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STRUCTURE OF THE GEORGES BANK ECOSYSTEM[1]

by

M. P. Sissenwine, E. B. Cohen, and M. D. Grosslein

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

ABSTRACT

Georges Bank is a highly productive fishing ground located off the northeast coast of the USA. Primary productivity is estimated as 6320 Kcal/m^{2}yr (400 g C/m^{2}yr). About 50% of primary productivity is necessary to support 350 Kcal/m^{2}yr of macrozooplankton production (with nanoplankton passing through a longer food chain including microzooplankton). The remaining primary productivity supports 200 Kcal/m^{2}yr of benthic production via a food chain including detritus and bacteria.

Total fish production (all species and sizes together) was 68.9 and 41.7 Kcal/m^{2}yr during 1964-1966 and 1973-1975, respectively. Fish consumed 33% of the suitable food during the latter period of low abundance and 56% during the earlier period of high abundance. Approximately half of demersal fish consumption is of young fish too small to be vulnerable to exploitation.

Gross estimates of early life stage mortality, based on egg production, larval abundance, and subsequent recruitment, confirm that late larval and postlarval mortality is extremely high. Year-class strength is probably determined during late larval or postlarval stages when only a very small difference in mortality rate is necessary to account for the difference between strong and weak year classes.

Introduction

The fishery yield of Georges Bank, like any other fishing ground, ultimately depends on the amount of solar energy stored by phytoplankton as organic carbon and the efficiency of transfer of this energy through the ecosystem to fish and eventually mankind. Biological productivity varies spatially as well as temporally at all trophic levels of the ecosystem, yet some geographic areas are consistently productive (Georges Bank) while others are not (Sargasso Sea). Temporal and spatial variability

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[1] ICES Rapp. Proces.-Verb, (in press).

in the physical environment and chance matches and mismatches of biological aggregations affect variability in productivity. Persistent biological and physical characteristics of the ecosystem (i.e. ecosystem structure) determine long term average productivity.

This paper is concerned with the persistent structure of the Georges Bank ecosystem. Georges Bank is a relatively shallow well mixed area (mean depth of about 50 m) off the northeast coast of the USA (Figure 1). Its surface area (within the 200 m depth contour) is about 53,000 km^2. The water over the central portion of the Bank is isothermal year round. Water on the Bank is maintained separately from the surrounding waters by a clockwise gyre, particularly during the warmer months. Hopkins and Garfield (1980) estimated the replacement time of water on Georges Bank as five months during summer and two months during winter.

Cohen et al. (1982) reported a gross static energy budget of Georges Bank. They did not consider production and consumption of early life stage fish which are too small for exploitation (generally less than 15 cm in length). We updated the energy budget to include these young fish. Our calculations are based on a simple energetic model of a cohort. The method is similar to the approach applied by Jones (1978).

The energy budget identifies critical energy pathways, i.e., where energy may limit production of a higher trophic level or where predation controls production of a lower trophic level. The energy budget may also indicate inconsistencies in calculated production.

We emphasize the partitioning of energy between components of the fish community in relationship to recruitment. Our results are interpreted in light of a cursory review of ichthyoplankton abundance as related to spawning potential and year-class strength.

Consumption and Production of Young Fish

Analytical Method:

We assume that the growth rate of a young fish is exponential (Jones 1978) and that its metabolic rate is a power function of body weight (Paloheimo and Dickie 1965),

$$\frac{dW}{dt} = GW \tag{1}$$

$$\frac{dQ}{dt} = \beta W^{\gamma} \tag{2}$$

where W is weight expressed in units of energy, Q is the amount of energy used for metabolism, G is the instantaneous growth rate and, β and γ are other parameters. The consumption rate is derived by rearranging Winberg's (1956) energy balance equation for an individual fish,

$$\frac{dc}{dt} = \frac{1}{\alpha}\frac{dW}{dt} + \frac{\beta}{\alpha} W^{\gamma} \tag{3}$$

where c is the energy consumed and α is the assimilation coefficient. Reproductive energy is not included in the energy balance equation since we are only considering young (immature) fish.

Let B equal the total energy content of a cohort and assume that B changes exponentially,

$$\frac{dB}{dt} = (G-Z)\ B \tag{4}$$

where Z is the instantaneous total mortality rate of the cohort. Then, the production (P) and the consumption (C) rates of the cohort are,

$$\frac{dP}{dt} = \frac{B}{W}\frac{dW}{dt} = GB \tag{5}$$

$$\frac{dC}{dt} = \frac{B}{W}\frac{dc}{dt} = \frac{1}{\alpha}\frac{dP}{dt} + \frac{\beta}{\alpha} BW^{\gamma-1} \tag{6}$$

By integration,

$$P = \begin{cases} \dfrac{GB_o}{Z-G}\,(1-e^{(G-Z)\Delta t}) & \text{when } G\neq Z \\ GB_o\Delta t & \text{when } G=Z \end{cases} \tag{7}$$

$$C = \frac{1}{\alpha}\,P + \frac{\beta}{\alpha} \cdot \frac{B_oW_o^{\gamma-1}}{Z-\gamma G}\,(1-e^{(\gamma G-Z)\Delta t}) \tag{8}$$

where B_0 and W_0 are the initial biomass (in energy units) of the cohort and of an individual fish, respectively. The interval during which the production and consumption occcurred is Δt. The derivations of Equations (6-7) are similar to the derivation of Baranov's (1918) catch equation (see Beverton and Holt 1957).

Application to Young Fish of Georges Bank:

Grosslein et al. (1980) calculated consumption and production of "exploitable size" fish (defined later) on Georges Bank based on annual estimates of population size in numbers, empirical growth and fecundity functions and an energy balance equation including reproduction. Their results were used by Cohen et al. (1982) in the computation of the Georges Bank energy budget. Since our purpose is to update the Georges Bank energy budget, we base our application of Equations (7-8) on Grosslein et al. (1980).

Grosslein et al. (1980) based parameters of Equation (2), the metabolic function, on an unpublished literature review of G. Laurence. Active metabolism was assumed to be twice resting metabolism (Winberg 1956, Fry 1957). Parameter β is adjusted to correspond to 10.C and annual energy utilization. The resulting parameter estimates are $\beta = 10.04$ kilocalories/year and $\gamma = 0.79$. The assimilation coefficient, α, was assumed equal to 0.8. We use the same parameter estimates herein.

Grosslein et al. explicitly consider six species: herring (Clupea harengus), mackerel (Scomber scombrus), silver hake (Merluccius bilinearis), cod (Gadus morhua) haddock (Melanogrammus aeglefinus), and yellowtail flounder (Limanda ferruginea). These species are a reasonable cross section of the exploited finfish community of Georges Bank (two pelagic, one semipelagic fish predator, two demersal roundfish and one demersal flatfish). Their analysis applied to exploitable fish of approximately one year and older and 100 g or Kcal and larger (assuming 1 g wet weight equals 1 Kcal). Relevant biological characteristics of early life stages of each population are given in Table 1.

The instantaneous growth rate (G) and the instantaneous rate of change in biomass of the cohort (G-Z) can be estimated by $(1/\Delta t)\ \log_e\ (W_r/W_o)$ and $(1/\Delta t)\ \log_e\ (B_r/B_o)$ where W_r and B_r are the energy content of an individual and the cohort at recruitment to the youngest exploitable size, respectively. Our model assumes that G and Z are time invarient. This assumption is particularly questionable for Z when applied to a time period including egg, larval, and early juvenile stages. On the other hand, Grosslein et al. (1980) note that the reproductive energy (B_o) of the six Georges Bank populations considered here approximately balanced recruitment energy (B_r); i.e., $G-Z \simeq 0$. Since the biomass of a cohort, B, is probably monotonically increasing (except for immediately after spawning when egg mortality occurs without growth), G-Z is not likely to exhibit significant variation. This conclusion is further supported by the general observation that G and Z are positively correlated (Beverton and Holt 1957, Pauly 1981). Our observation, that $B_o \simeq B_r$, is compatible with Sheldon's et al. (1977) hypothesis that biomass of pelagic organisms is uniform over a range of logarithmic size intervals. Kerr (1974) provides a theoretical argument that supports Sheldon's hypothesis.

If the biomass of a cohort is nearly constant, then production estimates are insensitive to the assumption that G is constant during the period Δt. Algebraically, based on Equation (7) with $G \simeq Z$, $P = G_1 B_o \Delta t_1 + G_2 B_o \Delta t_2 = (1/\Delta t_1)\Delta t_1\ \log_e(W_2/W_1)B_o + (1/\Delta t_2)\Delta t_2\ \log_e\ (W_3/W_2)B_o = \log_e(W_3/W_1)B_o = G B_o \Delta t$ where W_1, W_2 and W_3 are a sequence of weights separated by time intervals Δt_1 and Δt_2; $\Delta t = \Delta t_1 + \Delta t_2$; and G_1, G_2, and G apply to Δt_1, Δt_2, and Δt. Furthermore, if G-Z is nearly constant, then consumption estimates based on Equation (7) are insensitive to Z. Thus, Grosslein's (et al. 1980) observation that B_o approximately equals B_r has important practical consequences. Under these circumstances, our simplistic approach (Equations 7-8) provides useful new information.

Grosslein et al. (1980) report the average ratio of recruitment energy to exploitable fish biomass (B_r/B) for silver hake, haddock, cod, mackerel, herring, yellowtail flounder for the period 1963-1972. The B_r/B ratios were 0.10, 0,03, 0.05, 0.14, 0.16, and 0.09, respectively. They assumed that the ratio of the energy content of spawning products to exploitable fish biomass (B_o/B) was somewhat less than 0.10 on average. We have calculated B_o/B for the same six Georges Bank populations for 1963-1972 using unpublished results of Grosslein and co-workers. The B_o/B ratios were 0.07, 0.10, 0.08, 0.07.,0.08, and 0.04. The average values of B_r/B and B_o/B for the six populations were 0.071 and 0.077 respectively. The weighted (by exploitable biomass) averages were 0.12 for B_r/B and 0.08 for B_o/B. Based on the latter estimates of B_r/B and B_o/B, we estimate G-Z as 0.42 assuming Δt is one year (a reasonable assumption according to Table 1). Thus, $G-Z \neq 0$, but it is not far from it. Therefore, we conclude that Equations (7-8) are applicable.

We assume that the energy content of a typical fish egg is 4.3×10^{-4} Kcal. This assumption is based on the average weight of a haddock egg (0.076 mg dry weight; Hislop 1975) and the biomass to energy conversion rate for cod eggs (5.7 Kcal/g dry weight, Daan 1975). The typical fish size at recruitment to the exploitable population is about 100 Kcal (Table 1). Therefore, G = 12.36. Based on the parameter estimates noted above and Equations (7-8), $P/B_o = 15.36$ and $C/B_o = 45.24$ for young (pre-exploitable) fish, where B_o is the energy content of reproductive products of the exploitable population.

The results of a sensitivity analysis of P/B_o and C/B_o are given in Figure 2. For relatively small values of G-Z, P/B_o is nearly linear with G. C/B_o is insensitive to G. Over a realistic range of G-Z, P/B_o and C/B_o vary by about ±25%. These results are used later in the compilation of the energy budget.

Energy Budget

The Georges Bank energy budget is presented in Figure 3. Biomasses and flow rates are in units of Kcal/m^2 and Kcal/m^2 yr, respectively. The energy budget updates Cohen et al. (1982). In this version, primary productivity estimates are further updated, phytoplankton respiration is taken into account, zooplankton are partitioned into micro- and macro-components, the partitions of particular organic carbon (p.o.c.) between zooplankton and detritus has been revised, and young fish are included.

(1) Primary Production:

Although a great deal of phytoplankton work was done 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 is provided by Riley (1941). He estimated total water column production as 200-300 gC/m^{2}yr based on extrapolation from surface samples.

Based on a preliminary analysis of eleven cruises during 1975-1978, Cohen et al. (1982) concluded that Georges Bank primary production is higher than was previously believed. Primary productivity was measured using the $_{14}$C method (Strickland and Parsons 1968). This new information indicated that primary productiviiy was 400-500 gC/m^{2}yr. The data indicated a consistent annual cycle beginning with the spring bloom with production peaking in late summer or early autumn before declining to a winter low. This cycle is a distinct departure from a classic spring bloom - autumn bloom with low productivity during both summer and winter. The high summer productivity of Georges Bank 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 from the water column and the benthos to reach phytoplankton in the photic zone.

More recently, O'Reilly and Busch (1982) have reported on several additional cruises measuring primary productivity (using the $_{14}C$ method). Furthermore, they have revised their preliminary analysis of $_{14}C$ data considered by Cohen et al. (1982). It now appears that Georges Bank primary productivity is at the extreme low end of the range considered by Cohen et al. (1982). O'Reilly and Busch (1982) report about 450 gC/m^2 yr on the shallowest portion of the Bank and about 320 gC/m^2 yr over the remainder. Herein, we consider 400 gC/m^2 yr as a typical value.

Primary productivity on Georges Bank is high relative to other areas for which estimates have been reported. Parson et al. (1977) reported 250 gC/m^2 yr for the coastal waters of Long Island Sound. Steele (1974) reported 90 gC/m^2 yr for the North Sea. The high productivity of Georges Bank may be related to its unique topography and hydrography. As noted earlier, a clockwise gyre retains water on the Bank, nutrient rich waters from the slopes are advected onto the Bank and continuous mixing of the water column makes nutrients regenerated in the sediments available to phytoplankton. Yet, primary productivity is relatively high over the entire continental shelf of the northeastern USA; ranging from about 275-495 gC/m^2 yr, typically 350 gC/m^2 yr (O'Reilly and Busch 1982). Thus, the unique topography and hydrography of Georges Bank is not the only factor accounting for the high primary productivity of the Bank and the region.

Total organic carbon (T.O.C.) of primary productivity was partitioned into dissolved (D.O.C.) and particulate (P.O.C.) components and the particulate component was further partitioned into nano- and net plankton components based on Thomas et al.,(1978) O'Reilly and Busch (1979). Their results indicate that P.O.C. is 83% of T.O.C. and 63% of P.O.C. is nanoplankton. Primary productivity in gC was converted to Kcal using 15.8 Kcal/gC (Platt

1971). Accordingly, T.O.C. = 6320 Kcal/m^2 yr, D.O.C. = 1082 Kcal/m^2 yr, P.O.C. = 5238 Kcal/m^2 yr, 3300 Kcal/m^2 yr is nanoplankton and 1938 Kcal/m. yr is net plankton.

Some of the primary productivity measured by the $_{14}$C method is used for respiration. In essence, the $_{14}$C method measures something between net and gross productivity. O'Reilly (personal communication) estimated that respiration accounts for 10-50 of P.O.C. with 15 typical of a highly productive area like Georges Bank. Therefore, the remaining 4452 Kcal/m^2 yr of P.O.C. must be partitioned between zooplankton and detritus. Based on the production of macrozooplankton and trophic efficiency considerations described below, 23% of the P.O.C. remaining after respiration (1034 Kcal/m^2 yr) is assumed to be detritus. Thirty percent of the D.O.C. (323 Kcal/m^2 yr) is incorporated into bacteria (Parsons and Sekai 1971).

(2) 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). These early studies were for the most part qualitative in nature, e.g., the nets lacked flowmeters. Since then there have been numerous investigations of zooplankton, though usually on a small geographic scale and of short duration (some examples are Redfield 1939; Clarke et al. 1943; Riley and Bumpus 1947; Colton et al. 1962).

In 1971, the Northeast Fisheries Center (NEFC) began sampling zooplankton with 333 $^{\mu}$ bongo nets during spring and autumn. In 1976, coverage was expanded to several additional cruises per year and smaller mesh size samplers (165$_{\mu}$ and 255$_{\mu}$) were included. Unfortunately, only the data from the 333$_{\mu}$ mesh has been processed to date. Furthermore, processing of samples collected since 1976 is only partially complete.

The mean density of zooplankton during spring and autumn surveys of 1971-1975 was 1 g dry wgt m^2. Considering the fact that a

333μ mesh net undersamples copepodite stages 1-3 and relatively small zooplankton (such as Centropages and Pseudocalanus) and that the most productive summer months were not sampled, zooplankton biomass must be at a minimum 2 g dry wgt/m^2.

Riley and Bumpus (1946) report a range of zooplankton biomasses of 2.8-28.1 g dry wgt/m^2. Their estimates are probably too high since they use a wet volume to dry weight conversion of 25%; more recent estimates average about 10% (Kane 1979). Therefore, the available zooplankton data indicates a range of 2-15 g dry wgt/m^2 or 10.5-78.8 Kcal/m^2 (based on a conversion factor of 5.25 Kcal/g dry wgt, Laurence 1976). We assume a typical zooplankton biomass of 50 Kcal/m^2 A P/B ratio of 7.0, indicating 350 Kcal/m^2 yr, was applied to Georges Bank zooplankton (Crisp 1975).

Only the macro component of the zooplankton are retained by plankton nets; therefore, our estimate of 350 Kcal/m^{2}yr applies to macrozooplankton only. In general, the macrozooplankton prey on net phytoplankton and microzooplankton. Microzooplankton prey on nanoplankton. The longer food chain for nanoplankton is based on Parsons and Lebrasseur (1970). If hervibores and omnivores convert 32% and 20% of assimilated consumption (respectively) to growth (Steele 1974), both assimilate 70% of consumption (Crisp 1975), and 63% of the P.O.C. available to zooplankton is in the form of nanoplakton, then 3418 Kcal/m^{2}yr is necessary in order for the macrozooplankton to produce 350 Kcal/m^{2}yr. Microzooplankton consume 2154 Kcal/m^{2}yr in order to produce 482 Kcal/m^{2}yr. Unassimilated consumption (at all trophic levels) is converted to fecal material.

(3) Benthos:

Benthic production was estimated based on benthic biomass data and P/B ratios (Cohen et al., 1982). The most recent estimate of benthic macro-faunal biomass on Georges Bank is 240 g wet wgt/m (Wigley, personal communication). This estimated average biomass was converted into Kcal/m^2 using conversions in the literature for various groups of benthic invertebrates (Brawn et al. 1968; Cummin and Wuycheck 1971; and Thayer et al. 1973). The result was about 120 Kcal/m^{2}yr. A P/B ratio of 1.5 was then used to calculate the yearly production from the biomass data. This P/B ratio yields an estimate of macrobenthos production of 180 Kcal/m^2/yr.

Meiobenthos biomass estimates for Georges Bank are not available. We assume a macro to meiobenthos ratio of 48.0 recognizing that a range of 35.0-100.0 has been reported for various marine ecosystems (Cohen et al. 1982. Based on a P/B ratio of 8.0, a meiobenthos biomass of 2.5 Kcal/m^2 yields 20 Kcal/m^2 yr of production.

(4) Fish:

The Northeast Fisheries Center (NEFC) has conducted routine standardized research vessel bottom trawl surveys off the northeast coast of the USA (including Georges Bank) since 1963. Clark and Brown (1979) used these data and catchability coefficients, which they calculated, to estimate the finfish and squid biomass of the region. Grosslein et al. (1980) used Clark and Brown's catchability coefficients, NEFC bottom trawl survey data and unpublished results of NEFC virtual population analyses to estimate finfish and squid density on Georges Bank for 13 species or species groups for the periods 1964-1966 and 1973-1975. The former period corresponds to the beginning of the build-up of fishing pressure on Georges Bank by other than North American fleets. The latter period followed several years of intense fishing pressure when total biomass had declined to its lowest level (Clark and Brown 1979).

These estimates of biomass only apply to the portion of the fish and squid community vulnerable to fishing gear, generally about one year and older and 100 Kcal (assuming 1 Kcal/g wet wgt) and larger. This component of the finfish and squid is referred to as "exploitable".

Mean P/B and C/B ratios were calculated for six of the species (silver hake, haddock, cod, mackerel, herring, and yellowtail flounder) over a decade (1963-1972) and each age-class. These species were considered because age specific biomass estimates were available over a relatively long period of time. Production was based on empirical growth rate and fecundity functions. Consumption was calculated using an energy balance equation as described in an earlier section. The resulting P/B and C/B ratios for exploitable size fish are reported in Table 2.

Species-specific P/B ratios were applied when available. P/B ratios of 0.25 and 1.5 were assumed for redfish and squid reflecting their slow and rapid growth, respectively. Similarly, C/B ratios of 3.0 and 7.0 were assumed. For other species, P/B and C/B ratios of 0.46 and 4.1 (the mean of the values in Table 2) were applied. The resulting biomass, production and consumption estimates for each period are reported in Table 3. The results for 1973-1975 are used in our energy budget. Pelagic species are herring, mackerel, redfish, and squid. All other species are considered demersal.

The young (pre-exploitable) fish biomass is estimated by exponential interpolation between reproductive energy (B_0/B) x exploitable biomass or 0.08 x 23.6 = 1.9 for 1973-1975) and recruitment energy (B_r/B x exploitable biomass or 0.12 x 23.6 = 2.8 for 1973-1975). We estimate young biomass as 2.3 Kcal/m^2 Based on our earlier analysis, production and consumption are 15.36 and 45.24 times reproductive energy or 29.0 and 85.4 Kcal/m^2 yr, respectively for 1973-1975. Comparable calculations were made for the period 1964-1966. The results for the most recent period are reported in the energy budget (Figure 3), results for both periods are reported in Table 3.

Discussion of Energy Budget Implications on Fish

During 1973-1975, Georges Bank fish (of all ages) consumed 197.0 Kcal/m^2 yr or 33% of the total production of suitable prey (macrozooplakton, benthos and fish). Exploitable pelagics consume 15% of macrozooplankton, their primary prey. Similarly exploitable demersals consume 24% of their primary prey, benthos and fish. Of course, exploitable fish share macrozooplankton and benthic production with young fish.

Grosslein et al. (1980) note that only for Georges Bank haddock is there clear evidence of density dependent growth. There are some indicatons that growth rates of herring and silver hake are also density dependent. These observations are compatible with the energy budget. There is enough prey (in aggregate) for fish consumption, but certainly, prey abundance is not unlimited. In fact, during 1964-1966 (prior to peak distant water fishing fleet activity), fish consumed 56% of their potential prey, assuming that planktonic and benthic production was similar during both the earlier and late periods considered.

While prey production is sufficient to provide for fish consumption in aggregate, some prey and predator combinations may be more tightly bound. Figure 4 indicates the prey preference of several important Georges Bank species. Herring, mackerel and redfish prey on planktonic crustacea (macro-zooplankton). Haddock, yellowtail flounder and other flounder prey on <u>polycheta</u>, <u>Echinodermata</u> and benthic <u>Crustacea</u> (benthos). Cod and silver hake prey on <u>Pisces</u> (fish). Figure 4 is only a summary of much more detailed (size specific) data collected by the NEFC.

Cohen et al. (1982) noted that silver hake alone probably consume more fish than is produced by exploitable size fish. Therefore, silver hake must be partially dependent on young fish production. But, how significant is predation mortality by silver hake and other fish predators on young fish?

Cohen and Grosslein (1981) estimated that 74% and 38% of silver hake and cod consumption is fish. Their estimates are based on size specific feeding data and recent data on the size composition of the predators. Based on Table 3, silver hake and cod consumed 38.1 and 28.0 kcal/m^{2}yr during 1964-1966 and 1973-1975, respectively. Aggregate fish production (primarily young) during the same periods was 68.9 and 41.7 kcal/m^2 yr. Thus, fish predators must cause substantial young fish mortality. In fact, silver hake and cod consumption and fish production are so nearly equal that perhaps one or the other is in error.

The fish consumption rates are most sensitive to population size estimates. These are based on Virtual Population Analysis (VPA); as such population size is overestimated if catch is overestimated. This is unlikely. It is more likely that young fish abundance was underestimated. Some of the young fish are spawned by "other finfish". It is difficult to verify the accuracy of these estimates. Of course, some of the other finfish are important fish predators (e.g. spiny dogfish, goosefish). Therefore, if the abundance of this component of the fish community is significatly underestimated, then consumption is underestimated as well.

Sand launce (*Ammodytes americanus*) are a potentially important prey of silver hake and cod. The biomass estimates for fish used in the energy budget are based on bottom trawl survey data and/or commercial catch data. Sand launce are not well represented by either set of data. Based on ichthyoplankton data, Sherman et al. (1981) documented a recent increase in sand launce abundance, but this has largely occurred since 1975. Nevertheless, sand launce production during the periods considered in this paper may have been underestimated.

Young fish production would also be underestimated if G-Z and/or G were underestimated. Figure 2 indicates the potential magnitude of the error. If we overestimated and underestimated W_o and W_r by a factor of two, respectively, then G = 13.75 instead of 12.36. If a cohort nearly tripled in biomass during the young fish stage, then F-Z = 1.0 instead of 0.42. Accordingly, production might be about 50% higher. Of course, consumption by young fish would increase by a similar factor.

It seems likley that either silver hake and cod consumption of fish is overestimated and/or young fish production is underestimated, probably the latter. It is unrealistic that 60% of total fish production is consumed by silver hake and cod. On the other hand, there is probably inadequate benthic and macrozooplankton production to support substantially more young fish production on Georges Bank.

Some fish production energy may be imported to Georges Bank. Young herring are not found on Georges Bank. Some herring probably migrate to the Bank from nursery areas along the coast of Maine. Nevertheless, the net production that is potentially imported to Georges Bank must be quite small. Primary production is higher on Georges Bank than in surrounding waters. Furthermore, much of the production of young fish in areas like the Gulf of Maine must be necessary to support local predators, essentially the same species as are common on Georges Bank (e.g. silver, hake, cod, dogfish). Therefore, although our energy budget suffers from considerable uncertainty, fish predation clearly causes substantial young fish mortality. There is empirical evidence to support our conclusion.

The NEFC has conducted ichthyoplankton surveys of Georges Bank since 1971 (Bolz and Lough 1981; Smith et al. 1979). Not all of the data has yet been processed. We have used some readily available results to estimate larval abundance on Georges Bank (Table 4). Our abundance estimates were generated by expanding the number of larvae per unit area to the area of Georges Bank. This method produces a conservative estimate of abundance as it does not take into account cruise duration, spawning period, or mortality. By combining the results in Table 4 wih estimates of total egg production and subsequent recruitment for each population, it is possible to estimate early life stage mortality rates.

Anthony and Waring (1980) estimate the total egg production and recruitment of Georges Bank herring. During 1971-1976, the population typically produced 3.0×10^{13} eggs and 1.0×10^{8} recruits. The fishery collapsed in 1977 with virtually no spawning or recruitment subsequently. Larval abundance was typically about 3.0×10^{12} shortly after spawning and 3.0×10^{10} about three months later. Thus, the mortality of eggs and early larvae is 90.0%, the mortality of still later stage larvae and post larvae is 99.9667.

An unpublished NEFC VPA for cod indicates that, during 1974-1980, there were typically about 4.0×10^7 mature spawners and 2.5×10^7recruits. Average cod fecundity is about 5.0×10^6 eggs (Bigelow and Schroeder 1953). Larval abundance was typically 2.0×10^{11}. Therefore, egg and early larval mortality is 99.9000%. Late larval and post larval mortality is 99.9875%.

Clark's et al.(1982) VPA for Georges Bank haddock indicated typically (during 1974-1980) 1.0×10^7 recruits and 2.5×10^7 mature spawners. NEFC unpublished data indicates an average fecundity of 6.0×10^5eggs. Larval abundance was typically about 3.0×10^{11}. Therefore egg and early larval mortality is 98.000000 and late larval and post larval mortality is 99.996667%.

Thus, mortality of late larvae and post larvae is extremely high, typically as high as for eggs and early larvae. Predation by fish is probably one of the major causes. It is only necessary for this mortality rate to vary a small amount to account for the difference between poor and outstanding year classes. Silver hake appear to be a keystone predator as postulated by Edwards and Bowman (1979).

In Table 4 we have indicated the larval cohorts that resulted in the strongest year classes. There is no apparent relationship between larval abundance and subsequent year-class strength. Lough et al. (1980) examined the relationship in more detail for Georges Bank herring. They also found no evidence of a relationship. Smith et al. (1979) report no correlation between larval abundance and year-class strength of Georges Bank cod or haddock. Thus, it appears that year-class strength is established at a later life stage. Predation by larger fish is certainly one potential controlling mechanisms.

Hennemuth et al. (1980) describe the probability density function of year-class strength (recruitment) for eighteen fish populations, including several on Georges Bank. They noted that recruitment is highly variable and skewed with below average recruitment more frequent than above average recruitment. They also note a tendency toward more frequent outstanding year-classes than would be expected from the tail of routinely applied distributions (e.g. lognormal, negative binomial, Neyman types). These observations are comparable with our conclusions based on the energy budget.

A high young fish mortality rate essentially dictates highly variable recruitment since the difference between poor and outstanding year-classes is only a small change in an obscure digit of the mortality rate. Our conclusion that this high mortality rate extends beyond the larval stage implies that the probability density function of recruitment is probably a compound function reflecting sources of larval mortality and post-larval mortality (predation by fish).

Consider the possibility that the number of individuals that survive from egg to the size of vulnerability to fish predation is adequately described by a negative binomial distribution or other routine distribution noted above. If the number of post larval fish consumed by fish predators increases with prey abundance to an asymptote as predators become satiated, then fish predation would buffer recruitment so that the probability density function of recruitment would be more peaked about the mean than for the underlying negative binomial, but with nearly the same frequency of outstanding year-classes. If there were a threshhold to fish predation (i.e. assume predators feed on benthos when fish abundance is low), then the recruitment probability density function might be multimodal. On the other hand, if fish predators consume a nearly constant amount of pre-exploitables, then predation mortality would increase as prey abundance decreases and depensation would occur. Herring and haddock recruitment failures (1971-present and 1964-1974, respectively) might be indicative of depensation.

In summary, the energy budget indicates the potential for density dependent processes (growth and recruitment). While there is adequate production by macrozooplankton and benthos to support fish production, fish food is not unlimited. Density dependent recruitment is obscured by highly variable mortality of young fish. One major cause of this high mortality is predation. The relatively minor fluctuations in mortality of young fish, which distinguish between poor and outstanding year-classes, are probably caused by environmental factors and hence matches or mismatches of biological aggregations. The probability density function of recruitment must be a compound function reflecting both larval and post larval sources of mortality.

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Table 1. Relevant biological characteristics of early life stage herring, mackerel, silver hake, cod, haddock, and yellowtail flounder of Georges Bank.

	Silver Hake	Haddock	Cod	Mackerel	Herring	Yellowtail Flounder
Spawning Time	July	March	February	May	October	May
Egg Diameter (mm)	0.9	1.4	1.4	1.2	1.2	0.9
Larval Length at Hatching	3.0	4.0	4.0	3.2	5.5	3.0
Weight at Recruitment (g)[1]	32.0	101.0	170.0	95.0	87.0	39.0
Age at Recruitment (years)	1.0	0.7	1.0	0.7	1.2	1.2

[1] Weight and age is the minimum "exploitable" size and age considered by Grosslein et al. (1980).

Table 2. Geometric mean (over all ages and years considered) of production to biomass ratio (P/B) and consumption to biomass ratio (C/B) for "exploitable" individuals.

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 3. Georges Bank consumption and production in kilocalories per meter squared, 1964-1966 and 1973-1975 for exploitable individuals by species or species group and for young fish.

	1964-1966			1973-1975		
	Biomass	Consumption	Production	Biomass	Consumption	Production
Cod	1.9	5.6	1.1	0.9	3.0	0.6
Haddock	4.5	16.1	2.1	0.4	1.4	0.2
Redfish	<.1	0.1	<.1	0.1	0.2	<.1
Silver hake	10.1	48.6	5.8	7.4	36.3	4.4
Red hake	1.1	4.4	0.5	0.8	3.3	0.4
Pollock	0.3	1.1	0.1	0.1	0.5	0.1
Yellowtail flounder	0.6	2.9	0.4	0.5	2.2	0.3
Other flounder	0.3	1.3	0.1	0.2	1.0	0.1
Herring	19.3	87.5	5.4	6.2	28.5	1.8
Mackerel	1.3	5.4	0.4	2.7	11.7	0.9
Other finfish	1.7	6.9	0.8	2.3	9.3	1.0
Illex	0.2	1.6	0.2	1.7	12.0	2.6
Loligo	0.1	0.4	0.1	0.3	1.9	0.4
Pelagics	20.9	95.0	6.2	10.9	54.1	5.7
Demersal	20.4	97.1	11.1	12.7	57.2	7.0
Total	41.3	192.1	17.2	23.7	111.3	12.7
Young fish	4.1	152.2	51.7	2.3	85.4	29.0

Table 4. Larval abundance for several Georges Bank species.

			Larval Abundance (x 10^{-11})		
Year of Spawning	Herring Sep-Nov	Herring Dec-Feb	Cod Apr-May	Haddock Apr-May	Silver Hake Sep-Ded
1971	39.0	1.8**			14.0*
1972	27.0	13.0			5.3*
1973	68.0	0.7*			3.1
1974	60.0	1.1	2.0	0.7	17.0
1975	28.0	2.0	1.3**	1.7**	2.2
1976	3.0	0.2	0.2	1.0	3.8
1977	--	--	5.7	5.2	
1978	--	--	4.7*	5.3*	
1979	--	--	1.3	5.9	
1980	--	--	3.9	7.1*	

**the largest year-class (at recruitment) during period for which larval data is reported.

* the second largest year-class.

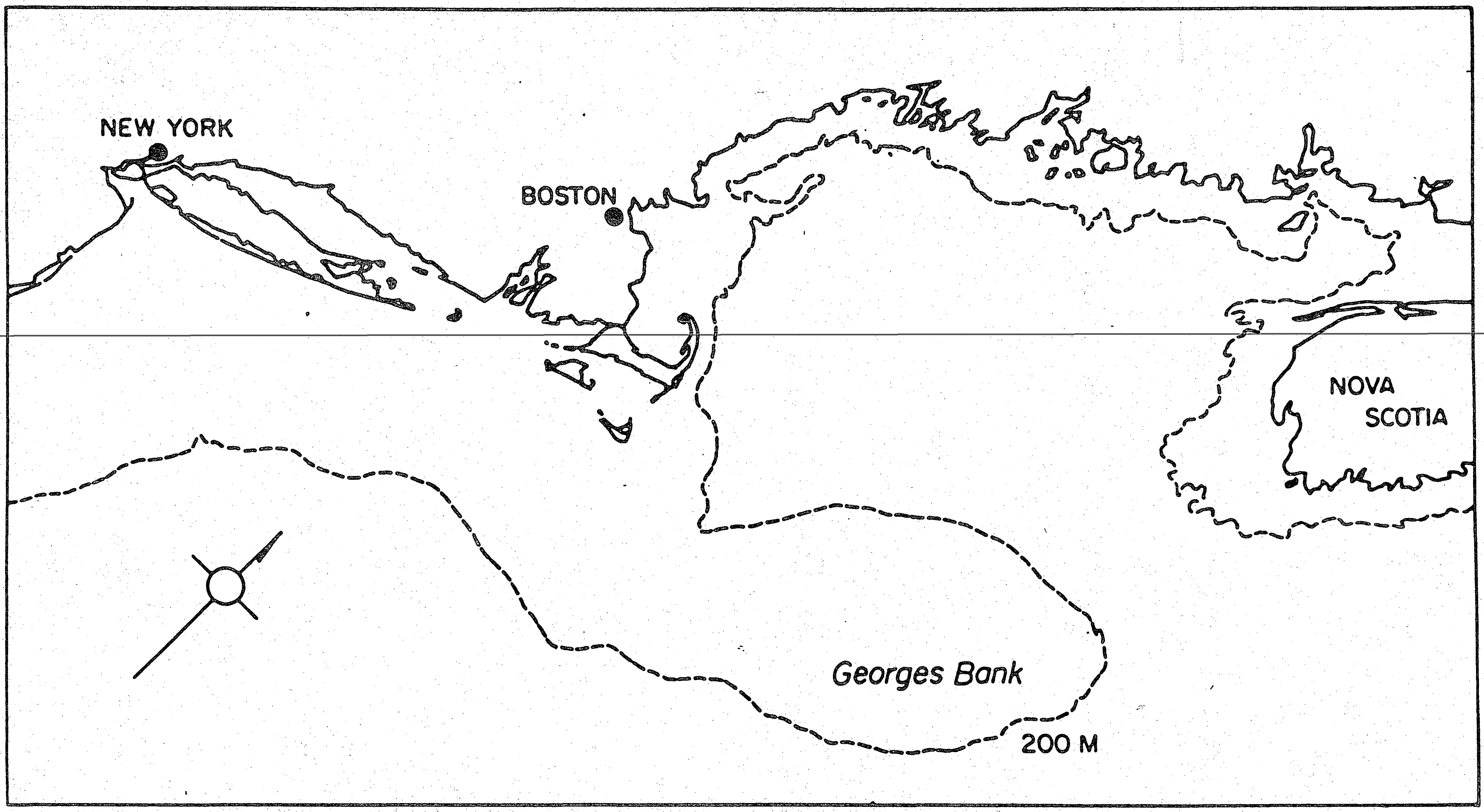

Figure 1. The location of Georges Bank.

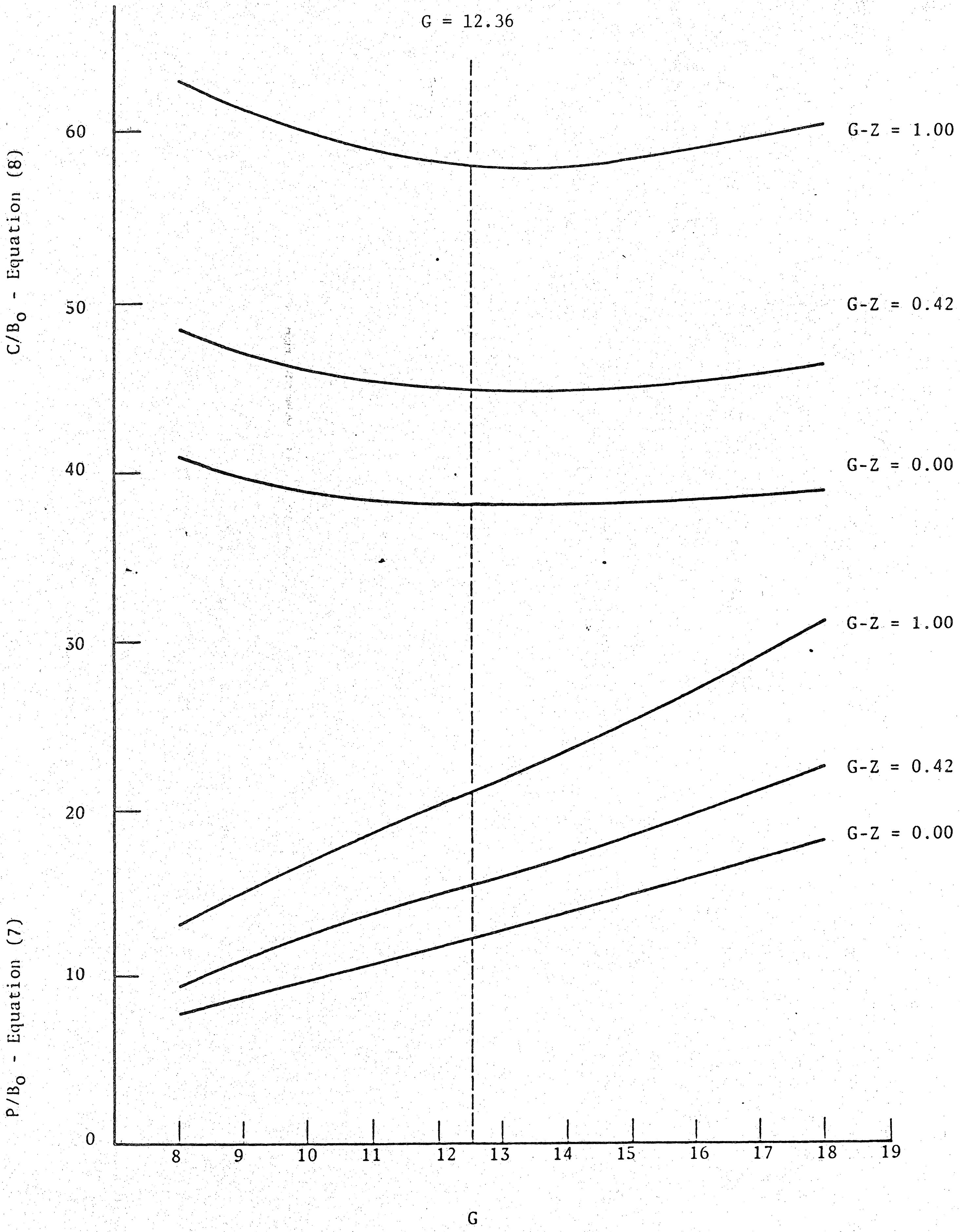

Figure 2. Sensitivity analysis for cohort model of production and consumption.

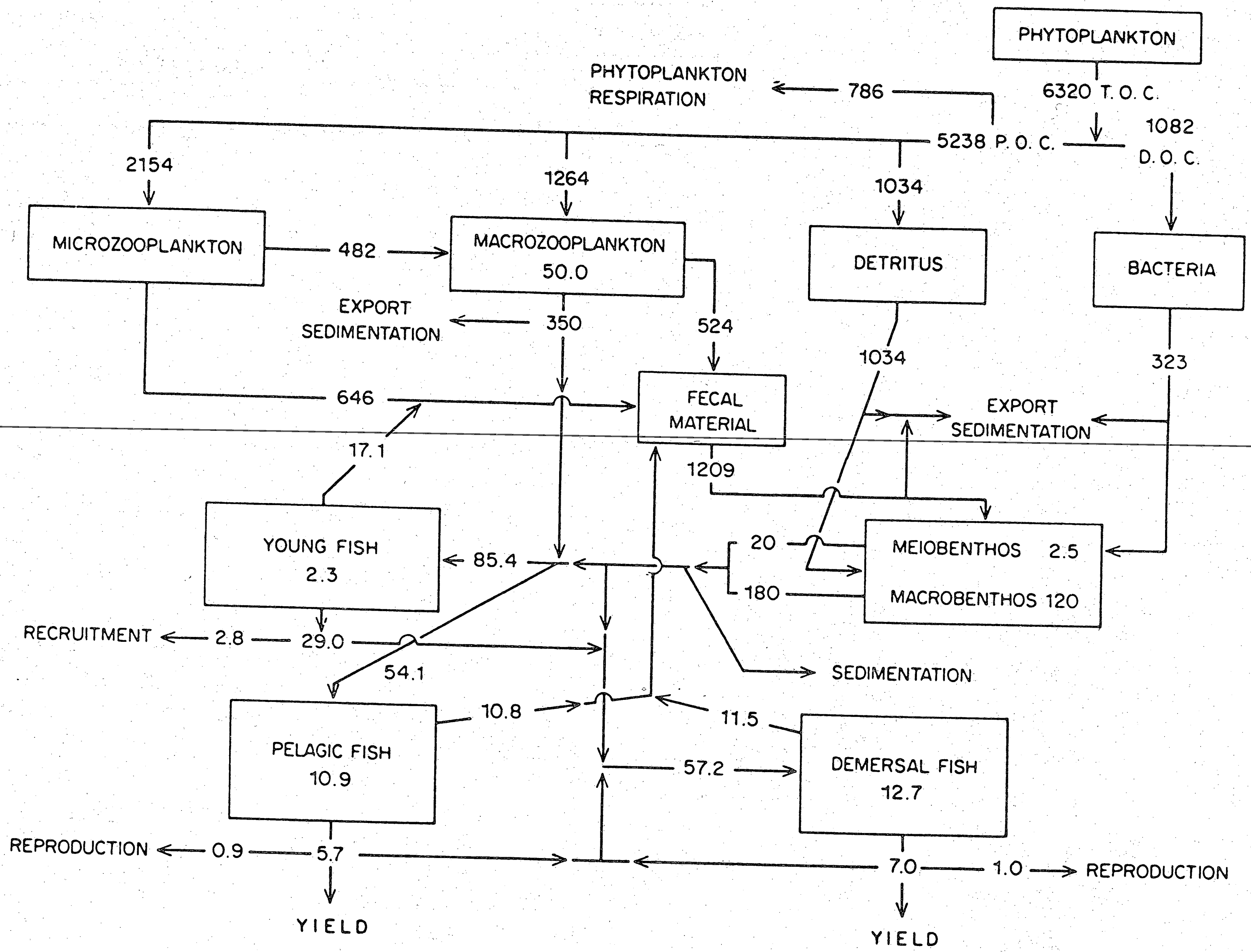

Figure 3. Georges Bank energy budget, 1973-1975. Biomass (enclosed in boxes) is in Kcal/m^2. Flow rates (on arrows) are in Kcal/m^2yr.

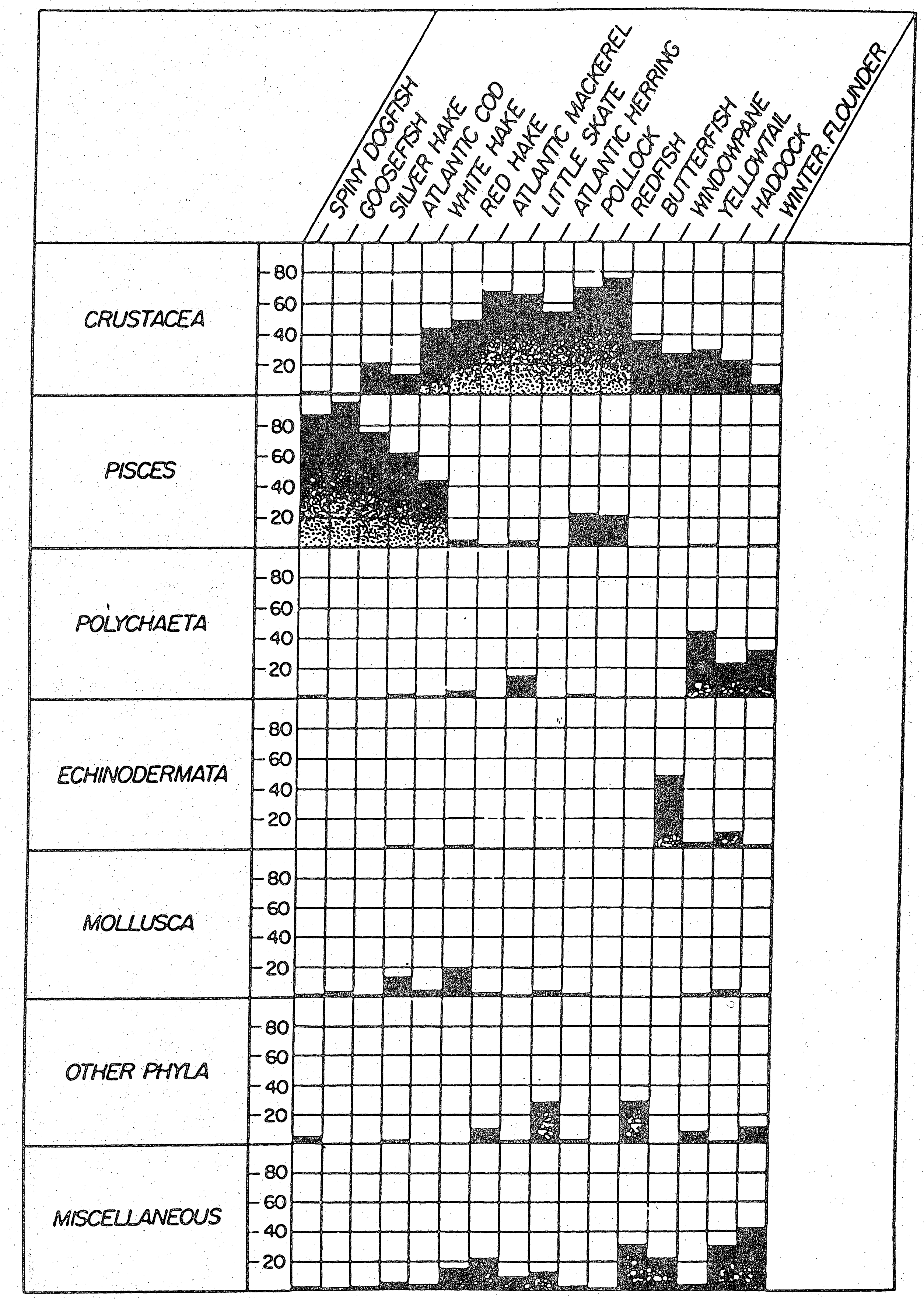

Figure 4. A diagrammatic representation of the prey of 16 species of fish collected on Georges Bank between the years 1969 through 1972. The data are expressed as percent weight.