted for birds and mammals but their energy requirements are thought to be relatively small in the Georges Bank area compared with that of the pelagic fish component.

Although we probably underestimated pelagic fish production on Georges Bank, it is unlikely that the estimate was low by a factor of 2.5, which is about the level of difference needed to bring the ratio of pelagic fish/

zooplankton production in line with the values for the North Sea. On the other hand, in order to account for the relatively low level of pelagic fish production on Georges through advective losses of plankton production, we have to assume about a 68% loss.

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. Crisp's estimates do not include production of reproductive material. Another factor to consider is that in any area a decade probably is not a sufficiently long time upon which to base estimates of average or sustainable fish production because of recruitment variations.

The average recruitment to biomass ratios (R/B) of herring, cod, mackerel, silver hake, yellowtail flounder, and haddock, are 0.16, 0.05, 0.14, 0.10, 0.06, and 0.03, respectively (Grosslein et al. 1980). Of course, R/B depends on the designated age at recruitment with this ratio increasing with age. In the North Sea, where small mesh nets are typically used, the R/B ratios are probably not significantly larger than those calculated for Georges Bank with age at recruitment designated as age 1 or 2. Assuming that annual reproductive energy is 10% of the biomass for sexually mature fish (as was assumed by Grosslein et al. (1980) for several species) 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. Clearly, both the production estimates reported by Crisp and those reported here underestimate the total production of the fish community (including all life stages). Further details of energy flow within the Georges Bank finfish and squid community are summarized in Figure 5.

Fig. 5 near here

It is also possible to compare finfish and squid consumption in the two areas. In the North Sea, the decline in biomass of herring and mackerel during the 1960s was accompanied by an increase in biomass of certain other species, particularly the gadids. 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 gadids. In the case of Georges Bank (1964-1966 vs 1973-1975), the decline in herring and mackerel biomass was also 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 by exploitable size fish of nine species considered by Jones and Richards for the North Sea declined by 33% between the early and late 1960s. 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: 8.03×10^5 vs 2.3×10^5 $J \cdot m^{-2}$ (192 vs 55 $KCal \cdot m^{-2}$) for the high biomass period and 4.64×10^5 vs 1.51×10^5 $J \cdot m^{-2}$ (111 vs 36 $KCal \cdot m^{-2}$) 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%, respectively, of the total Georges Bank consumption during the two periods. The North Sea values typically apply to fish age 2 and older whereas the Georges Bank values apply to age 1 and older (except for herring). Nevertheless, it is likely that total consumption per unit area is higher on Georges Bank than in the North Sea, as would be expected with a higher density of fish.

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 1960s). Consumption per unit area on Georges Bank appears to be higher than in the North Sea. While finfish and squid production per unit area is probably higher on Georges Bank than in the North Sea, the difference is surprisingly small considering the difference in productivity at other trophic levels.

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. Our knowledge of the benthos is very 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. Information on zooplankton production is also very limited and only recently has more complete seasonal coverage of the zooplankton been implemented.

One of the big surprises to arise out of the energy budget exercise was the very high level of primary production on Georges Bank. Previous estimates had been in the range of 200 to 300 $gC \cdot m^{-2} \cdot yr^{-1}$. We have revised the estimate upwards to 400-500 $gC \cdot m^{-2} \cdot yr^{-1}$ and a picture is emerging of a seasonal cycle possibly different from the classical spring-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 combination of recycling and advection. The shallowness of Georges Bank coupled with wind and tidal mixing allows a constant supply of regenerated nutrients from the water column and benthos to reach the phytoplankton in the photic zone. Also a supply of nutrient-rich water is available from the Gulf of Maine and slope water that is advected onto Georges Bank by tidal mixing and other mechanisms. However, some of this productivity is surely lost through transport, and better understanding of the nutrient flux and circulation on Georges Bank is needed to clarify this question.

With regard to fish it is only in the production of pelagic species that there appears to be a significant discrepancy between the Georges Bank and North Sea ecosystems. More accurate accounting of the possible energy "losses" from Georges Bank may explain part of this discrepancy. However if we examine fish production from the entire New England shelf region

from Cape Hatteras to the Gulf of Maine, including Georges Bank (corresponding to ICNAF statistical areas 5 and 6) we see that demersal fish production per unit area is about the same as for the North Sea but pelagic fish production per unit area is still lower by a factor of at least two. The total MSY of finfish and squid for the entire New England area is on the order of 1.3×10^6 tons or about 5 tons$\cdot$km^{-2} (Hennemuth 1976). Although the MSY value overestimates actual production of recruited size fish, in this case the value is probably conservative in comparison with the North Sea estimates of "production," which include contributions from smaller size "pre-recruits" due to the smaller mesh used in the North Sea. The MSY for the New England area is roughly equivalent to a production of 2.09×10^4 J$\cdot$m^{-2} (5 KCal$\cdot$m^{-2}, assuming 1 g wet weight of fish = 1 KCal = 4.18×10^3 J) of which slightly more than half, 1.09×10^4 J$\cdot$m^{-2}, is attributed to the major pelagic species (herring, mackerel, squid, and menhaden). The comparable production for the North Sea is 4.39×10^4 J$\cdot$m^{-2} (10.5 KCal$\cdot$m^{-2}) of which 3/4 or 3.35×10^4 J$\cdot$m^{-2} (8 KCal$\cdot$m^{-2}) is attributed to pelagic fish. Thus it appears that pelagic fish production per unit area is substantially lower on the New England Shelf than in the North Sea even though the primary production levels in the Gulf of Maine and in the Middle Atlantic Bight are thought to be at least as high as 100 gC$\cdot$m$^{-2}\cdot$yr^{-1}. Unique hydrographic features in the New England area such as the relatively deep waters of the Gulf of Maine and the extreme seasonal temperature ranges encountered in the Middle Atlantic Bight (causing large scale migrations in and out of the area) may reduce the productive potential somewhat. Also, losses of coastal water may occur through entrainment by Gulf Stream rings and other processes.

Mills and Fournier (1979) and Mills (1980) examined the structure and dynamics of the marine ecosystem off the coast of Nova Scotia. Primary production on the Scotian Shelf is slightly higher than in the North Sea and considerably lower than on Georges Bank. Like Georges Bank, the efficiency of energy transfer to higher trophic levels is lower for the Scotian Shelf than for the North Sea. In particular, there appears to be a deficit in pelagic fish production for both Northwest Atlantic continental shelf ecosystems when compared to the North Sea. Mills and Fournier (1979) apply a P/B ratio of 0.60 for pelagic fish, approximately double the ratio estimated for Georges Bank. Thus, the deficit in pelagic fish production for the Scotian Shelf might be even greater than reported by Mills and Fournier (1979).

On Georges Bank it is noteworthy that the consumption of one finfish species, silver hake, exceeds total productivity of the exploited finfish and squid community. Silver hake (like cod and squid) feed heavily on other finfish (Grosslein et al. 1980), therefore much of its consumption must be of prerecruit fish. The impact of prerecruit consumption of silver hake and other fish predators is unknown, but its potential significance is very great, particularly since its effects might be partially controlled through management.

In summary, Georges Bank seems to be more productive at all trophic levels than the North Sea, per unit area, but the paths of energy flow in each system appear to be quite different. The amount of zooplankton and benthic production is lower relative to primary production on Georges Bank than in the North Sea. Pelagic fish production on Georges Bank seems to be very much lower relative to primary production and zooplankton production

compared to the North Sea. The discrepancy implies a difference in the whole food web, not just in the zooplankton portion. The ratio of demersal fish production to primary production is about the same in the two areas but again differences in the food web are apparent. Further study is needed to examine the possible export of particulate matter from Georges Bank, and in particular to elucidate the food webs in quantitative terms for comparisons with other marine ecosystems. Even after the effects of variable recruitment are accounted for, we may see some significant differences in the utilization of energy in various ecosystems.

Literature Cited

Arntz, W. E. 1978. The "Upper Part" of the benthic food web: the role of macrobenthos in the western Baltic. Rapp. P.-v. Reun. Cons. Int. Explor. Mer, 173:85-100.

Bigelow, H. B. 1926. Plankton of the offshore waters of the Gulf of Maine. Bull. U.S. Bur. Fish. 40, Part II:1-509.

Bowman, R., R. Maurer, and J. Murphy. 1976. Stomach contents of 29 fish species from five regions in the Northwest Atlantic. Data Rept., NEFC, Woods Hole, MA, Lab. Ref. 76-10, 37 pp.

Brawn, V. M., D. L. Peer, and R. J. Bentley. 1968. Caloric content of the standing crop of benthic and epibenthic invertebrates of St. Margaret's Bay, Nova Scotia. J. Fish. Res. Board Canada, 25:1803-1811.

Butman, B., M. A. Noble, R. C. Beardsley, J. A. Vermersch, R. A. Limeburner, B. Magnell, and R. J. Schlitz. 1980. The mean circulation of Georges Bank as measured by moored current meters. ICES C. M. 1980/C:34.

Choi, Chung L. 1972. Primary production and release of D.O.C. from phytoplankton in the western N. Atlantic Ocean. Deep-Sea Res. 19(10):731-737.

Clark, S. H., and B. E. Brown. 1977. Changes in biomass of finfishes and squids from the Gulf of Maine to Cape Hatteras, 1963-74, as determined from research vessel data. Fish. Bull. 75:1-22.

Clark, S. H., and B. E. Brown. 1979. Trends in biomass of finfish and squid in ICNAF subarea 5 and statistical area 6, 1964-1977, as determined from research vessel survey data. Investigacion Pesquera, 43(1):107-122.

Clarke, G. L. 1933. Diurnal migration of plankton in the Gulf of Maine and its correlation with changes in submarine irradiation. Biol. Bull. 65:402-436.

Clarke, G. L. 1934. Further observations on the diurnal migration of copepods in the Gulf of Maine. Biol. Bull. 67:432-455.

Clarke, G. L., E. L. Pierce, and D. F. Bumpus. 1943. The distribution and reproduction of Sagitta elegens on Georges Bank in relation to hydrographical conditions. Biol. Bull. 85:201-226.

Clarke, G. R., and D. J. Zinn. 1937. Seasonal production of zooplankton off Woods Hole with special reference to Calanus finmarchicus. Biol. Bull. 73:464-487.

Cohen, E. B., M. D. Grosslein, M. P. Sissenwine, and F. Steimle. 1978. Status report on production studies at the Northeast Fisheries Center. NEFC Woods Hole Lab. Ref. Doc. 78-14, 33 p.

Cohen, E. B., and W. R. Wright. 1979. Primary productivity on Georges Bank with an explanation of why it is so high. NEFC Woods Hole Lab. Ref. Doc. No. 79-53, 6 p.

Colton, J. B., Jr., R. F. Temple, and K. A. Honey. 1962. The occurrence of oceanic copepods in the Gulf of Maine - Georges Bank area. Ecology, 43:166-171.

Crisp, D. J. 1975. Secondary productivity in the sea, p. 71-90. In D. E. Reichle, J. F. Franklin, and D. W. Goodal(eds.), Productivity of World Ecosystems. National Academy of Science, Washington, D.C.

Cummins, K. W., and J. C. Wuycheck. 1971. Caloric equivalent for investigation in ecological energetics. Internat. Assoc. Theor. and Applied Limn., Communication No. 18, 158 pp.

Elmgren, R. 1976. Baltic benthos communities and the role of the meiofauna. Contrib. Asko. Lab., Univ. Stockholm, Sweden, 14:1-31.

Fish, C. J., and M. W. Johnson. 1937. The biology of the zooplankton in the Bay of Fundy and Gulf of Maine with special reference to production and distribution. J. Biol. Board Can., 3:189-322.

Gerlach, S. A. 1971. On the importance of marine meiofauna for benthos communities. Oecologia 6:176-190.

Grosslein, M. D., R. W. Langton, and M. P. Sissenwine. 1980. Recent fluctuations in pelagic fish stocks of the Northwest Atlantic, Georges Bank region, in relationship to species interaction. Rapp. P.-v. Reun. Cons. Int. Explor. Mer, 177:374-404.

Hennemuth, R. C. 1976. Fisheries and renewable resources of the Northwest Atlantic Shelf, pp. 146-166 in: Effects of Energy-related Activities on the Atlantic Shelf. Ed. B. Manowitz. Brookhaven National Laboratory, Upton, N.Y.

Hopkins, T. S., and N. Garfield III. (In press). Physical origins of Georges Bank water. J. Mar. Res.

Jones, R., and J. Richards. 1976. Some observations on the interrelationship between the major fish species in the North Sea. ICES, C.M. 1976/F:36.

Kane, J. 1979. Relationships between zooplankton wet volumes and dry weight. Nat. Mar. Fish. Serv., Northeast Fisheries Center, Narragansett Lab. Ref. 79-56.

Laurence, G. C. 1976. Caloric values of some North Atlantic calanoid copepods. Fish. Bull. 74:218-220.

McIntyre, A. D. 1978. The benthos of the western North Sea. Rapp. P.-v. Reun. Cons. Int. Explor. Mer, 172:405-417.

Mills, E. L. 1980. The structure and dynamics of shelf and slope ecosystems off the Northeast Coast of North America. In K. R. Tenore and B. C. Coull (eds.) Marine Benthic Dynamics, Univ. of South Carolina Press.

Mills, E. L., and R. O. Fournier. 1979. Fish production and the marine ecosystems of the Scotian Shelf, Eastern Canada. Marine Biology 54:101-108.

Moiseev, P. A. The Living Resources of the World Ocean. Jerueslem: Israel Program for Scientific Transalation. 1971. Transalated from Izdatelstvo Pishchevaya Promyshlennost, Moscow 1969. 334 p.

Mullen, M. M. 1963. Comparative ecology of the genus Calanus in the Gulf of Maine. Ph.D. Thesis, Harvard Univ., Cambridge, MA, 97 pp.

Odum, E. P. 1971. Fundamentals of Ecology (W. B. Saunders, Philadelphia), p. 46.

O'Reilly, J. E., and D. A. Busch. 1979. Summary of primary productivity made during MARMAP surveys (Belogorsk 78-01, 78-03, 78-04) NOAA, NMFS, NEFC Report, SHL-79-09.

O'Reilly, J. E., and J. P. Thomas. 1979. A manual for the measurement of total daily primary productivity using ^{14}C simulated in situ sunlight incubation. NEFC Sandy Hook Lab. Rept. No. SHL-79-06.

Parsons, T. R., and R. L. Lebrasseur. 1970. The availability of food to different trophic levels in the marine food chain, pp. 325-343. In J. H. Steele (ed.), Marine Food Chains, Oliver and Boyd, Edinburgh.

Parsons, T. R., and H. Seki. 1971. Importance and general implications of organic matter in aquatic environments, pp. 1-27. In D. W. Hood (ed.), Organic matter in natural waters. Inst. Mar. Sci., U. of Alaska, Publ. No. 1.

Parsons, T. R., M. Takahashi, and B. Hargrave. 1977. Biological oceanographic processes. Pergamon Press, Oxford. 332 pp.

Pavshtics, Ye. A. 1963. Distribution of plankton and summer feeding of herring in the Norwegian Seas and on Georges Bank. ICNAF, Spec. Pub. 6 583-590.

Pavshtics, Ye. A., and M. A. Gogoleva. 1964. Plankton distribution in the area of Georges and Browns Banks in 1962. Translation Series, U. S. Naval Oceanographic Office, Trans. 420.

Platt, T. 1971. The annual production by phytoplankton in St. Margaret's Bay, Nova Scotia. J. Cons. int. Explor. Mer, 33:325-333.

Polk, Ph. 1978. The sluice dock at Ostend. Rapp. P.-v. Reun. Cons. Int. Explor. Mer, 173:43-48.

Ramp, S. R., and W. R. Wright. 1979. Northeast Channel flow: the view after one year's measurements. ICES C.M. 1979/C:54.

Ramp, S. R., R. J. Schlitz, and W. R. Wright. 1980. Northeast Channel flow and the Georges Bank nutrient budget. ICES C.M. 1980/C:35.

Raymont, J. 1963. Plankton and productivity in the oceans. Pergamon Press, 660 pp.

Redfield, A. C. 1934. On the proportions of organic derivatives in sea water and their relation to the composition of plankton, p. 176-92 in James Johnstone Memorial Volume, Liverpool Univ. Press. 68 pp.

Redfield, A. C. 1939. The history of a population of *Limacina retroversa* during its drift across the Gulf of Maine. Biol. Bull. 76:26-47.

Redfield, A. C., and A. Beale. 1940. Factors determining the distribution of populations of chaetognaths in the Gulf of Maine. Biol. Bull. 79:459-487.

Redfield, A. C., and A. Beale. 1941. The effect of the circulation of waters on the distribution of the Calanus community in the Gulf of Maine. Biol. Bull. 80-86-110.

Riley, G. A. 1941. Plankton Studies IV. Georges Bank. Bull. Bingham Oceanog. Coll. 7:1-73.

Riley, G.A. 1942. The relationship of vertical turbulence and spring diatom flowerings. J. Mar. Res. 5:67-82.

Riley, G. A. 1946. Factors controlling phytoplankton populations on Georges Bank. J. Mar. Res. 6:54-73.

Riley, G. A. and D. F. Bumpus. 1946. Phytoplankton-zooplankton relationships on Georges Bank. J. Mar. Res. 6:54-76.

Riley, G. A., and D. F. Bumpus. 1947. A theoretical analysis of the zooplankton population on Georges Bank. J. Mar. Res. 6:104-113.

Sanders, H. 1956. The biology of marine bottom communities. Bull. Bingham Oceanog. Coll., Yale Univ. 15:344-414.

Sherman, K. 1966. Seasonal and areal distribution of zooplankton in coastal waters of the Gulf of Maine, 1964. U.S. Fish Wildl. Serv., Spec. Sci. Rept. No. 530.

Sherman, K. 1968. Seasonal and areal distribution of zooplankton in coastal waters of the Gulf of Maine, 1956 and 1966. U.S. Fish Wildl. Serv., Spec. Sci. Rept. No. 562.

Sherman, K. 1970. Seasonal and areal distribution of zooplankton in coastal waters of the Gulf of Maine, 1967 and 1968. U.S. Fish Wildl. Serv., Spec. Sci. Rpt. No. 594.

Sherman, K., and H. C. Perkins. 1971. Seasonal variations in the food of juvenile herring in coastal waters of Maine. Trans. Amer. Fish. Soc. 110(1):121-124.

Steele, J. H. 1974. The structure of marine ecosystems. Harvard Univ. Press, Cambridge, MA. 128 p.

Strickland, J. D. H., and T. R. Parsons. 1968. A practical handbook of seawater analysis. Bull. Fish. Res. Board Can. 167:1-311.

Sverdrup, H. O. 1953. On the conditions for the vernal blooming of phytoplankton. J. Cons. Explor. Mer, 18:287-295.

Thayer, G. W., W. E. Schaaf, J. W. Angelovic, and M. W. LeCroix. 1973. Caloric measurements of some estuarine organisms. Fish. Bull. 21:289-296.

Thomas, J. P., J. E. O'Reilly, C. N. Robertson, and W. D. Phoel. 1978. Primary productivity and respiration over Georges Bank during March and July 1977. ICES C.M. 1978/L:37.

Walsh, J. J., T. E. Whitledge, F. W. Barvenik, C. D. Wirick, and S. O. Howe. 1978. Wind events and food chain dynamics within the New York Bight. Limnol. Oceanogr. 23:659-683.

Whiteley, G. C. 1948. The distribution of larger planktonic crustaceans on Georges Bank. Ecol. Monogr. 18:233-264.

Wigley, R. L. 1961. Benthic fauna of Georges Bank. Trans. 26th Northw. Amer. Wildl. and Nat. Res. Conf., pp. 310-371.

Wigley, R. L. 1968. Benthic invertebrates of the New England fishing banks. Underwater Natur. 5:8-13.

Wigley, R. L., and K. O. Emery. 1968. Submarine photos of commercial shellfish off northeastern United States. Comm. Fish. Rev. 30:43-49.

Wigley, R. L., and A. D. McIntyre. 1964. Some quantitative comparisons of offshore meiobenthos and macrobenthos south of Martha's Vineyard. Limnol. and Oceanog. 9:485-493.

Wigley, R. L., and R. B. Theroux. 1970. Sea-bottom photographs and macrobenthic collections from the continental shelf off Massachusetts. U. S. Fish Wildl. Serv., Spec. Sci. Rept.-Fish. No. 613, 12 pp.

Yentsch, C. S., and J. N. Ryther. 1959. Relative significance of the net phytoplankton and nanoplankton in the waters of Vineyard Sound. Cons. Perm. Int. Explor. Mer, J. du Cons. 24:231-238.

Zenkevitch, L. 1956. Biology of the seas of the U.S.S.R. Geo. Allen and Unwin Ltd., London, 955 pp.

Table 1. Geometric mean (over all ages and years considered) of production to biomass ratio (P/B) and consumption to biomass ratio (C/B).

Species	P/B	C/B
Herring	0.29	4.6
Cod	0.60	3.3
Mackerel	0.34	4.3
Silver hake	0.69	4.9
Yellowtail flounder	0.63	4.6
Haddock	0.41	3.2
All six species combined	0.46	4.1

Table 2. Biomass, consumption, and production of finfish and squid on Georges Bank in millions of joules per kilometer squared.

Species group	1964-1966			1973-1975		
	Biomass	Consumption	Production	Biomass	Consumption	Production
Cod	7,908	22,430	4,481	3,849	12,703	2,770
Haddock	18,719	67,434	8,983	1,854	5,933	761
Redfish	96	25	25	222	707	54
Silver hake	42,058	203,288	24,393	31,012	151,955	18,297
Red hake	4,535	18,594	2,088	3,351	13,740	1,540
Pollock	1,163	4,770	536	494	2,025	226
Yellowtail flounder	2,615	12,025	1,669	2,013	9,259	1,268
Other flounder	1,305	5,351	602	1,000	4,100	460
Herring	80,588	366,188	22,564	25,945	119,349	7,523
Mackerel	5,498	22,635	1,866	11,422	49,116	3,883
Other finfish	7,046	28,886	3,243	9,456	38,769	4,351
Illex	967	6,766	1,033	7,192	50,346	10,791
Loligo	264	1,845	397	1,142	7,996	1,715
Total	172,766	803,596	71,797	98,952	465,955	53,179

LIST OF FIGURES

Figure 1. Mean primary production ($gC \cdot m^{-2} \cdot day^{-1}$) versus time of year for 11 cruises on Georges Bank between late 1975 and late 1978. Each point is a mean of from 4 to 27 individual determinations. Standard deviation varied from 0.36 to 3.02 $gC \cdot m^{-2} \cdot day^{-1}$, with an average of 1.0.

Figure 2. Vertical section through Georges Bank at 68°W showing distribution of temperature (heavy lines, °C) and nitrate (light lines, $\mu g \cdot at \cdot l^{-1}$) measured from R/V ANTON DOHRN (Federal Republic of Germany) in November 1975. Vertical exaggeration about 2000:1. Heavy line on inset map shows location of section.

Figure 3. Georges Bank energy budget (1973-75). All values in $J \cdot m^{-2} \cdot yr^{-1}$. Arrows indicate direction of energy flow.

(1) Estimated 17% of primary production released as dissolved organic carbon (D.O.C.) (Thomas et al., 1978 and O'Reilly and Busch (1979). Assumes that $1gC=6.6x10^4 J$ (15.8 KCal) (Platt 1971). Total production $2.97x10^7 J \cdot m^{-2} \cdot yr^1$.

(2) Zooplankton production based on mean biomass value of 8.5 g dry $wgt \cdot m^{-2}$ and P/B ratio as described in text. Assumes that zooplankton graze only 50% of primary production.

(3) Assumption that 30% of D.O.C. is incorporated into benthic bacteria which attach to particles and enter benthos (Parsons and Sekai 1970).

(4) Assume assimilation efficiency of 70% (Crisp 1975).

(5) Benthic production actually derived from biomass extimates and P/B ratios as described in text.

(6) Pelagic and demersal fish production based on P/B ratios as described in text.

Figure 4. North Sea energy budget (modified from Crisp 1975). All values in $J \cdot m^{-2} \cdot yr^{-1}$. Arrows indicate direction of energy flow.

(1) Estimated 17% of primary production released as dissolved organic carbon (D.O.C.) (Thomas et al. 1978, O'Reilly and Busch 1979). Assumes 1gC = 6.61×10^4J (15.8 KCal) (Platt 1971).

(2) Assume 30% of D.O.C. incorporated into benthic bacteria which attach to particles and enter benthos (Parsons and Seki 1970).

(3) Assumption that 75% of phytoplankton is consumed by zooplankton; remainder is detritus (Crisp 1975). Zooplankton production based on biomass estimate of 6.3 g dry $wgt \cdot^{-2}$ and P/B ratio of 7 (Crisp 1975).

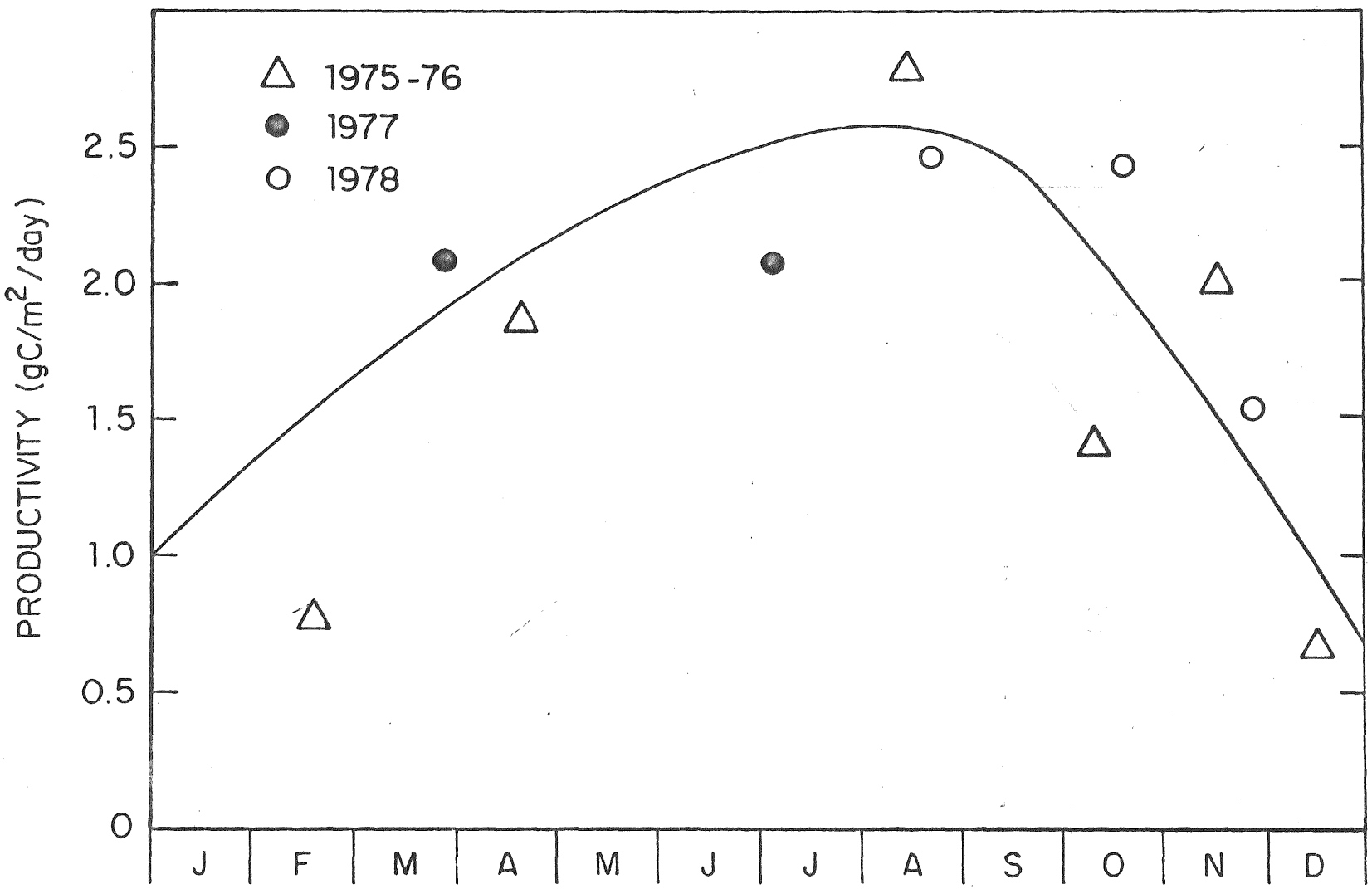
(4) Assume assimilation efficiency of 70% (Crisp 1975).

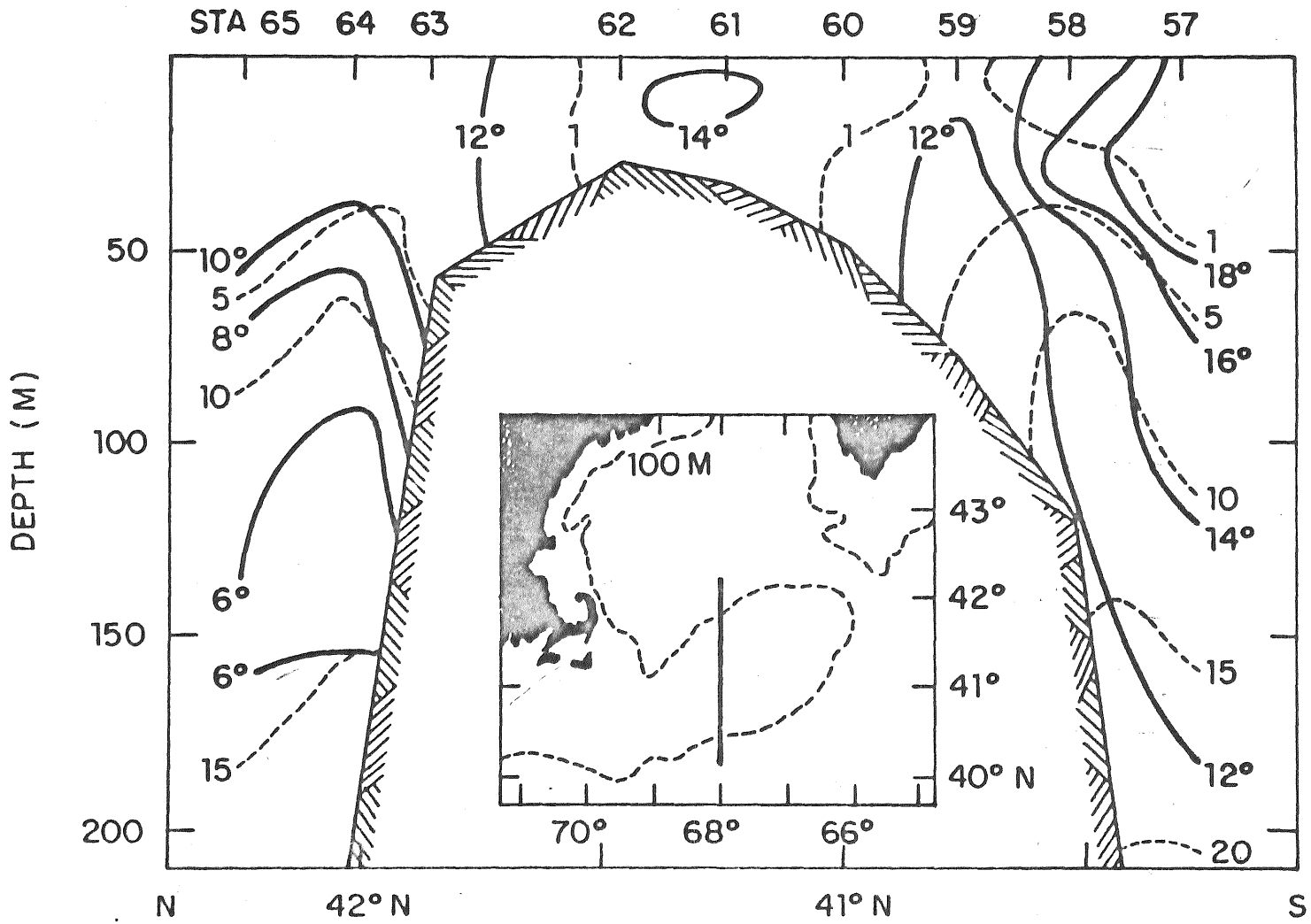
(5) Macrobenthic production calculated from benthic biomass (8.37×10^4 $J \cdot m^{-2} \cdot yr^{-1}$) and P/B ratio of 3 (Crisp 1975).

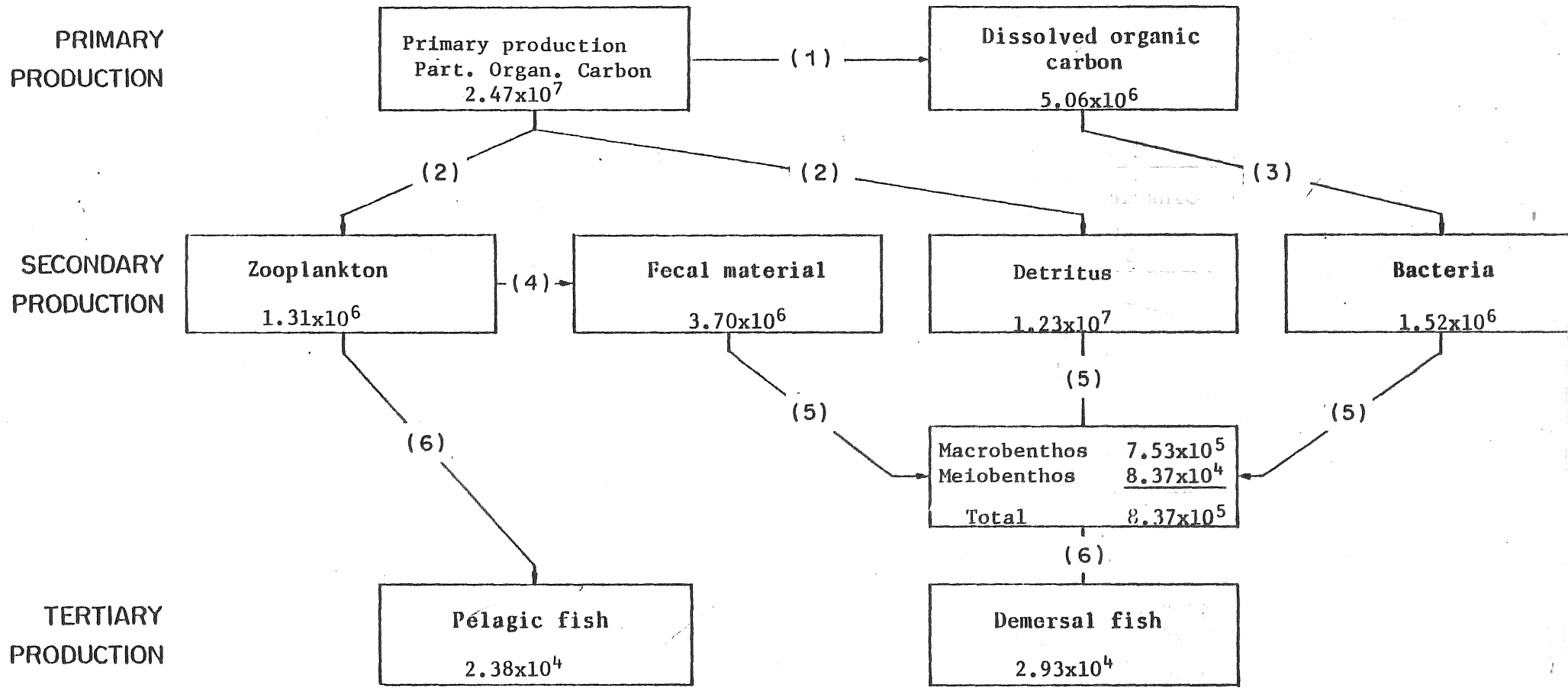
(6) Assumption that 13% of total energy available to benthos is left over for meio- and microbenthos (from Crisp 1975) with further assumption of 30% ecological efficiency for meio- and microbenthos.

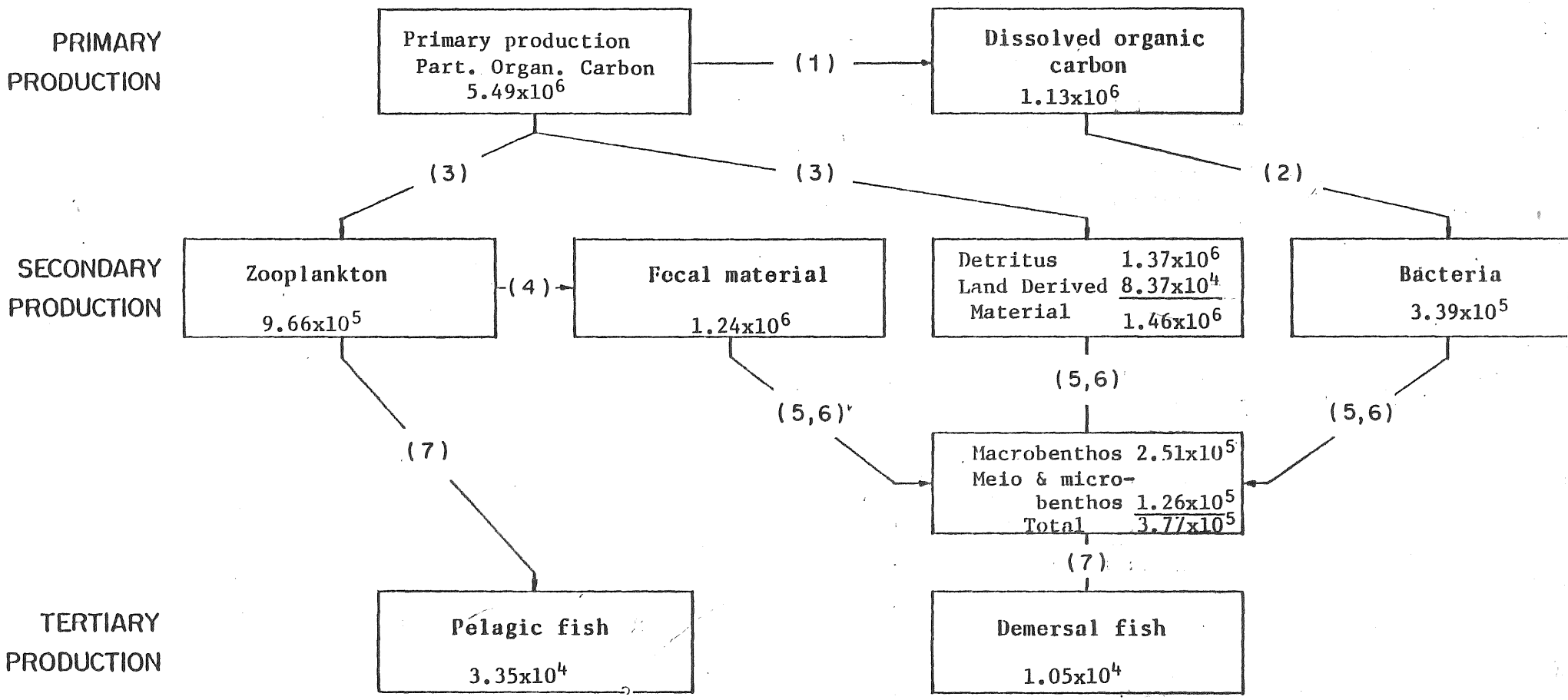
(7) Pelagic and demersal fish production based on catch data of $1.67 \times 10^4$and 8.37×10^3 $J \cdot m^{-2} \cdot yr^{-1}$, respectively (Crisp 1975).

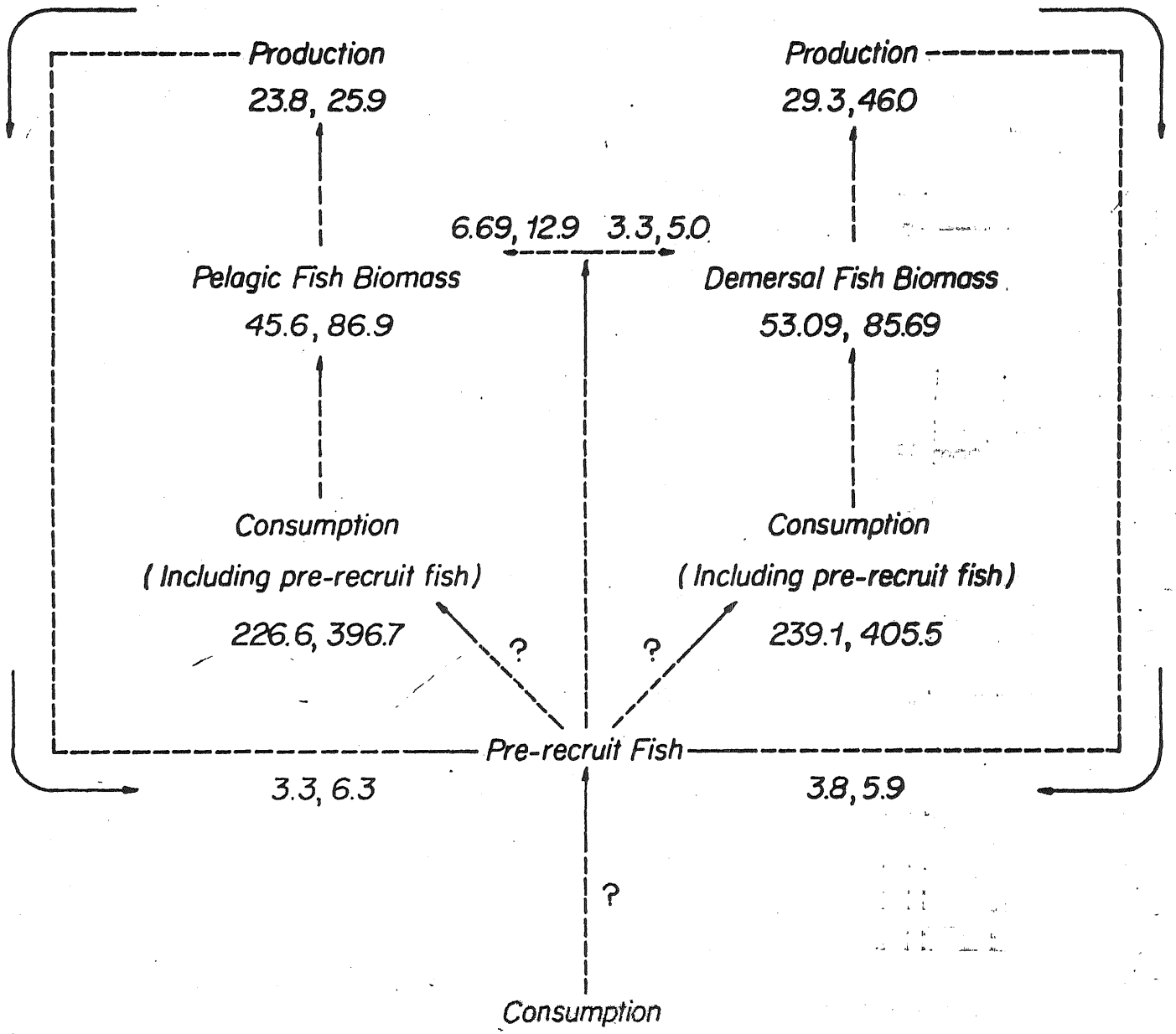
Figure 5. Energy flow of Georges Bank finfish and squid community expressed in $J \cdot 10^3 \cdot m^{-2}$ or $J \cdot 10^3 \cdot m^{-2} \cdot yr^{-1}$. First entry of each item is for 1973-1975, second entry is for 1964-1966. A recruitment to biomass ratio of 0.15 and 0.06 is assumed for pelagics and demersals, respectively. Egg production is assumed to be 7% of fish biomass annually.


1975-76
1977
1978
PRODUCTIVITY (gC/m²/day)
2.5
2.0
1.5
1.0
0.5
0
J
F
M
A
M
J
J
A
S
O
N
D


STA 65 64 63 62 61 60 59 58 57
DEPTH (M)
50
100
150
200
N
42° N
41° N
S
12°
1
14°
1
12°
10°
5
8°
10
6°
6°
15
1
18°
5
16°
10
14°
15
12°
20
100 M
43°
42°
41°
40° N
70°
68°
66°


PRIMARY PRODUCTION
SECONDARY PRODUCTION
TERTIARY PRODUCTION
Primary production
Part. Organ. Carbon
2.47x10^7
(1)
Dissolved organic carbon
5.06x10^6
(2)
(2)
(3)
Zooplankton
1.31x10^6
(4)
Fecal material
3.70x10^6
Detritus
1.23x10^7
Bacteria
1.52x10^6
(5)
(5)
(5)
(6)
Macrobenthos 7.53x10^5
Meiobenthos 8.37x10^4
Total 8.37x10^5
(6)
Pelagic fish
2.38x10^4
Demersal fish
2.93x10^4


PRIMARY PRODUCTION
SECONDARY PRODUCTION
TERTIARY PRODUCTION
Primary production
Part. Organ. Carbon
5.49x10^6
(1)
Dissolved organic carbon
1.13x10^6
(3)
(3)
(2)
Zooplankton
9.66x10^5
(4)
Fecal material
1.24x10^6
Detritus 1.37x10^6
Land Derived 8.37x10^4
Material 1.46x10^6
Bacteria
3.39x10^5
(5,6)
(5,6)
(5,6)
(7)
Macrobenthos 2.51x10^5
Meio & micro-
benthos 1.26x10^5
Total 3.77x10^5
(7)
Pelagic fish
3.35x10^4
Demersal fish
1.05x10^4


Production
23.8, 25.9
Production
29.3, 46.0
6.69, 12.9
3.3, 5.0
Pelagic Fish Biomass
45.6, 86.9
Demersal Fish Biomass
53.09, 85.69
Consumption
(Including pre-recruit fish)
226.6, 396.7
Consumption
(Including pre-recruit fish)
239.1, 405.5
?
?
Pre-recruit Fish
3.3, 6.3
3.8, 5.9
?
Consumption