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PRODUCTION DYNAMICS OF A MARINE FLATFISH POPULATION: AN ENERGETICS MODEL

by

James C. MacKinnon

Submitted in partial fulfillment of
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PRODUCTION DYNAMICS OF A MARINE FLATFISH POPULATION: AN ENERGETICS MODEL

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J. C. MacKinnon

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ABSTRACT

The seasonal pattern of production processes in the American plaice (*Hippoglossoides platessoides*) population of St. Margaret's Bay, Nova Scotia was analyzed with a model based upon energy principles. Results are presented for field and laboratory investigations designed to provide energetics data required by the model. Estimates derived from the model are given for seasonal and annual energy flows of the population in its present unexploited state and in states that might be attained as a result of fishing.

Annual net production and ingestion of the unexploited population were estimated at 2.3 kcal/m^2 and 11.0 kcal/m^2 respectively. Larvae and 0+ fish accounted for 20% of total ingestion by the population and 34% of net production while their biomass constituted only 4% of the population total. Production during summer months by fish aged 1 and up exceeded the corresponding net annual production by a factor of two as a result of the use of stored energy for metabolism and gonad maturation during winter.

Highest fishing yields are predicted by the model for equilibrium states where it is assumed that population response mechanisms have been able to maintain ingestion at its pre-exploitation value whereas lower yields are obtained when situations of less complete response are considered. The reaction of the population to fishing is in accord with

theoretical ecological considerations which postulate increased productivity in association with decreased diversity and homeostatic capacity as expoitation is intensified.

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INTRODUCTION

An analysis of the production process is a primary objective of theoretical models of exploited fish populations. This analysis involves the application of energy principles to all components of the fish population system (eggs, larvae, immature and mature fish) and to interactions of the system with other components of the particular ecosystem of which it is a part. The energetics considerations must be integrated with the "traditional" population dynamics analysis of changes in numbers via birth and death processes, and attention should also be given to the ability of the population to adapt to environmental change, including exploitation, by a variety of regulatory mechanisms. These statements summarize the main concepts underlying a production model which is developed in this thesis; the model is used for evaluating changes in production dynamics and fishing yields obtainable from exploitation of stocks of a common Atlantic flatfish species.

Details concerning structure of the production model and choice of parameter values are presented in the first section of the thesis along with a discussion of model predictions concerning the changes in production dynamics which are caused by fishing. Supporting data obtained in field and laboratory studies are presented in two subsequent sections.

Emphasis on production and the use of energy principles in the analysis of fish population dynamics has evolved in parallel with the emergence of energetics as an important aspect of ecological research. The early papers of Winberg[1] gave a major impetus to the use of energetics concepts in studies of fish metabolism, growth and food requirements. Paloheimo and Dickie subsequently explored in greater detail the relationships between food and growth of individual fishes while Mann extended the use of energetics methods to the fish population level. In more recent papers, the ecological context of fish populations as production systems has been emphasized and "food-chain" models for the assessment of fishery resources have become widely used.

Earlier models such as those of Beverton and Holt which were concerned with the dynamics of exploited fish populations focused attention on yield and its relationship with parameters affecting the processes of growth, recruitment and mortality. A detailed comparison of features of the present model with those of Beverton and Holt models is included as an appendix of the thesis.

In the yield models of Beverton and Holt the effects of fish/fishery **interactions** were examined in detail whereas other ecological relationships, such as those between the population and its food supply, were given relatively little attention. The simple population production models of Paloheimo and Dickie were the first to demonstrate how

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[1] References to papers by authors mentioned in this introduction are found after the three sections of the thesis.

energetics concepts could be used to develop relationships among yield, production, physiological parameters and characteristics of the food supply and the physical environment. The production model presented in this thesis is an extension of this line of research and includes, in addition, consideration of regulation mechanisms whose adaptive significance has been emphasized by Russian researchers such as Nikolsky.

SECTION A

A Production Model for Estimation of Equilibrium Yields from a Marine Flatfish Population

by

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INTRODUCTION

Models for the prediction of yields from exploitation of a fish stock in relation to various fishing strategies are of fundamental importance for fisheries management policies. Yield may be viewed as the direct consequence of interference with the production dynamics of a fish stock so that incorporation of the main features of population production processes into these models must be a basic objective (Dickie and Mann, 1972). However, production was not given this emphasis in earlier models (Beverton and Holt, 1957); attention was focused on the concept of yield as the result of interaction between fishing gear and characteristics of the exploited phase of a fish population.

Production is the result of a complex of energy transfer and conversion processes and any quantitative description of the production process must therefore involve consistent application of energy principles (Winberg, 1962). Paloheimo and Dickie (1970) have demonstrated with simple population production models that energetics concepts can be used to develop relationships between yield, production, physiological parameters and characteristics of the food supply and physical environment. The type of data required for such models was collected by Mann (1965) for a community of freshwater fishes and later used in evaluating energy flows for the particular river ecosystem (Mann *et al*, 1971). Energetics data have been obtained for a number of freshwater fish populations but the approach has seldom been used in investigations of marine fish populations. The few marine studies include Lasker's (1970) analysis of a Pacific sardine (*Sardinops caerulea*) population and the investigation by Steele and Edwards (1970) of O-group plaice (*Pleuronectes platessa*) and dabs (*Limanda limanda*) in Loch Ewe.

Fishing activity causes significant alterations in the structure of the population being exploited and thereby stimulates regulatory mechanisms which enable the population to respond to this disturbance. The mechanisms act to match population numbers and mass with the food supply and to maintain adequate reproduction features appropriate to the environment (Nikolsky, 1969a). Since the exploited population interacts with other ecosystem components (Mann, 1969) the disturbances to the production process which are initiated by fishing activity are far-reaching and extremely complex to analyze in detail.

In this paper, a production model is presented, based upon energy principles and the energetics data (MacKinnon, 1972 a, b) now available for the unexploited American plaice, (*Hippoglossoides platessoides*) population of St. Margaret's Bay, Nova Scotia. This model is used to evaluate the seasonal patterns of energy transfer and conversion within the population and to estimate annual energy flows and efficiency parameters for the unexploited steady state (Beverton and Holt, 1957) of the population.

The direct effects of fishing activity and the subsequent response of the population through its regulation mechanisms are theoretically investigated with the model. The analysis concerns steady states attained by systematically varying population structural parameters that are commonly observed to be altered by fishing. Equilibrium yields are computed for these sequences of states and fishing strategies (defined primarily through the effects on age composition) and are evaluated in terms of potential catches and reproduction consequences.

The production model is also used to estimate ecological efficiency parameters which are required by models for evaluation of potential yields from demersal fish stocks as a whole (Gulland, 1970). Since American plaice is a typical demersal flatfish stock, an examination of the factors and processes which have significant effects on ecological efficiency of a plaice population may provide conclusions that are relevant to demersal fish stocks in general.

ECOLOGY OF AMERICAN PLAICE

A brief review of literature on the ecology of American plaice provides essential background information and data relevant to the population production model presented in this paper.

American plaice, *Hippoglossoides platessoides*, is a common commercial flatfish with a wide distribution along the Atlantic coast of Canada (Leim and Scott, 1966). The species is most abundant on fine sand or soft mud bottoms at depths of 40 to 200 meters and temperatures of -1 to 3°C.

Stocks of plaice in the Northwest Atlantic region are thought to be genetically homogeneous although there is little overall movement of adults from one region to another. Bakken (1972) found that the plaice of St. Margaret's Bay constitute an essentially separate resident stock with little migration in or out of the Bay. Pitt (1963) observed a low degree of variability in vertebral numbers of plaice from the Northwest Atlantic region and concluded that populations in the different areas were genetically similar. However tagging studies, such as those by Powles (1965) in the Gulf of St. Lawrence, indicate that distinct populations of larger fish can be identified in various areas.

Some seasonal movement of American plaice has been observed but the pattern appears to be related to the annual feeding-overwintering-spawning sequence of events rather than being a direct response to some environmental parameter such as temperature. Powles (1965) has described the seasonal movement of plaice in the Gulf of St. Lawrence. During the summer months the fish feed inshore at depths of 40 to 100 meters and temperatures of -1 to 0°C. Gradual movement offshore begins in the fall and overwintering occurs at depths of 180 - 450 meters and temperatures of 2 - 5°C. In early spring, prior to spawning, plaice move inshore to resume feeding at depths of 75 to 150 meters where temperatures average 2°C.

American plaice feed intensively during summer months and store large amounts of energy which are used during the overwintering period for maintenance metabolism and gonad development. Observations by Powles (1965) of stomach volumes of specimens from the Gulf of St. Lawrence indicated that fish of all sizes contained essentially no food during January and February and that only moderate feeding occurred during November and April. This seasonal variation in feeding intensity is accompanied by large changes in the energy content of individual fish (MacKinnon, 1972a).

Spawning times from April to June have been reported for plaice in the Northwest Atlantic region but bottom water temperatures do not appear to have a direct influence on timing. Pitt (1966) reported spawning times for the Newfoundland and Labrador region and found no indication that low temperatures retarded the spawning period. However, there is evidence that spawning occurs earlier in more southern areas such as the Gulf of Maine (Bigelow and Schroeder, 1953).

Pelagic eggs of plaice hatch within two to three weeks after spawning, the period of larval growth occupies three to four months and fry migrate to the bottom soon after metamorphosis. When the eggs are opaque and ripening in the ovary, they are about 0.8 mm in diameter (Pitt, 1964). As spawning approaches the eggs become translucent, with diameters of 1 - 1.25 mm, and at spawning they swell to 2 - 2.5 mm and float to the sea surface (Huntsman, 1918). In the Gulf of Maine, Bigelow and Schroeder (1953) reported an average egg size of 2.5 mm and an incubation period to hatching of 11 to 14 days at 4°C. Larvae are 4 - 6 mm long at hatching and metamorphosis is complete when a length of about 25 mm is attained. By the beginning of winter, the fry are approximately 50 mm long and at one year fish are commonly 75 mm although differences in size at this age are apparent in different regions (Huntsman, 1918).

American plaice appear to be predominantly visual feeders and they consume a wide variety of food organisms.

Groot (1969) concluded from experiments on sensory faculties and observations on comparative anatomy that *Hippoglossoides platessoides* belongs to a group of flatfish species which find their food in or near the bottom during the day and are visual feeders but may use chemical cues in their search for food. This conclusion is supported by laboratory observations that plaice remain on the bottom during the day while swimming in the water column at night (Verheijen and Groot, 1967) and by data showing higher trawl catches during the day (Pitt, 1967a). The diet of young plaice (under 30 cm) was observed by Powles (1965) to consist mainly of amphipods, small echinoderms and annelids while larger fish consumed echinoderms and pelecypods primarily. Smaller amounts of other organisms, including euphausiids and fish, are also eaten (Bigelow and Schroeder, 1953).

Significant differences in growth rate and maximum size of plaice are evident in various locations within the Northwest Atlantic region. Pitt (1967b) and Yanulov (1962) studied growth in the Newfoundland area and found that females attained lengths of 50 cm at 20 years on the Labrador Shelf versus 60 cm at 20 years on the Southwest Grand Bank. Prior to the existence of the commercial trawl fishery on the Grand Banks, plaice of up to 72 cm were found (Templeman and Andrews, 1956). In the Cape

Cod region growth rates are much higher and females attain maximum lengths of 50 cm at 12 years of age (Lux, 1970).

The relatively slow growth rate of American plaice is consistent with their low environmental temperature and associated metabolic rate. MacKinnon (1972b) found that plaice displayed essentially no adaptation to low temperature in their level of metabolism and that respiration rates were relatively unresponsive to temperature within the range normally experienced by the species in St. Margaret's Bay.

Size at maturity varies between areas in conjunction with growth rate and the evidence suggests that onset of maturity is more closely correlated with attainment of a certain size rather than with a certain age. Data are available on the size at maturity of plaice in a number of locations in the Northwest Atlantic (Pitt, 1966; Powles, 1965; Bakken, 1972).

The European subspecies, *Hippoglossoides platessoides limandoides*, found in the Firth of Clyde matures at a much smaller size and has a much higher fecundity than does a fish of the American subspecies of the same size (Bagenal, 1957; Pitt, 1964). Growth rates of the European subspecies in the Clyde (Bagenal, 1955) are comparable with the highest growth rates reported in the Northwest Atlantic for the Cape Cod area but the maximum sizes attained are 30 cm and 50 cm respectively.

Aside from miscellaneous natural causes of death, major influences on mortality rate are predation by cod on fish less than 30 cm and fishing of the larger size plaice where this occurs. Cod are often abundant over the grounds where plaice occur and Powles (1965) found that plaice were volumetrically the second most important fish in the stomachs of Atlantic cod in the Magdalen Shallows. Mortality estimates for adult plaice in the Magdalen Shallows were reported by Powles (1969); the response of an unexploited stock to initiation of intensive fishing is clearly shown in these data.

The only estimates of absolute density for plaice are those by Bakken (1972) for the St. Margaret's Bay stock. Because this stock appears to be confined year-round to depths of 30 to 100 meters in the Bay and close attention was paid to the determination of trawling efficiency one can have a fair degree of confidence in these estimates. One must rely upon catch statistics for approximate estimates of abundance in other areas.

American plaice constitute the main resident component of the demersal fish community in St. Margaret's Bay, N.S., and analysis of the production dynamics of the plaice population is an important part of a productivity study of the Bay ecosystem (Platt, 1971; Sameoto, 1971; Mann 1972).

Winter flounder (*Pseudopleuronectes americanus*) is the major demersal fish species in the near-shore regions down to depths of about 30 meters. A number of other species such as cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinis*) are present in smaller concentrations on a predominantly seasonal basis. References to work on the plaice population have been cited elsewhere in this survey. The energy content of invertebrates which constitute the food supply of demersal fish in the Bay was assessed by Brawn, Peer, and Bentley (1968), while Peer (1970) determined the productivity of one of the major species, *Pectinaria hyperborea*. The structure of the invertebrate community and its relationship to sediment type has been analyzed by Hughes, Peer and Mann (1971).

DESIGN OF THE PRODUCTION MODEL

The production model to be described is based upon the application of energy principles (Winberg, 1962) to the production processes of a typical demersal fish population. Two basic assumptions of the model are: (1) the age distribution is stable, and (2) the population is confined to the same general area throughout the year. These features are commonly found in flatfish populations (Beverton, 1962) and they apply to American plaice in the Gulf of St. Lawrence (Powles, 1965) and St. Margaret's Bay (Bakken, 1972).

The seasonal pattern of energy storage and conversion processes is analyzed in detail by the model once the initial equilibrium state is specified. If an assessment of the production dynamics associated with changes of state over a period of years is required, an appropriate sequence of changes in population structure must be postulated.

1. Structure of the Model

A. General Features

Calculations with the model start at an initial time assigned to an appropriate reference date and continue by evaluating the energy changes during successive time intervals until a year's cycle is completed. For convenience, the reference date used is the day following an idealized "date" on which the population spawns.

The initial state is defined in principle by data listed in Table 1 but it is desirable to represent the state by various other properties which are computed from these data. The most important of these properties is the total population energy per unit area but other properties of interest include total numbers of eggs and fish per unit area, overall sex ratio, biomass per unit area and age structure diversity.

Population energy changes associated with a change of state during an interval of time are the result of changes in numbers (n) or the energy content (e) or both of individuals in each age class. The energy E of the population can be expressed as

$$E = \sum_{i} n\ e \tag{1}$$

where i = the age class. Changes in population energy during a time interval dt are then given by the equation

$$\frac{dE}{dt} = \sum_{i} n\ \frac{de}{dt} + \sum_{i} e\ \frac{dn}{dt} \tag{2}$$

which implies

[change in population energy] = [production] - [elimination].

When calculations are performed for a finite time interval, it is therefore necessary to assign suitable average values of n and e for each age class and to evaluate the changes in numbers (Δn) and energy of individuals (Δe) of the age class during that interval. It should be noted that, for all time intervals within a given year, changes in numbers must be zero or negative so that the second term on the right in equation (2) is esentially always negative.

Changes in numbers per age class are computed from numbers present at the start of a time interval and the appropriate mortality rate. In the present analysis, it is assumed that the mortality rate is constant throughout the year, with a value dependent upon the annual mortality rate defined by the stable age distribution at population equilibrium. Seasonal variations in mortality rate of larger fish caused by annual feeding patterns of natural predators or by fishing activity could be considered by making minor changes in the model. In the case of eggs, larvae and O+ fish, however, the instantaneous mortality rate is assumed to vary with stage of development.

The change in energy of individuals during any time interval is computed directly from data used to define the seasonal energy storage cycle (MacKinnon, 1972a) and the net yearly increases in weight and length which are specified by weight/length and length/age regressions. It is assumed that length changes occur only during a certain part of the year and that the rate of length increase is constant during that period.

Because of the assumptions of population equilibrium, the net change in population energy over an annual cycle is zero; this can be expressed formally, using equation (2), as

$$\oint \frac{dE}{dt} = \oint \sum_i n \frac{de}{dt} + \oint \sum_i e \frac{dn}{dt} = 0$$

so that,

$$\oint \sum_i n \frac{de}{dt} = -\oint \sum_i e \frac{dn}{dt} \qquad (3)$$

The term on the left side of equation 3 represents the net annual production of the population due to the change in energy of individuals, including eggs, larvae and older fish. The term on the right represents the elimination (including yield) of energy from the population by removal of individuals. It should be noted that the stable age or equilibrium assumption does not imply that population production during a particular time interval ($\sum_i n \, \Delta \, e$) must equal elimination ($\sum_i e \, \Delta \, n$) and that this will generally not be the case when the population experiences a significant annual energy storage cycle. This situation is found in many temperate zone fish populations in which production takes place principally during summer months while elimination and energy expenditures for maintenance occur throughout the year. Also it should be noted that net annual production is not in general equal to annual elimination of a particular age class; production exceeds elimination in younger age classes and vice versa in older age classes.

Production ($n\Delta e$) and elimination ($e\Delta n$) are computed with the model for each time interval and age class and then summed to give annual population values. For reasons outlined previously a distinction is made between gross annual production (including energy that is stored and used for population maintenance at other times of year) and net annual production which must equal annual elimination.

Yield as a component of elimination is evaluated by computing the decrease in numbers (Δn) due to fishing from a consideration of natural and fishing mortality rates.

Because of the primary importance of estimating the rate of energy intake as food by the population (Mann, 1967) a model describing metabolic processes of an individual fish was developed and the details are presented in the following section.

B. Metabolic Model for an Individual Fish

Food requirements and maintenance energy expenditures are computed with the metabolic model from data defining the seasonal pattern of energy storage in an individual fish. The model is based upon application of the energy conservation equation to an individual fish (Winberg, 1956), and distinction between various components of metabolic expenditure and energy storage by an approach similar to that of Kerr (1971).

An important feature of the model is the provision for use of energy from body stores to meet energy requirements for metabolism and gonad maturation during periods of starvation. Body energy stores are also assumed to be used as required when feeding levels are between maintenance and starvation.

Total metabolism is assumed to consist of standard metabolism and activity requirements plus heat released during food processing (specific dynamic action) to provide energy for these requirements and for energy storage (Fig. 1). Additional assumptions include: (1) standard metabolism depends upon fish size, season and temperature but is independent of feeding level, (2) activity metabolism for foraging and swimming is a fraction of standard metabolism at starvation and increases linearly with total metabolic level, (3) food is processed with a constant conversion efficiency (see **equation** 5) which is similar for standard and activity metabolism and for somatic and gonad energy storage requirements, (4) during starvation, energy may be transferred from body energy stores and converted to gonad materials with a certain constant efficiency.

The standard metabolism requirement (M_s) is computed from a laboratory-derived expression relating metabolic rate and weight at different temperatures and seasons (Winberg, 1956). In accord with the assumption mentioned above, the activity metabolism can then be evaluated from the expression:

$$M_A = a_1 M_s + a_2 (M - M_s) \qquad (4)$$

where a_1 and a_2 are constants and M represents total metabolism.

For each energy requirement (E), an amount of assimilated food energy (E/ε_p) must be processed and a quantity of energy $\{(1 - \varepsilon_p)/\varepsilon_p\}E$ released as heat. This is a direct consequence of defining food processing efficiency (ε_p) as the ratio of an energy requirement (E) to the energy of food that must be processed to meet this requirement. The amount of heat released during food processing (Q_p) to meet all requirements for an individual fish can then be written as

$$Q_p = \{(1 - \varepsilon_p)/\varepsilon_p\} (M_s + M_A + G_B + G_G) \qquad (5)$$

where G_B and G_G are the amounts of energy storage in body and gonad components respectively.

When the feeding level is above maintenance, the total metabolic energy expenditure for a particular time interval is computed from the various components mentioned above according to the expression:

$$M = M_s + M_A + Q_p \qquad (6A)$$

or, when equations (4) and (5) are introduced, by the equation

$$M = \{b_1 M_s + b_2(b_1 M_s + G_B + G_G)\}/b_3 \qquad (6B)$$

where $b_1 = 1 + a_1 - a_2$; $b_2 = (1 - \varepsilon_p)/\varepsilon_p$;

and $b_3 = 1 - a_2 - a_2 b_2$.

The corresponding amount of energy intake as food *(I)* can then be calculated from Winberg's (1956) energy equation:

$$I = \frac{1}{a}(M + G) \qquad (7)$$

where ε_a = assimilation efficiency and $G = G_B + G_G$ = total amount of energy storage in the fish during the time interval.

For situations between complete starvation and maintenance of body energy, it is convenient to make use of a parameter c which is a dimensionless measure of the feeding level appropriate to these situations. At starvation, the total metabolism *(M*)* can be expressed as

$$M^* = (1 + a_1)\, M_s + \{(1 - \varepsilon_t)/\varepsilon_t\}\, G_G \qquad (8)$$

where ε_t = efficiency of energy transfer from body to gonad. Assuming that gonads continue to develop during starvation, the decrease in body energy under these circumstances $(G_B{}^*)$ must meet requirements for metabolism and gonad growth so that

$$-G_B{}^* \quad = \quad M^* + G_G \tag{9}$$

At maintenance the requirements for metabolism and gonad growth are met completely by intake and processing of food so that the maintenance food intake (I^1) can be computed from

$$I^1 \quad = \quad \frac{1}{\varepsilon_a} \; (M^1 + G_G) \tag{10}$$

where M^1 is calculated from equation (6B) with $G_B = 0$. At intermediate feeding levels metabolism and food requirements are therefore determined by the equations:

$$M \quad = \quad -G_B{}^* \; + c \; (\varepsilon_a \; I^1 + G_B{}^*) \; - \; G_G \tag{11}$$

$$I \quad = \quad cI^1 \tag{12}$$

where c is found from the relationship $(1 - c) = -G_B/G_B{}^*$. This definition of c was chosen so that $c = 0$ at starvation and $c = 1$ at maintenance.

Slightly different metabolic models are used for calculations concerning eggs and larvae. In the case of eggs the energy for metabolism is provided by the decrease in yolk energy; the total decrease in egg energy during the development period is defined by a yolk utilization efficiency (Lasker, 1962) so that the daily expenditure can be found once development time is known. For larvae a constant growth efficiency is specified and food consumption is computed directly; metabolic expenditures are then determined from the energy equation.

2. Choice of Parameters

Sufficient data are available from direct observations concerning the American plaice population of St. Margaret's Bay to provide almost complete specification of parameter values for the production model. A few parameter values must be determined from information applicable to other plaice populations and fish in general.

Although spawning occurs from April to June in the St. Margaret's Bay population, 31 May was chosen as the idealized date of spawning and 1 June as the reference date for starting the production analysis. The time interval for calculation of energy changes is arbitrary but should be of the order of days; an interval of four days was found to be satisfactory.

Data required to specify the initial state of the St. Margaret's Bay population are presented in Table 1. Age 8 was chosen as the reference age class because these fish were fully vulnerable to the net used and relatively abundant in the catch. Annual mortality rates of vulnerable age classes were estimated graphically from length frequency and age/length data(Bakken, 1972); mortality rates of larvae and smaller fish were estimated by combined extrapolation forward from the total egg production and backward from relative numbers in vulnerable age classes.

Female plaice in the Bay mature at 6 to 15 years while males mature from 2 to 9 years; although data on percentage mature at age appear to follow an s-shaped curve in these ranges, a linear relationship is adequate. Length/age and weight/length regressions have been reported by Bakken (1972) while gonad weights at spawning and energy content of body and gonad materials were given by MacKinnon (1972a). Fecundity data are not available for St. Margaret's Bay plaice so that the fecundity/weight regression of Pitt (1964) for plaice in the Newfoundland area was assumed to apply.

Instantaneous changes in numbers per age class of older fish are determined by the annual mortality rate data, but additional information is required to describe the mortality pattern of eggs, larvae and 0+ fish. In view of the information outlined previously on ecology of plaice, it was assumed that hatching occurs at 18 days, transition to active feeding is completed at 23 days, and metamorphosis occurs at 108 days from 1 June. Mortality during the periods defined by these dates was described by estimates of probabilities of survival for each period; several sets of these probabilities were used and values will be given later in the paper. In the case of 0+ fish, it was considered desirable, in view of data for European plaice (Steele and Edwards, 1970), to assume a relatively higher mortality rate during the first few months after metamorphosis. Overall mortality rate of 0+ fish was therefore computed from assumed numbers of surviving larvae and numbers of age 1 fish estimated by back extrapolation from data for vulnerable age classes; the mortality rate during the first three months of this period was arbitrarily assumed to be twice that of subsequent months.

The seasonal energy storage pattern of St. Margaret's Bay plaice can be computed from the data on seasonal changes in weight relative to length (condition) and percent dry weight of materials, the annual gonad weight cycle and variations in the energy per unit dry weight of body and gonad materials (MacKinnon, 1972a). Direct information on the seasonal pattern of length change is not available for this population; the only relevant information concerns observations on smaller plaice in the Newfoundland area (Pitt, 1966). In view of this information and data on seasonal variations in feeding intensity, it was assumed that the annual length increase in St. Margaret's Bay plaice occurred during the period from 1 June to 30 November.

The standard metabolic rate of American plaice as a function of size, season and temperature can be computed directly from laboratory data (MacKinnon, 1972a) but constants a_1 and a_2 of the metabolic model (equation 4 etc.) must be determined before the activity component of metabolism can be found. Estimates for these constants have been obtained for plaice under laboratory conditions (Ware, D., personal communication). Since no method of checking was available, the laboratory value of $a_2 = 0.067$ was assumed to apply to field conditions. A value for a_1 was chosen so that daily ingestion computed with the metabolic model was approximately zero during winter months when the observed decrease in body energy is equal to the energy expenditures for standard and activity metabolism. The estimate of $a_1 = 0.3$ obtained by this method is approximately equal to that for laboratory conditions.

Assimilation efficiency was taken as 80% (Winberg, 1956) and food processing efficiency was assumed to be 65%, although there is evidence that the latter may vary with diet and activity (Warren, 1971). Kerr (1971) found that for trout the cost of food processing was 29% of the energy intake; assuming an assimilation efficiency of 80% this gives a food processing efficiency of 64%. Edwards, Finlayson and Steele (1969) concluded that for 0+ European plaice amounts of food in excess of maintenance were converted to fish flesh with a maximum efficiency of 55%; when corrected for assimilation this implies a food processing efficiency of 69%. Feeding experiments with American plaice (Ware, D., personal communication) provide further confirmation of the 65% estimate.

No information is available on the efficiency of transferring energy from body materials and converting it for storage in ovary materials. However, biochemical considerations suggest that the efficiency might be around 90% (Blaxter, 1967).

A yolk utilization efficiency of 65% was assumed on the basis of information reviewed by Lasker (1962) on energy conversion in eggs. Net growth efficiency of larvae was estimated at 50%, a value slightly higher than the maximum efficiency reported by Edwards, Finlayson and Steele (1969) for the smallest 0+ European plaice.

3. Computer Program Description

A Fortran program for the model was written for execution on a Control Data 3150 Computer. The program comprises:

(1) a preliminary section for data input and calculat-

ion, with printout, of properties defining the initial population state;

(2) a main loop for calculations required for each successive time interval throughout the year, with provision for printout of information at particular times of year as required;

(3) a final section for summation of production parameters over all age classes and time intervals to give annual population production characteristics which are then printed out.

In the main loop energy changes of individual fish of each age class are first evaluated for the time interval from input data and metabolic expenditures and food requirements are computed with the metabolism sub-model. This information is then combined with changes in numbers during the time interval to give production, metabolism, food requirements, elimination and yield for each male and female age class. These calculations are performed for fish of age 1 and up and finally, depending upon the time of year, the corresponding computations are made for eggs, larvae or 0+ fish as appropriate. At the end of the loop, the various production parameters and other quantities of interest are summed over all age classes to give overall population parameters appropriate to the particular time interval.

RESULTS AND DISCUSSION

1. Productivity of St. Margaret's Bay Plaice

The productivity of any fish population depends upon a complex of energy flows (Fig. 2) which are associated with processes of energy conversion and storage within the population. Estimates for the seasonal variation in these energy flows and the net annual values were computed with the production model from data for the St. Margaret's Bay plaice population.

When the population is in its initial state on 1 June the total population energy per unit area is 4.20 kcal/m^2; fish aged 1 and up constitute 4.02 kcal/m^2 of this amount and eggs constitute the remaining 0.18 kcal/m^2. The biomass equivalents of this energy are 41.6 kg/ha and 1.22 kg/ha for fish and eggs respectively. Biomass per age class ranges from 0.021 gm/m^2 for females aged 1 to a peak of 0.29 gm/m^2 at age 12; corresponding values for males are 0.030 gm/m^2 at age 1 to 0.22 gm/m^2 at age 10. Density at this time is 728 fish per hectare, overall sex ratio is 0.96:1, and the number of eggs present is 7.3×10^6 per ha.

Daily body growth rates, metabolism and food consumption of individual fish attain peak values in summer and gross growth efficiencies of about 40% are estimated for this period (Fig. 3). During winter months, food consumption decreases to zero, metabolic rate declines, body growth rate becomes negative and growth efficiency is zero. In the case of mature females gonad growth continues during winter months at the expense of body energy stores.

Although the curves shown in Figure 3 represent the main seasonal features of energy conversion and storage processes in an individual American plaice several points should be noted concerning interpretation of their detailed significance. After assuming that increase in length occurs only during a certain period in the year, the body growth rate curve is generated directly from observational data so that the detailed shape of this curve is greatly influenced by variability in these data. For population estimates it was assumed that although absolute values of growth rate differ, fish of all age classes exhibit a similar seasonal growth pattern; this assumption was necessary because data were available only for 30-40 cm females and 20-30 cm males. Metabolism and food requirements are computed from growth data with the metabolic sub-model and the magnitudes of these quantities are affected by uncertainties in parameter values used in the model. On the other hand, several checks on the reliability of these patterns are available. The period of negative body growth rate is consistent with observations that food is virtually absent from the stomachs of plaice during that time of year (Powles, 1965). For the winter period the observed rate of decrease in body energy is approximately equal to the energy requirements for metabolism and gonad maturation computed with the model; in this case the metabolism approaches the standard level which is estimated independently from laboratory data (MacKinnon, 1972b) while gonad growth rate is found directly from field data. During the summer months the estimated rates of food consumption and growth efficiencies are similar to those observed in laboratory feeding experiments for American plaice (Ware, D., personal communication) and other flatfishes (Pandian, 1970; Edwards, Finlayson and Steele, 1969) when food is relatively abundant.

The seasonal variations in production, metabolism and food consumption of each age class follow patterns similar to those for individuals in the age class (Fig. 3) while elimination, because of the constant mortality rate assumption, has little seasonal variation. In August, for example, age 11 females ingest 38 kcal/ha day while production is 13.6 kcal/ha day and elimination is 1.2 kcal/ha day. During March a metabolic expenditure of 6.4 kcal/ha day plus gonad production of 0.7 kcal/ha day is balanced by the decrease in body energy and elimination is 1.0 kcal/ha day.

Distributions among age classes of population biomass and annual metabolic expenditure and food consumption (Fig. 4) have peak values near the median age of the population. The estimated biomass magnitude is directly dependent upon population density data while the biomass distribution is influenced primarily by mortality rate data. Metabolism and food consumption estimates are directly related to the biomass magnitude and distribution.

Since an increase in mortality rate with age is commonly found in unfished populations (Nikolsky, 1969a) appropriate rates for various age class ranges of the St. Margaret's Bay population were estimated graphically from catch data. This interpretation, however, cannot be distinguished statistically from an assumption of constant mortality rate for all vulnerable age classes and different estimates for biomass, production, etc. are obtained if the latter assumption is used. In the present analysis the annual instantaneous natural mortality rate of females aged 4-12 is assumed to be 0.13 whereas according to a method used by Huntsman (1918) this figure is approximately equal to the mortality rate for all vulnerable age classes. If the mortality rate of 0.13 is assumed to apply to all vulnerable age classes, higher estimates for biomass, production, etc. of older fish are obtained than in the present analysis. However, the rate obtained by Huntsman's method is very strongly influenced by numbers of fish in the younger age groups and when a slightly different method is used (Robson and Chapman, 1961) a value of 0.26 is obtained. In the latter case, assuming the density of age 8 fish as given in Table 1, estimated biomass, production, etc. is lower for ages 8-12 relative to those of the present analysis but estimates for older age classes are relatively higher.

The distribution of production and elimination among age classes (Fig. 5) is such that net production exceeds elimination in younger age classes whereas the converse is true for the older fish. In age 1 females, for example, the ratio of net production to elimination is 2.1 whereas in age 20 females the ratio is 0.33. This population feature is clearly an important requirement for the generation of an equilibrium biomass distribution with a constant rate of elimination. However, no major significance can be attributed to the sharp peaks in the body production and elimination curves because these are a consequence of assuming different constant mortality rates for various age class ranges. If mortality rate was assumed to vary continuously with age class, these peaks would be flattened somewhat but the production/elimination ratio of the younger age classes would remain greater than 1. The mortality pattern will have similar effects on egg production and elimination of gonad materials and will, therefore, alter the relative contribution of eggs at spawning from the various age classes.

Estimates of production parameters for larvae and 0+ fish are profoundly influenced by the mortality pattern.

Specification of mortality rates is however very difficult because data are scarce and substantial year-to-year variations can be expected even when the population has a reasonably stable age distribution. Energy flows were therefore computed for several mortality patterns - a most probable situation and more extreme cases (Table 2).

Information from a variety of literature sources was considered in estimating mortality rates used in the calculations for Table 2. The assumed annual mortality rate for plaice in their first year of life is comparable with the decrease in numbers by 4-5 decades reported by Gulland (1965) for Arctic cod. In the same paper, Gulland gave values of 5-17% for survival of cod and haddock eggs whereas Kipling and Frost (1970) considered that 70% of pike eggs survived to hatching. A figure of 0.25 was chosen as the mean survival probability to hatching for a plaice egg, with 0.10 and 0.50 considered to represent extreme values. In view of Gulland's observation that 23-29% of "late" cod and haddock eggs survived to become larvae, the mean survival probability for plaice during this period was taken to be 0.25, with 0.10 and 0.50 as extreme values. Kipling and Frost (1970) assumed 22% of hatched pike larvae survived to start feeding on zooplankton. Larval fish mortalities of 90-98% are common according to the data surveyed by Farris (1960) so that for plaice it was judged reasonable to assume a mean larval probability of survival to metamorphosis of 0.03 and extreme values of 0.10 and 0.01. If the survival probabilities given above for plaice are used together with numbers of eggs and age 1 fish from Table 2, the computed mortality rates for O+ fish are 6.1, 9.7, and 1.9 yr^{-1} for mean, extreme high and extreme low larval mortalities respectively. These mortality rates for O+ fish are similar to those reported by Steele and Edwards (1970) for O+ European plaice.

Net annual production of the St. Margaret's Bay plaice population is estimated at 2.3 $kcal/m^2$ when the most probable figures for larval and O+ fish production are used. Larval production accounts for 0.5 $kcal/m^2$ and gonad production for 0.2 $kcal/m^2$. The remaining component of total production, 1.6 $kcal/m^2$, may be compared with the estimated demersal fish yield of 1.7 $kcal/m^2$ for the North Sea (Gulland, 1970). Production of North Sea demersal fish must exceed the yield figure by at least a factor of two (Steele, 1965). However, as will be shown later in this discussion, the plaice in St. Margaret's Bay consume about half of the estimated benthic production so that production of the demersal fish community in the Bay may well amount to twice the estimate for plaice. According to these rough estimates, therefore, demersal fish productivity in St. Margaret's Bay is equal to that of the North Sea.

The production/biomass ratio for the plaice population, including larvae, is 0.4 while the ecological efficiency (production/ingestion) is 17%. When larvae are excluded from the calculations these figures become 0.3 and 12% respectively. The production/biomass ratio is low but the value is close to that expected for a population dominated by large, slow-growing fish (Mann, 1969). The ecological efficiency of 12% for that part of the population consuming benthos is within the 5-15% range appropriate to a variety of populations (Odum, 1971).

Gonad production constitutes 8.5% of total population production and 13% of production by fish aged 1 and up. Mann (1965) reported that germ cell production amounted to 9.5% of production by fish aged 1 and up in a freshwater fish community but, when revised estimated for O+ fish production (Mann *et al*, 1971) are considered, gonad production constitutes 3.2% of the total production.

Larvae and O+ fish together account for 20% of total ingestion by the plaice population and 34% of net production but the biomass of this component of the population is about 4% of the total. In the freshwater fish community studied by Mann *et al* (1971) the production of O+ fish constituted 70% of the total but these populations consisted of fish with life spans of about 6-9 years as compared to 24 years in the plaice population.

Production by the population during the summer months (i.e. gross production) is approximately twice the annual net production. Winter metabolic requirements amount to 49% of gross production; the quantity remaining is divided between net body production (44%) and gonad production (7%). Summer metabolism accounts for 80% of total annual metabolism and winter metabolism for 20%; aside from the fact that the summer feeding period is 1.4 times the overwintering period, the main factor contributing to the relatively high summer metabolism is the heat released during food processing.

2. Effects of Fishing on Stock Structure and Productivity

Extensive changes in stock structure and production dynamics are produced when a previously unexploited population is subjected to fishing. The model described in this paper can be used to analyze these changes by evaluating the production characteristics of populations in various equilibrium states.

Fishing activity gives rise to changes of population state through direct and indirect modification of population structure parameters. Changes in age class structure and density are among the most direct and immediate consequences of fishing. More indirect changes result when the population responds by modification of a complex of interrelated characteristics such as growth rate, mortality, density, age at maturity and fecundity (Nikolsky, 1969a). This active response operates through a variety of mechanisms with time delays ranging from the order of days to years and the overall process is extremely complex to analyze. Although one cannot now predict the complex of stock structure modifications that might arise directly or indirectly from a particular fishing strategy, there is sufficient information available to estimate the extent of structural changes that might be expected. Given this information, sets of equilibrium states that might result from fishing can be defined and the associated production dynamics evaluated.

The data available for American plaice populations provide a unique opportunity to examine the relationships between stock structure, production dynamics and fishing activity. A convenient reference is provided by the equilibrium state (defined by structure parameters and energy flows) of the unexploited population in St. Margaret's Bay. Some indications of the equilibrium states that might be induced by fishing activity are provided by changes in stock characteristics which have been documented for plaice in the Gulf of St. Lawrence (Powles, 1969) and on the Grand Banks (Pitt, T. K., personal communication) during periods when fisheries in these areas were initiated and then intensified.

Changes in the production dynamics of plaice populations as fishing is intensified were studied by considering sequences of equilibrium states or paths which are attained by modifying selected structural parameters. The choice of a sequence of states is, in principle, arbitrary but it is convenient to use sequences which represent approximately the various types of response to fishing that one expects the population to display. In an actual situation there will be simultaneous changes in a number of the structural parameters and the path followed in response to changes in fishing pressure would be very complex. If a prediction of this path is desired it is necessary to define the mechanisms underlying the changes in structural parameters. However, in this paper the main concern is with the production characteristics associated with equilibrium states having specified structural parameters and the conclusions are not affected by the path taken to reach these states.

The age structures and relative densities for a postulated sequence of states of an American plaice population subjected to fishing are shown in Figure 6. This sequence illustrates the more immediate changes one expects from fishing a previously unexploited stock in which fish aged 1 to 4 are assumed not vulnerable to capture; mortality rates of older fish increase while densities decrease as fishing is intensified. State (1) corresponds to the unexploited situation of the St. Margaret's Bay population. States of moderate exploitation (2) through (6) represent situations observed in the exploited stocks of the Gulf of St. Lawrence and the Grand Banks. Intensively fished situations are represented by states (7) to (10) where mortality rates are comparable with those reported for European plaice in the North Sea (Beverton and Holt, 1957).

The equilibrium states of Figure 6 are conveniently represented by values of a diversity parameter (D) based upon the distribution of individual fish among age classes and computed according to Shannon's formula for information. Margalef (1968) discussed the use of such a parameter for sardine populations and in a later paper (Margalef, 1969) indicated the value of relating productivity with measures of diversity in general. Although age class diversity is not often considered in ecological theory, it can be used in a manner directly analogous to that of community diversity at the ecosystem level. In later parts of this discussion, it will be shown that many of the events associated with changes in community diversity (Regier and Henderson, 1971) have analogous implications at the population level when age class diversity is considered. In the present discussion the various equilibrium states of Figure 6 will, for convenience, be referenced by numbers 1 to 10; it should be noted, however, that diversity values can be assigned to each state and that there is an inverse relationship between diversity and state number.

Computed values of production, yield, ingestion and biomass for states (1) to (10) are plotted in Figure 7. In calculating the steady-state yield, the usual assumption that natural mortality rate (M) is unaffected by fishing (Beverton and Holt, 1957) was made; the fishing mortality rate (F) was then computed from the known total mortality rate (Z) and the definition $Z = F + M$. On this basis, the yield/elimination ratio for age 4-12 females, for example, increases from 0.35 for light fishing (state (1)) to 0.74 for moderate fishing (state (5)) to 0.84 for heavy fishing (state (8)). The total transient yield obtained during the time period required for each change of state is equal to the decrease in biomass; by arbitrarily assuming a time interval between states of one year, the corresponding annual transient yields can be computed and these are plotted in figure 7.

As fishing is intensified and population ingestion decreases (Fig. 7) relatively more food is made available to survivors and the growth rate of individuals may increase. This "density-dependent" effect is a common response of fish populations (Backiel and LeCren, 1957) and Pitt (personal communication) has observed such changes in growth rate in American plaice on the Grand Banks.

Alterations in population energy flows because of growth rate changes were investigated with the production model by changing the parameter ℓ_∞ of the length/age regression. Beverton and Holt (1957) discussed this method of changing ℓ_∞ as an empirical description of the relationship between growth and population density and incorporated it into their population models. Information on changes in ℓ_∞ of exploited American plaice stocks has not yet been reported in the literature but estimates of expected changes in ℓ_∞ were made on the basis of preliminary data now available (Pitt, personal communication). The production model was therefore used to compute energy flows for a series of states obtained by varying ℓ_∞; values for females were varied from 85.5, when the stock is unexploited, to 105 while those for males ranged between 45.5 and 55.3.

If a population with specified density and age structure is considered an increase in growth rate will result in a relative increase in population ingestion, biomass, production and elimination. An increase in ℓ_∞ from 85.5 to 100 for females and from 45.5 to 52.6 for males for a population in state (5) (Fig. 6), for example, would give the following: ingestion = 6.4 kcal/m^{2}yr; biomass = 2.3 gm/m^2; net body production = 1.05 kcal/m^{2}yr. These values can be compared with those for state (5) in Figure 7 where it is assumed that no growth rate changes occur. Elimination and yield from a population with this structure (diversity = 1.8) are shown in Figure 8.

Increases in population density as a consequence of reproduction response mechanisms also provide a compensation for a decrease in food supply utilization. If it is assumed that removal of older fish does not affect the total amount of energy that can be taken from the food supply, the density increase required for an exploited population to maintain energy intake equal to that for no exploitation can readily be calculated. The density of an unexploited population in state (1) (Fig. 6) decreases from 728 fish per hectare to 540 per hectare for the exploited state (5) while ingestion decreases from 11.0 kcal/m^{2}yr to 4.2 kcal/m^{2}yr. Population ingestion would be restored to its initial value if the density corresponding to population structure (5) were increased to (11.0/4.2) (728) = 1900 fish per hectare. Assuming that the food supply is limited, a population with a density of 1900 per hectare and age structure (5) has completely compensated for the effects of exploitation. Elimination and yield for states having this complete response (∞ response) are plotted in Figure 8 for comparison with values for states having neither growth nor density response (ϕ response).

In general, one expects a particular population to respond to exploitation by a combination of growth rate and density effects; this should give states with elimination and yield values which, for a given diversity, lie between the zero and complete response lines shown in Figure 8. Higher yields are clearly made attainable by the population's response to exploitation but it is important to note that such yields will be theoretically possible only after the response mechanisms have had sufficient time to operate. Whether or not these yields can be sustained depends upon the effects of such exploitation on the reproduction characteristics of the population.

If no population response occurs the alteration of age class structure and density by fishing (Fig. 6) results in an exponential decrease in gonad production and spawn (Fig. 9). Reproduction is adversely affected not only by the decrease in gonad production but also by the decrease in spawn/gonad production ratio from 0.84 for no exploitation to 0.45 for heavy exploitation (diversity = 1.6).

When the population experiences a growth rate increase, gonad production will increase proportionately; a decrease in age at maturity may also occur and this would cause a further increase in gonad production. There is considerable evidence to suggest that maturity is correlated to a greater extent with size than with age of fish (Alm, 1969) and consequently one expects maturity to be attained earlier when growth rate is increased. This phenomenon has apparently occurred as a result of growth rate changes in the Grand Banks plaice stocks (Pitt, T. K., personal communication).

Estimates of gonad production for a series of states with reasonable, but arbitrary, growth rate increases assigned are shown in Figure 9.

Fecundity of individual fish in the population may also change if growth rate and age at maturity are altered (Nikolsky, 1963). This effect has not been reported for any American plaice population but substantial year-to-year variations in fecundity have been observed (Bagenal, 1966) and these may have been due to yearly changes in growth conditions.

Another form of population reproductive response to the higher mortality rates associated with exploitation is for fish to attain maturity at a smaller size (Nikolsky, 1969a). Assuming size at maturity is genetically determined to a significant extent, natural selection under exploitation would provide a mechanism for reducing the mean size at maturity of the population. It is interesting to note that *Hippoglossoides platessoides* females in the Firth of Clyde attain 50% maturity at 20-21 cm and a maximum size of approximately 30 cm (Bagenal, 1957). Although plaice in St. Margaret's Bay attain maximum sizes of about 55 cm the ratio of size at maturity to maximum size is 0.6, a value close to the ratio of 0.65 for the Firth of Clyde stock. Fish in the latter population also have a significantly higher fecundity and gonad weight for a given size, suggesting that the population is adapted to a relatively higher mortality rate. These differences may have arisen as a long-term consequence of different selective pressures on the two populations. With this concept in mind, gonad production was computed for a series of states for which it was assumed that the maturity/maximum size ratio is equal to 0.60 and gonad weights at a given size are assigned values between those for the extreme situations mentioned above (Fig. 9).

An increase in growth rate plus a decrease in age, but not necessarily size, at maturity appears to be an effective method for maintaining population numbers in response to relatively low levels of exploitation. The immediate consequences of the start of exploitation (removal of a number of older fish and a proportionate decrease in the number of eggs laid) are probably similar to those associated with normal annual fluctuations in fecundity; adjustments in larval and young fish mortality rates could be expected to adequately compensate for these disturbances. Within one or two years a significant increase in growth rate could occur and the initial level of gonad production and number of eggs laid by the population would tend to be restored. In the absence of any response the number of eggs laid by a population in state (3) for example, would be 30% of the number for the unexploited population. A population with the same age structure but a higher growth rate (Fig. 9) by contrast, sheds 55% of the number of eggs of the unexploited population.

As fishing is intensified and high adult mortality rates are attained the numbers of eggs laid by the population, even allowing for a growth response, drop to 0.5-5% of the pre-exploitation values and result in a decline in population numbers. If, however, the postulated genetic response involving a decrease in size at maturity and increase in individual fecundity has had time to take place the number of eggs laid by the population would not fall below 13% of the pre-exploitation value (Fig. 9). The genetic response also assumes a significant decrease in egg size so that the reproductive advantages of this mechanism may not be as great as the calculations concerning the number of eggs laid would suggest.

3. Potential Yields From Demersal Fish Stocks

Ecological relationships between a fish population and its food supply, natural predators, and the fishery must be considered in any realistic assessment of the yield potentially available from the population. In the previous section, the production dynamics associated with changes in internal characteristics of a population subjected to fishing were analyzed. Additional ecological implications will now be considered.

The ecological situation of a demersal fish population can be conveniently represented (Fig. 10) in terms of an energy input from the food supply and a set of efficiency parameters (Dickie, 1971). Three of these parameters of particular interest here are: (1) foraging efficiency, (ε_{BF}), the fraction of food supply production ingested by the fish population, (2) production or conversion efficiency (K_F), the net amount of fish biomass synthesized and stored per unit food intake, (3) fishing efficiency (ε_{YF}) the yield to fishing as a fraction of fish production. In view of these definitions, yield to fishing (Y) can be related to food supply production (P_B) by the expression

$$Y = (\varepsilon_{BF} K_F \varepsilon_{YF}) P_B \tag{13}$$

Since larger fish are most affected by fishing activity, attention will here be focused on the benthic food supply and that part of the population comprised of fish older than one year.

Annual production of the invertebrate community in the deeper parts of St. Margaret's Bay where plaice are abundant is roughly estimated to be 25 kcal/m^2. This figure was obtained from recent biomass data (D. L. Peer, unpublished), the calorific values of Brawn, Peer and Bentley (1968) and an estimated average production/biomass ratio of 3.1 based upon observations of Peer (1970) on

Pectinaria hyperborea and the general considerations of Waters (1969). The estimate is comparable with that of Steele (1965) for the North Sea where the type of bottom community (McIntyre, 1961) is similar to that of St. Margaret's Bay. Steele estimated macrobenthos production at 3 gmC/m^2yr; assuming a conversion factor of 10 kcal/gmC (Odum, 1971) this is equivalent to 30 $kcal/m^2yr$.

Foraging efficiency and conversion efficiency of the St. Margaret's Bay population were estimated at 0.44 and 0.12 respectively. Net conversion efficiency (Fig. 11) and ingestion of fish aged 1 and up (Fig. 2) were given previously as output from the production model. Foraging efficiency was computed from ingestion and the estimate given above for invertebrate production.

Intensification of fishing is accompanied by a decrease in age structure diversity and changes in all three of the efficiency parameters as shown in Figure 11. Population ingestion and hence foraging efficiency (ε_{BF}) decrease because of the decline in density which results from fishing (Fig. 11A). Removal of older fish from the population involves a relative increase in the numbers of smaller fish with higher growth efficiencies; the associated change in population conversion efficiency (K_F) computed with the production model is shown in Figure 11B. Yield as a fraction of total elimination increases with fishing pressure and there is a corresponding increase in fishing efficiency (ε_{YF}) (Fig. 11C). The latter efficiency is computed from the ratio of fishing mortality to total mortality rate parameters and is easily obtained if the usual assumption of constant natural mortality rate is made. If this last assumption is not appropriate the fishing efficiency may be relatively greater. The effect on fishing efficiency of allowing natural mortality rate to decrease proportionately to half its initial value at state (10) is shown in Figure 11C.

The efficiency parameters of Figure 11 may also change as a consequence of the operation of population response mechanisms. Fishing causes an initial mismatch between population ingestion and the amount of energy available from the food supply; the population may respond by increasing growth rate or recruitment, or both. For a given density and age structure an increase in growth rate will result in increased ingestion, foraging efficiency and conversion efficiency relative to an exploited population which exhibits no response (Fig. 11A,B). The growth rate is subject to limitations inherent in each species and it is unlikely that ingestion could be restored to its initial value by this mechanism. However, recruitment processes would be capable of maintaining ingestion and foraging efficiency constant for the given range of age class structures (Fig. 11A); this could be accomplished through an increase in density of fish in the younger age classes. The fishing efficiency as defined above is not affected by population density changes, but if one considers that increased effort is required to sustain a specified fishing mortality rate as stock density declines, it is apparent that "inefficiency" of fishing must increase at low densities.

Productivity of the invertebrate food supply may be stimulated by the changes in predation pressure which accompany alterations in the fish population structure. The effects would be analogous to those produced in the fish population by fishing activity. In the present discussion, however, it will be assumed that benthic production remains constant.

Potential equilibrium yields from exploitation of the St. Margaret's Bay plaice population were computed for various sequences of population states and a constant food supply production of 25 kcal/m^{2}yr. The estimates were obtained from equation 13 and the information given in Figure 11.

Highest yields are predicted for states in which population ingestion is maintained at its pre-exploitation value whereas lowest yields are predicted for states representing no population response to exploitation. A density response involving an increase in the numbers of smaller fish is sufficient to maintain ingestion constant; this mechanism would make it possible to attain the sequence of states shown as line 1 in Figure 12. Under these circumstances the relative increases in both conversion efficiency and fishing efficiency affect the yields obtainable as exploitation is intensified. When no population response occurs, the low yields shown as line 2 (Fig. 12) are associated with states where population ingestion is significantly less than the energy potentially available from the food supply. If interaction occurs between natural and fishing mortality processes, the fishing efficiency may improve as fishing is intensified (Fig. 11C) and yields shown as line 4 (Fig. 12) would be obtained in situations involving no population response.

Removal of larger fish may make some food items unavailable to the population and thereby cause the foraging efficiency to decrease. In this case yield shown by line 3 (Fig. 12) will be less than for constant ingestion even though a density response occurs to match ingestion with the available food.

Populations with a large number of age classes require times of the order of years for density responses and one expects an increase in growth rate of individuals as a more immediate response to any mismatch between population ingestion and food availability. The extent of the growth response is, however, limited and, if no density response occurs, yields obtained for postulated maximum growth rates are as shown in line 5 of Figure 12. Population ingestion for these states is lower than for states along line 3 where it is assumed that the food supply is fully utilized.

In general a population may react to exploitation by a combination of growth and density responses so that yields lying within the region defined by lines 2 and 3 in Figure 12 can be expected. If fishing pressure is suddenly intensified so that population response mechanisms have not had time to operate the population might, for example, attain a diversity of 1.9 (state (4)) and have a predicted equilibrium yield of 0.3 kcal/m^{2}yr. A growth response alone might then occur and the yield would rise to a maximum of 0.45 kcal/m^{2}yr. During this period and subsequent years, a density response might result in a gradual increase in yield to the value of 0.7 kcal/m^{2}yr. which corresponds to a state of full use of the food supply. Once this last state is reached, the growth rate may decline towards its initial value.

The above description of states attained by a population in response to exploitation is clearly an idealization and the actual path of states for a particular population must in general be very complex. In order to describe the sequence of states in time the details of the density and growth rate mechanisms must be defined. Furthermore, it is questionable whether a sequence of equilibrium states would constitute an adequate description of the process; wherever ingestion and food supply are mismatched the response mechanisms come into operation to change the population state.

The attributes of mature ecosystems (Odum, 1971) are comparable with those of an American plaice population in the unexploited state (1). A relatively large biomass is supported and productivity is low (P/B = 0.3). The population structure has a high diversity; there are 24 age classes of females, for example, and diversity D = 2.3. Other aspects of diversity or "intraspecific variability" (Nikolsky, 1969b) are apparent (e.g. age at first maturity is spread over nine age classes of females) but these are more difficult to quantify. Life cycles are long and adult fish attain a relatively large size. The population exhibits stability and good regulation (Regier and Henderson, 1971) since the age class structure appears to remain unchanged from year to year and the fluctuations in numbers per age class are not great.

Calculations with the production model indicate a response to fishing which is in accord with the general ecological considerations of Regier and Henderson, 1971.

The production/biomass ratio of the American plaice population increases from 0.3 for no exploitation to 0.45 for moderate fishing intensity (state (5)) and 0.6 for high fishing intensity (state (10)). The corresponding values of age structure diversity (D) are 2.3, 1.8 and 1.5 respectively. Although it is not possible to make a quantitative prediction with the present model it seems reasonable to suggest that the decrease in diversity will be accompanied by decreases in stability and effectiveness of regulation. The changes in gonad production, spawn, and number of eggs laid as fishing is intensified have been analyzed previously (Fig. 9); if fishing pressures change very quickly so that there is not adequate time for population response mechanisms to operate, an unstable situation might result. At high fishing intensity (e.g. state (10)) the population has about 11 age classes so that one would expect such a population to be less effective at regulating population numbers and biomass in response to variations in year class strength, for example, than the unexploited population with 24 age classes.

Equilibrium yields of American plaice (Fig. 12) attain maximum values, according to the present model, when fishing is intensified at a rate such that the population can fully respond to the change. If a "pulse fishing" strategy (Regier and Henderson, 1971) is adopted the population may be forced into an unstable situation in which it would be less effective at exploiting its relatively constant food supply. At the same time a large mismatch between population ingestion and energy available from the food supply would be created; this food may then be consumed by a competing species so that the food supply of the plaice population is effectively reduced and the corresponding potential yield is diminished.

In the absence of information about rates of the population response mechanisms one must conclude that a policy of gradual intensification of fishing plus detailed analysis of the resultant changes in production dynamics constitutes the best strategy for attaining high sustainable yields. Demersal fish communities appear to have system properties which are analogous with those of the plaice population considered in this paper; the conclusion above regarding maximum yields from this population may also be relevant to the demersal fish community as a whole.

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Table 1 Information required to specify an initial state for the production model, with data for the St. Margaret's Bay plaice population.*

		Females	Males
(1) Density for reference age classes -numbers per hectare (age class)		16.7 (8)	16.7 (8)
(2) Annual mortality rates, with age range in years		0.40 (1-4) 0.13 (4-12) 0.51 (12-24)	0.40 (1-4) 0.14 (4-10) 0.75 (10-17)
(3) Age range of first maturity (years)		6-15	2-9
(4) Constants for length l(cm), gutted weight w (gm), and age t (years) regressions $l = l_\infty (1-e^{-k(t+t_0)})$ $w = c_1 l^{c_2}$	l_∞	85.5	45.0
	k	0.04	0.10
	t_0	1.23	0.98
	c_1	0.0047	0.0047
	c_2	3.099	3.099
(5) Constants for gonad weight w_G(gm), fecundity f, and gutted weight w (gm) regressions (at spawning time) $w_G = c_3 l^{c_4}$ $f = c_5 w^{c_6}$	c_3	0.0252	0.020
	c_4	1.261	1.00
	c_5	1094.0	--
	c_6	0.9010	--
(6) Energy per unit dry weight (cal/gm) of body and gonad materials at spawning time	body	900	990
	gonad	1430	613

*Data from Bakken, 1972 (1,2,3,4); MacKinnon, 1972a(5,6); Pitt, 1964 (5 - c_5, c_6).

Table 2 Estimates of production parameters for larvae and 0+ fish of the St. Margaret's Bay plaice population[(a)]

Estimate:	larvae probable	 high	 low	0+ fish probable	 high	 low
Energy Flows ($kcal/m^2$ yr)						
Ingestion	1.49	11.29	0.145	1.25	7.35	0.349
Metabolism	0.52	3.95	0.0506	0.74	4.24	0.208
Production	0.52	3.95	0.0506	0.27	1.63	0.071
Elimination	0.42	2.33	0.0475	0.35	3.27	0.269
Averages biomass (gm/m^2)	0.125	1.06	0.0108	0.066	0.286	0.0248
Energy Ratios						
Production/Ingestion	0.35	0.35	0.35	0.22	0.22	0.203
Elimination/Production	0.81	0.59	0.94	1.30	2.01	3.79
Production/Biomass[(b)]	4.15	3.72	4.69	4.09	5.70	2.86

(a) Assuming 7.32×10^6 eggs per hectare at spawning, 190 fish at age 1 and the following survival probability estimates:

		probable	high	low
egg:	spawn/hatching	0.25	0.50	0.10
larva:	hatching/active feeding	0.25	0.50	0.10
larva:	active feeding/metamorphosis	0.03	0.10	0.01

(b) Conversion factor of 1 kcal/gm assumed.

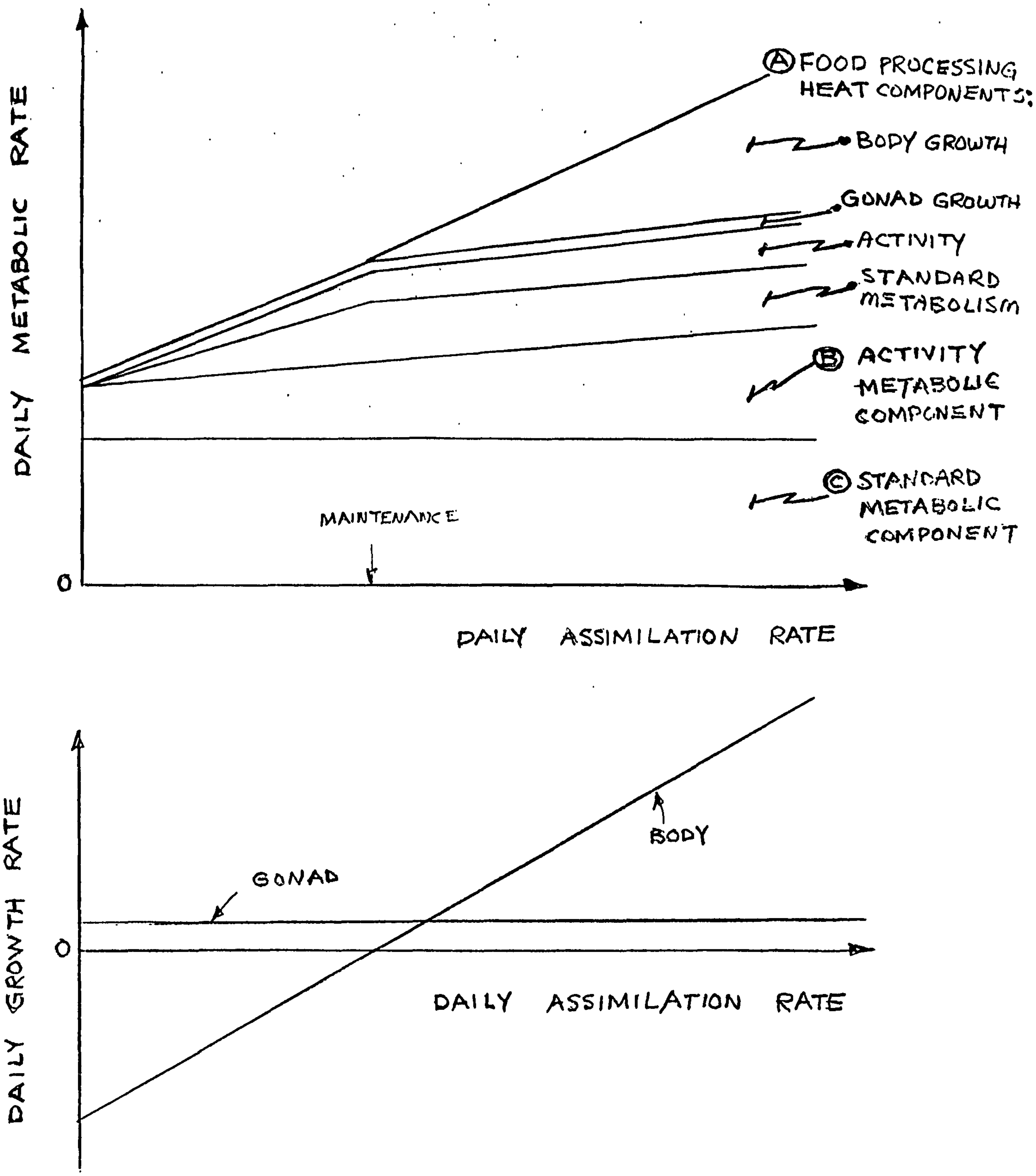


Figure 1. Relationships between metabolism, assimilated food requirements and body/gonad growth rate according to the metabolic model for an individual fish.

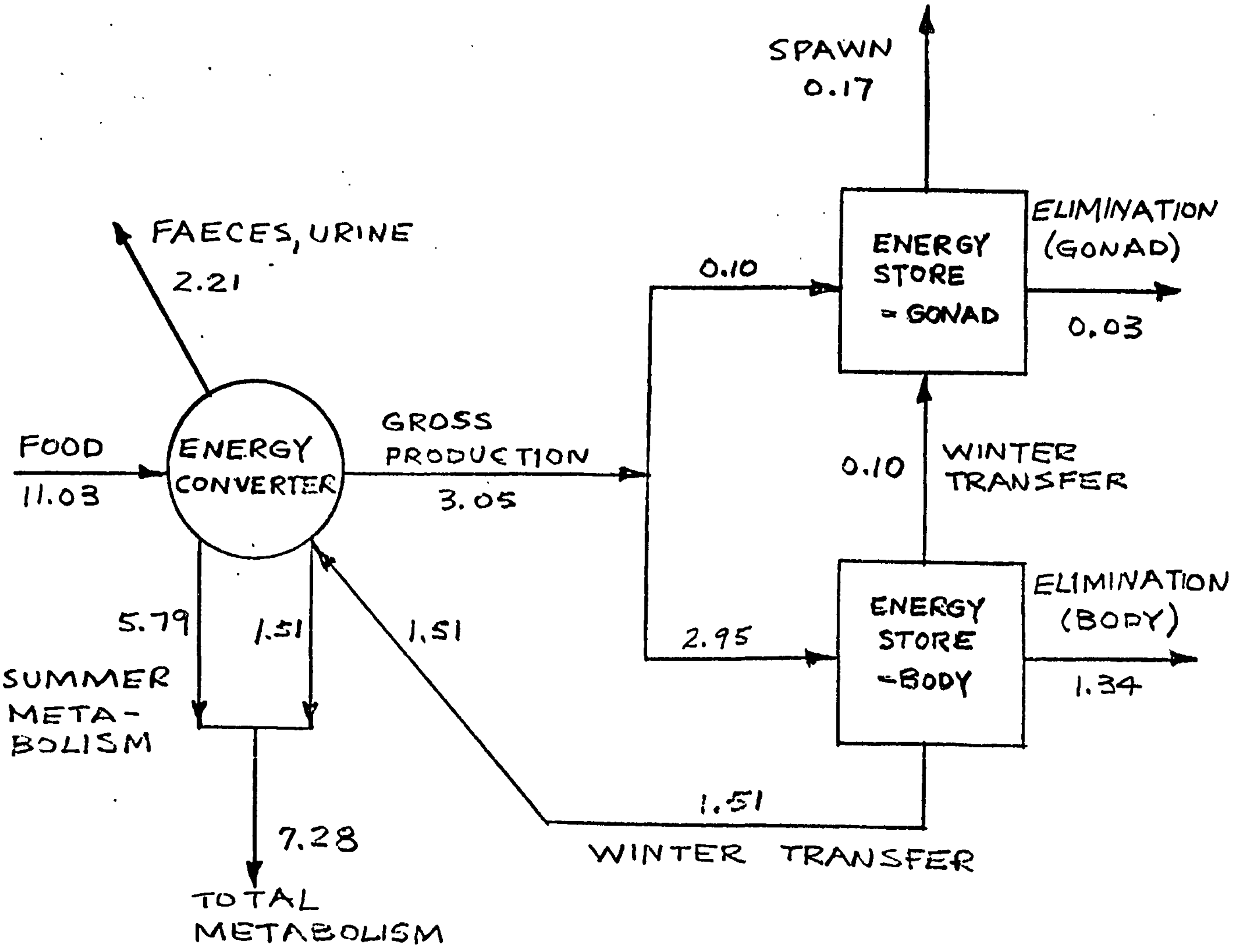


Figure 2. Annual energy flows for the American plaice population (fish aged 1 and up) of St. Margaret's Bay. Numbers are kcal/m^2.

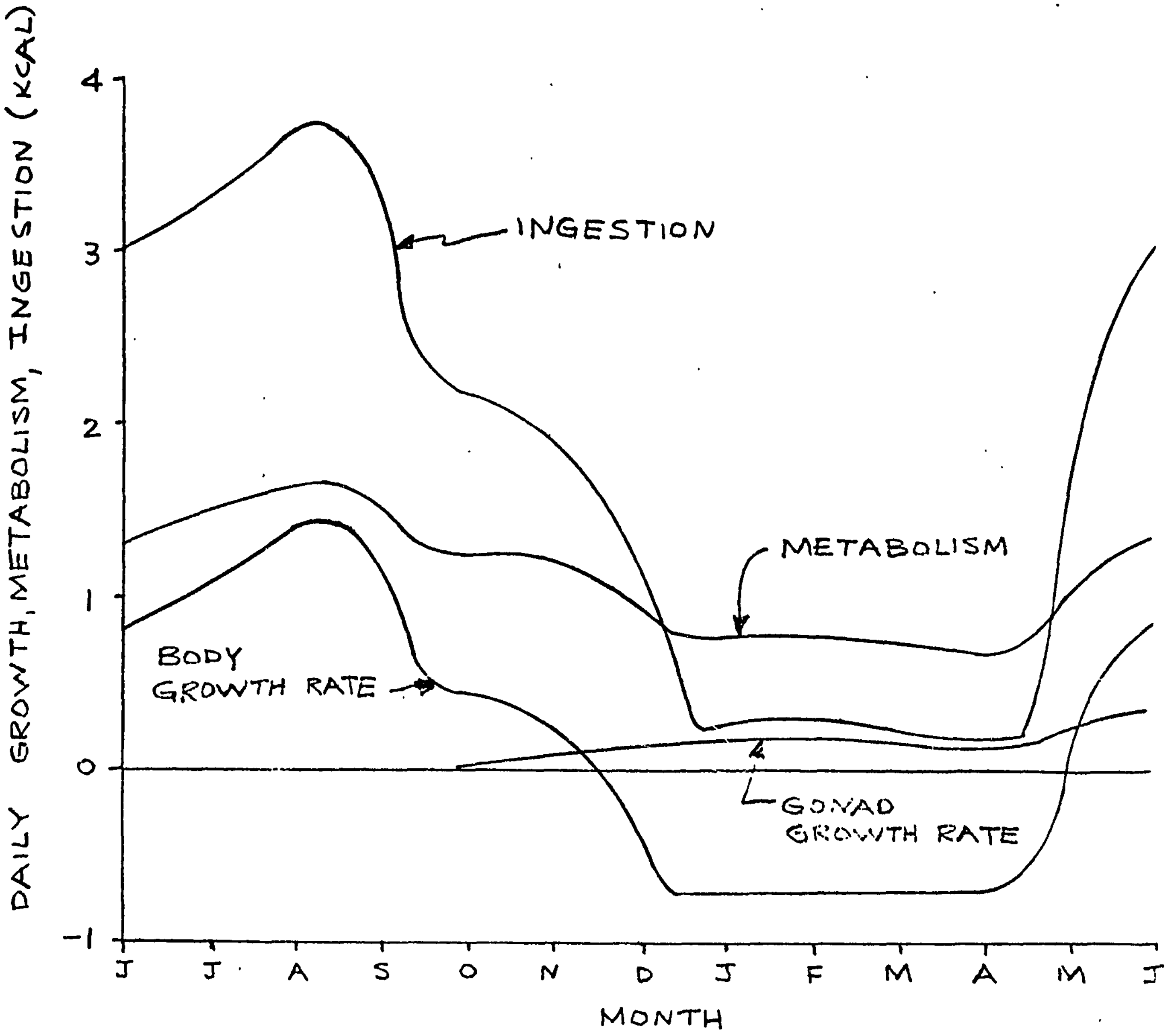


Figure 3. Seasonal variation in daily growth rate, metabolism and food requirements of a mature 35 cm. female American plaice.

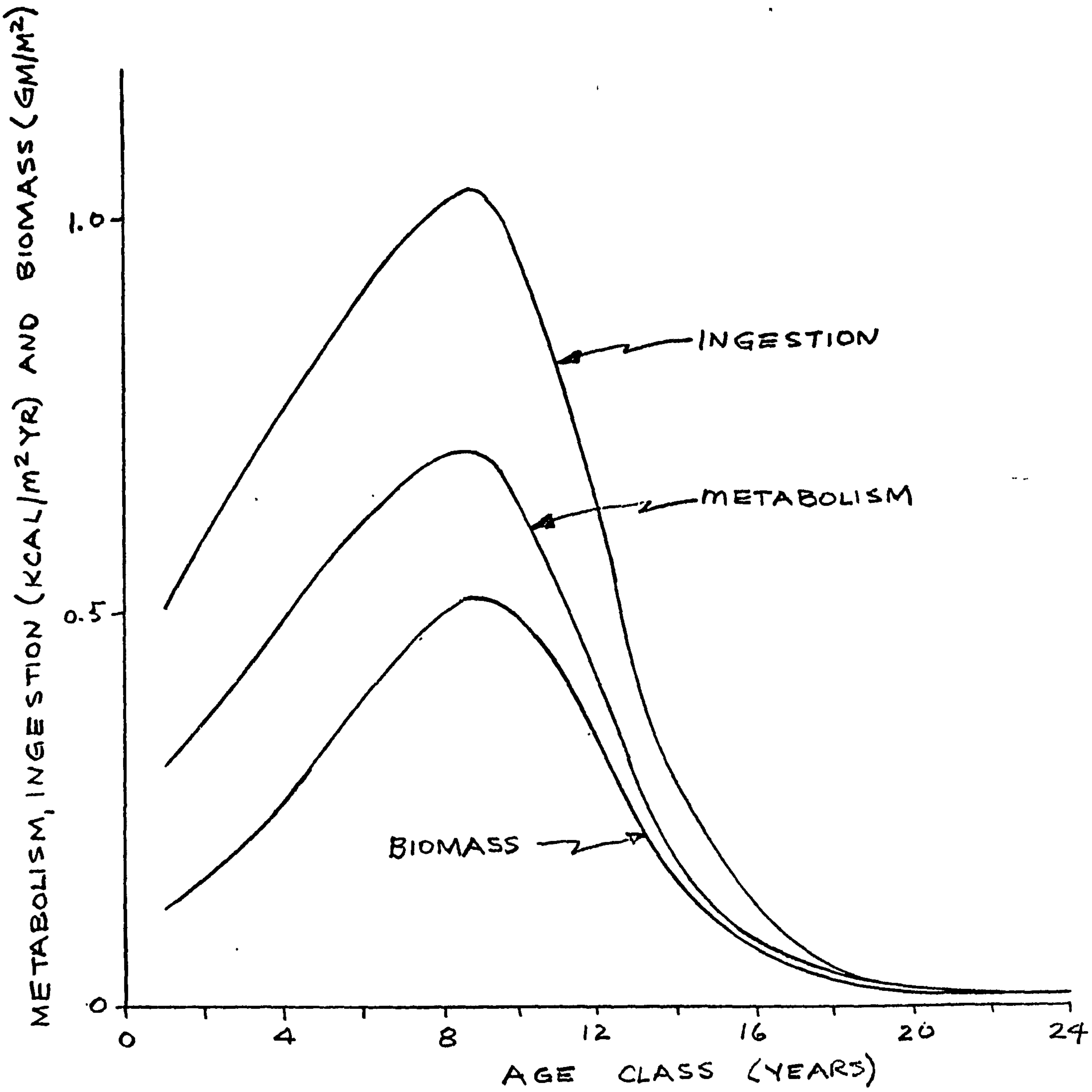


Figure 4. Distribution among age classes of biomass, ingestion and metabolic expenditure for the American plaice population of St. Margaret's Bay, N. S.

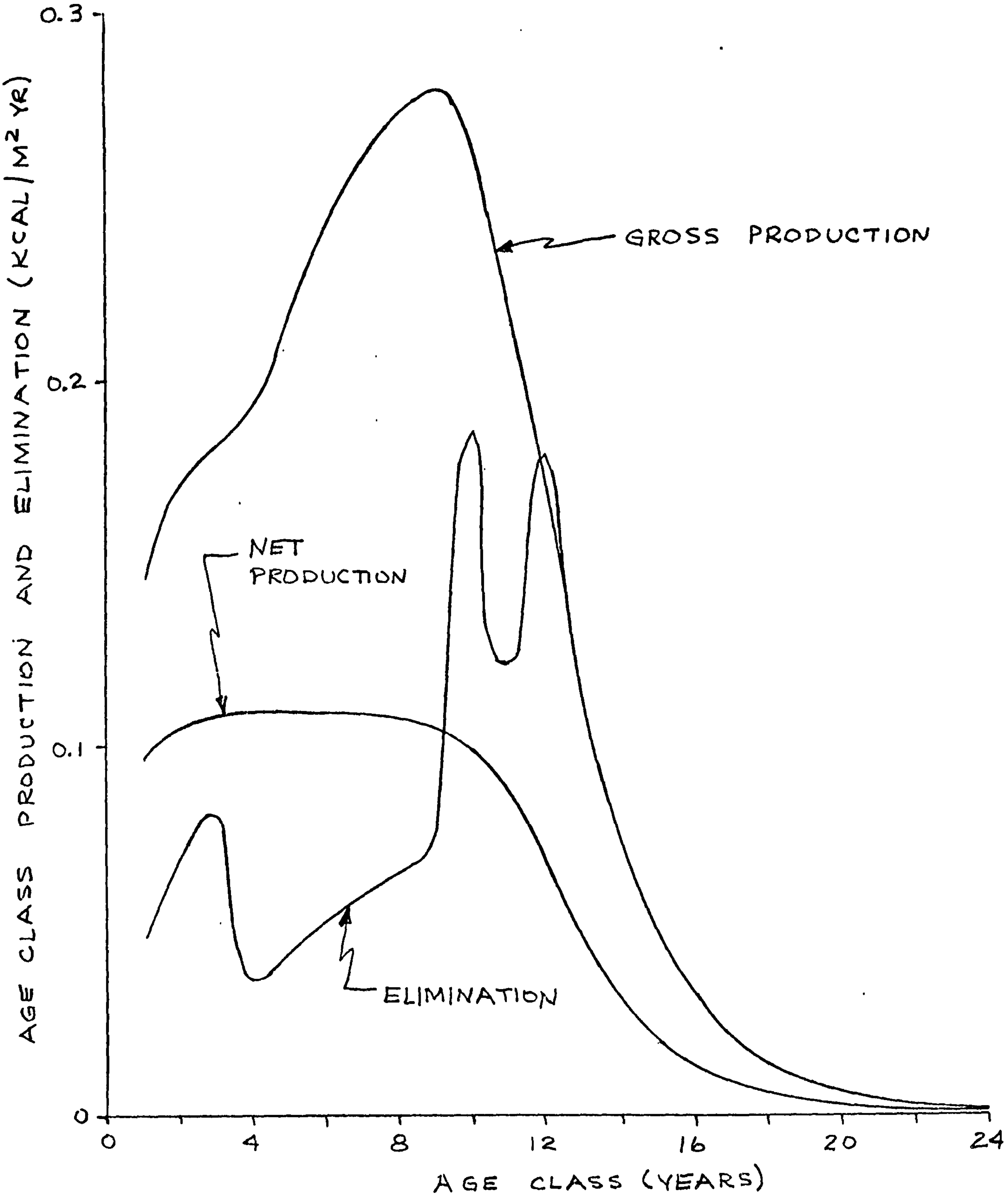
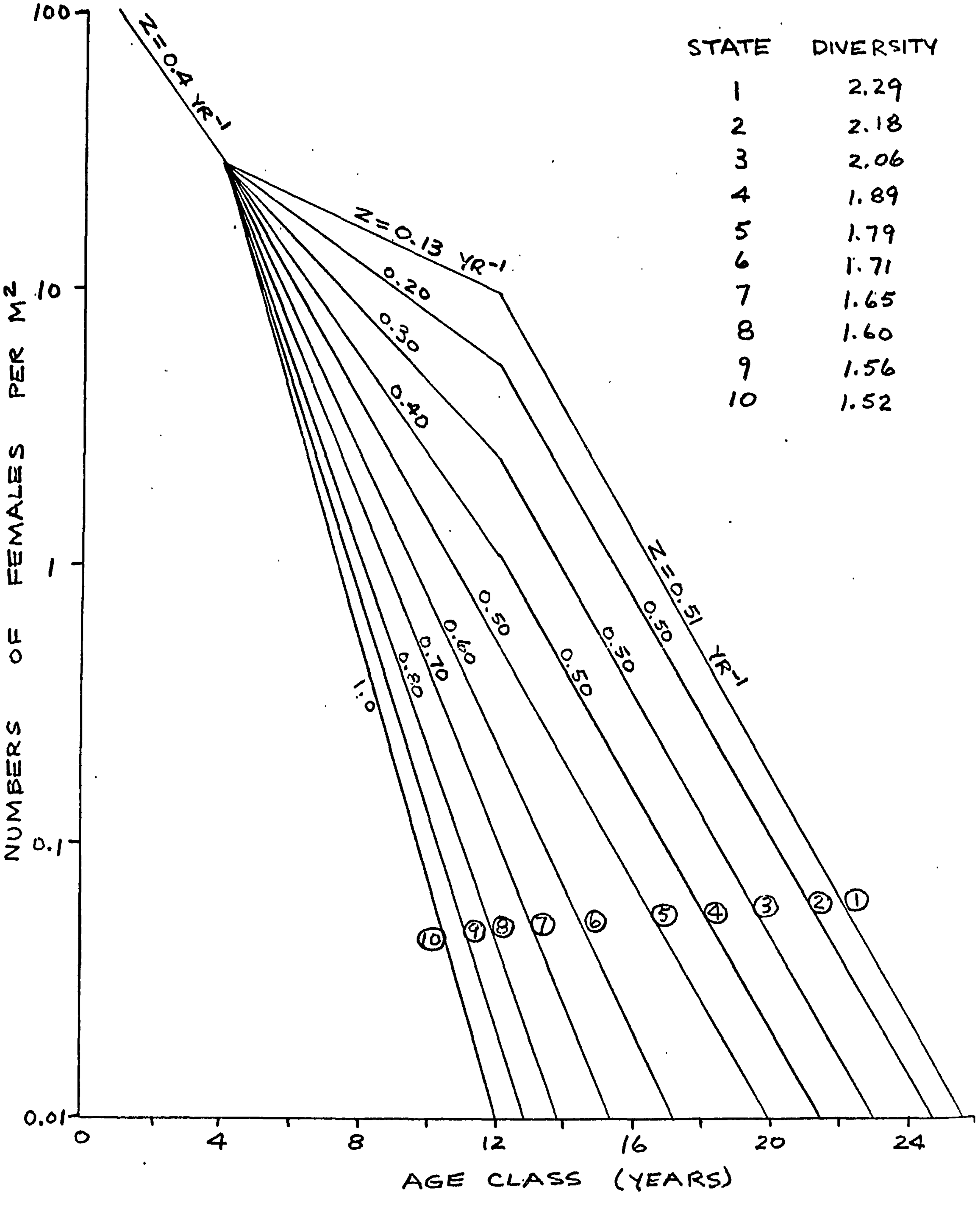


Figure 5. Distribution among age classes of annual production and elimination for the American plaice population of St. Margaret's Bay, N. S.



STATE	DIVERSITY
1	2.29
2	2.18
3	2.06
4	1.89
5	1.79
6	1.71
7	1.65
8	1.60
9	1.56
10	1.52

Figure 6. Postulated equilibrium states representing various intensities of fishing of the St. Margaret's Bay plaice population.

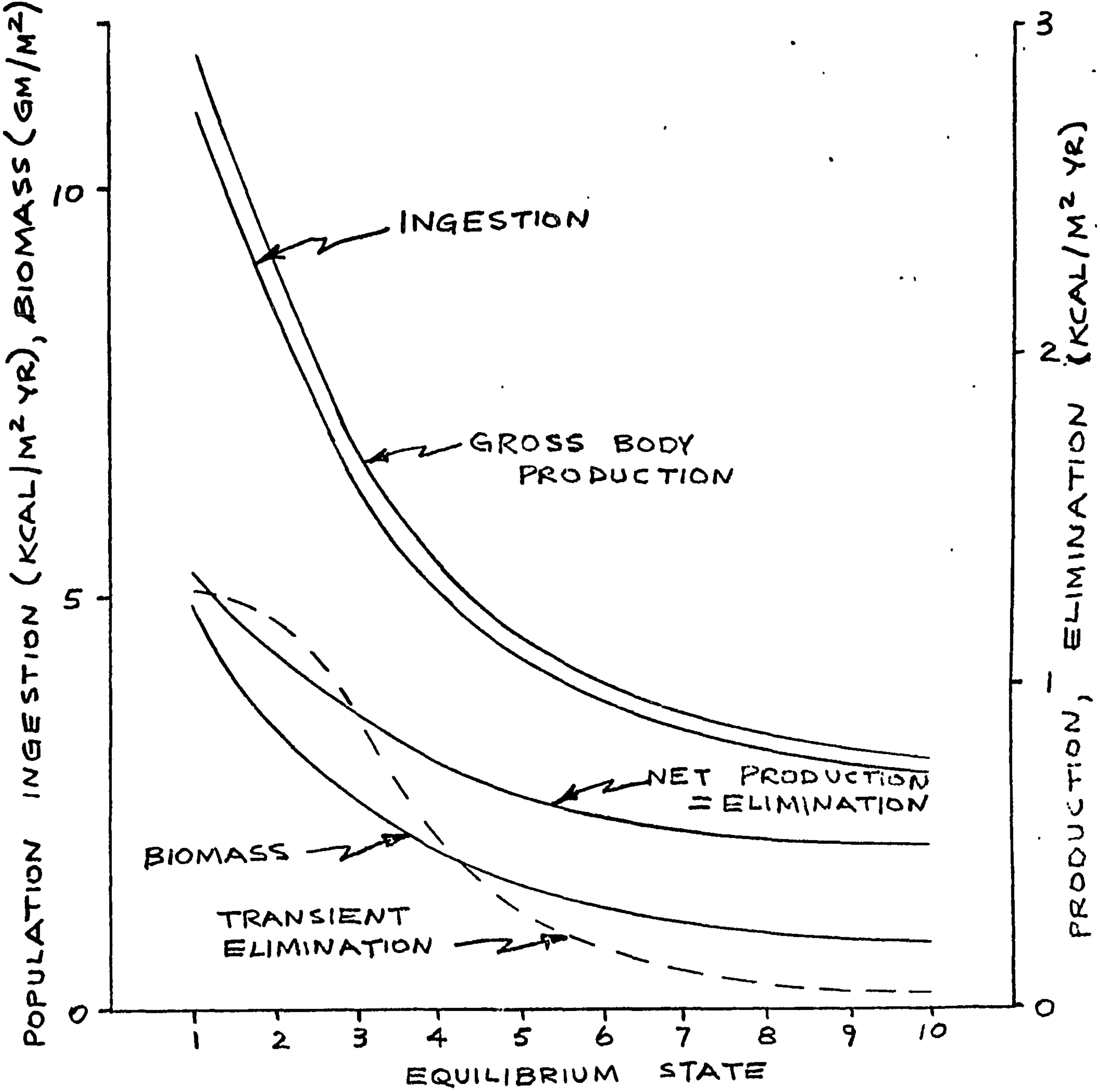


Figure 7. Variation of population ingestion, production, transient elimination and annual mean biomass for the postulated sequence of states resulting from fishing.

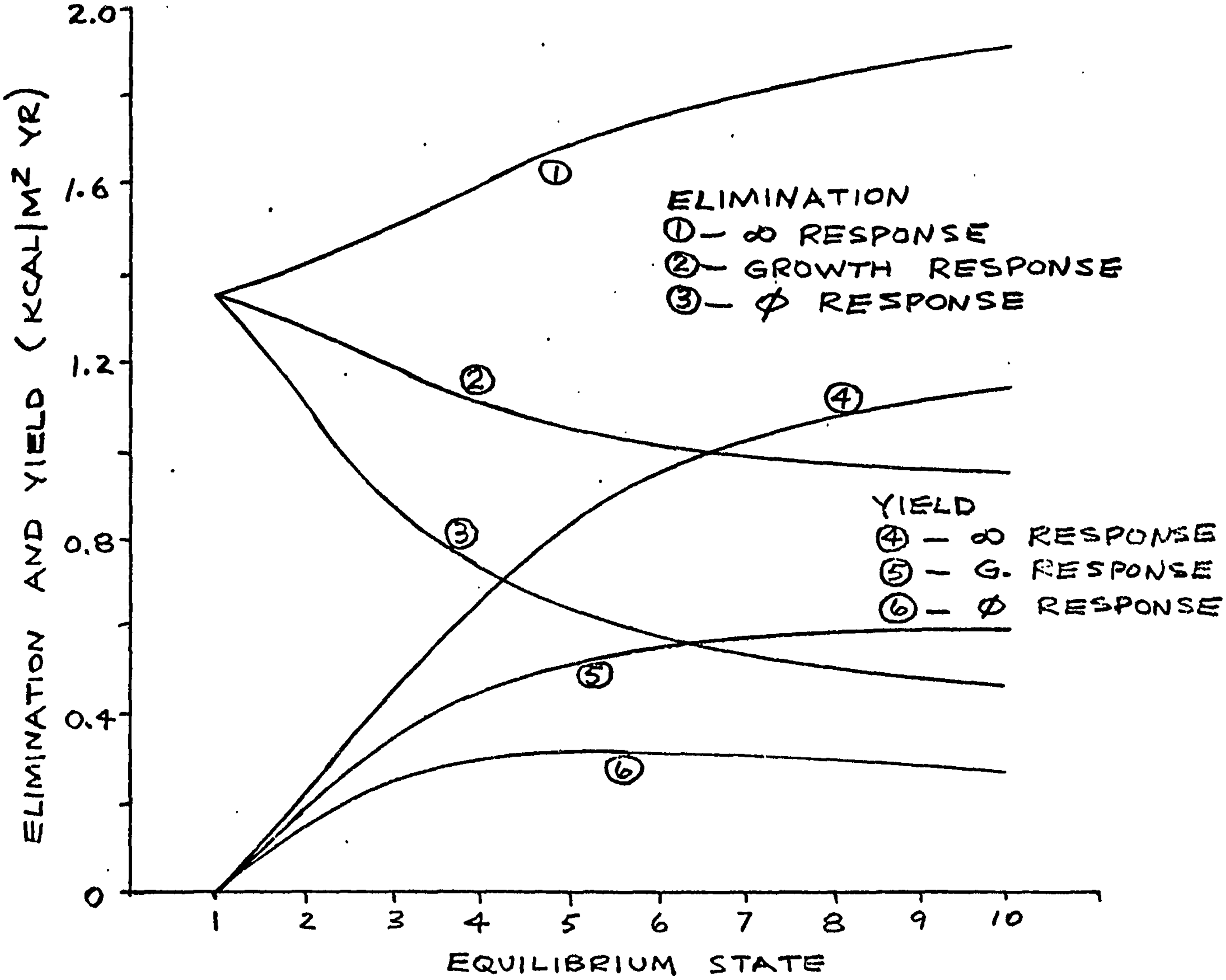


Figure 8. Variation of elimination and yield for equilibrium states resulting from fishing. Population is assumed to respond in three different ways as described in the text.

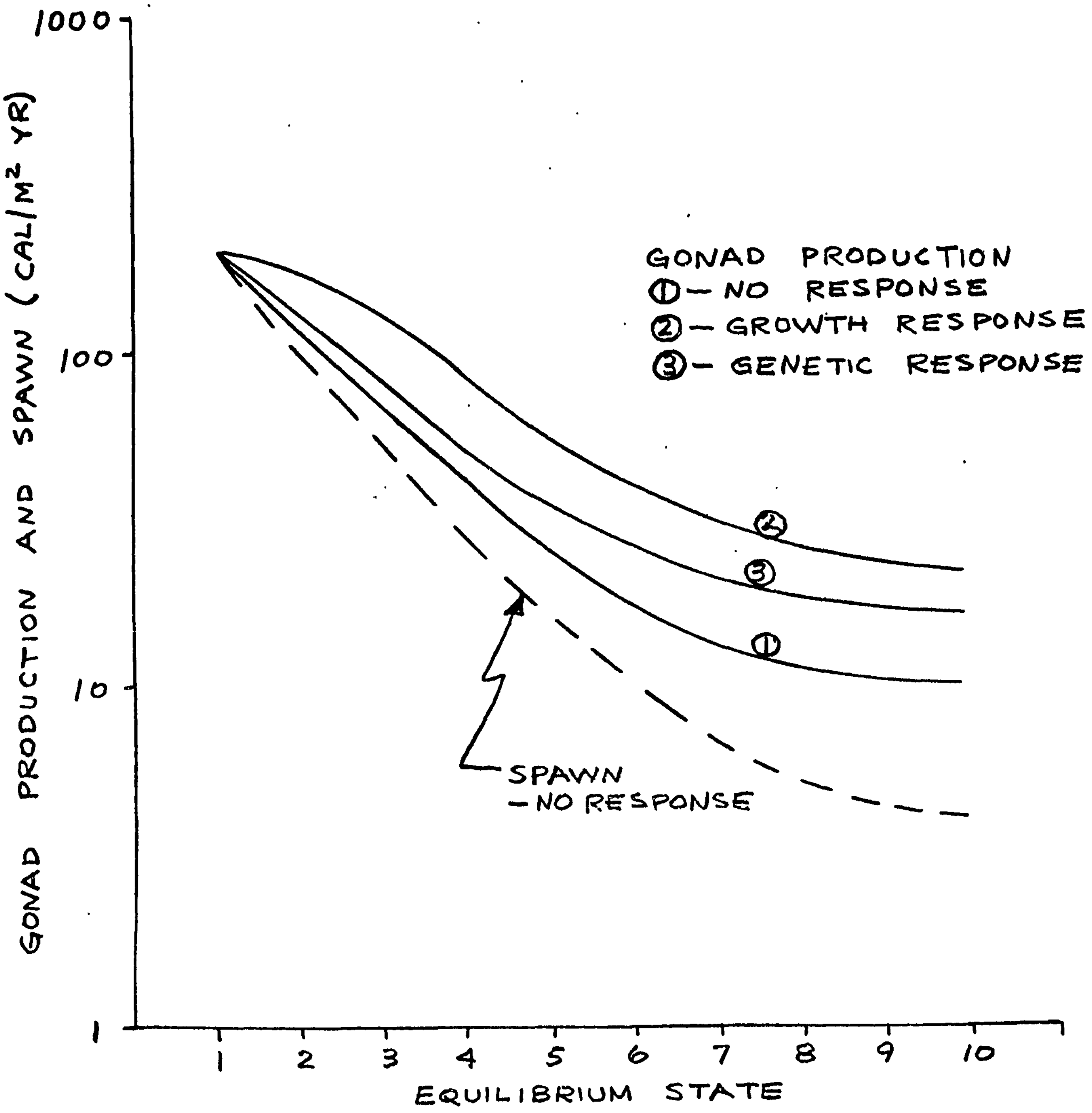


Figure 9. Variation of population reproduction parameters for the postulated sequence of states resulting from fishing.

A. Variation in gonad production and spawn energy. Population is assumed to respond in three different ways as described in the text.

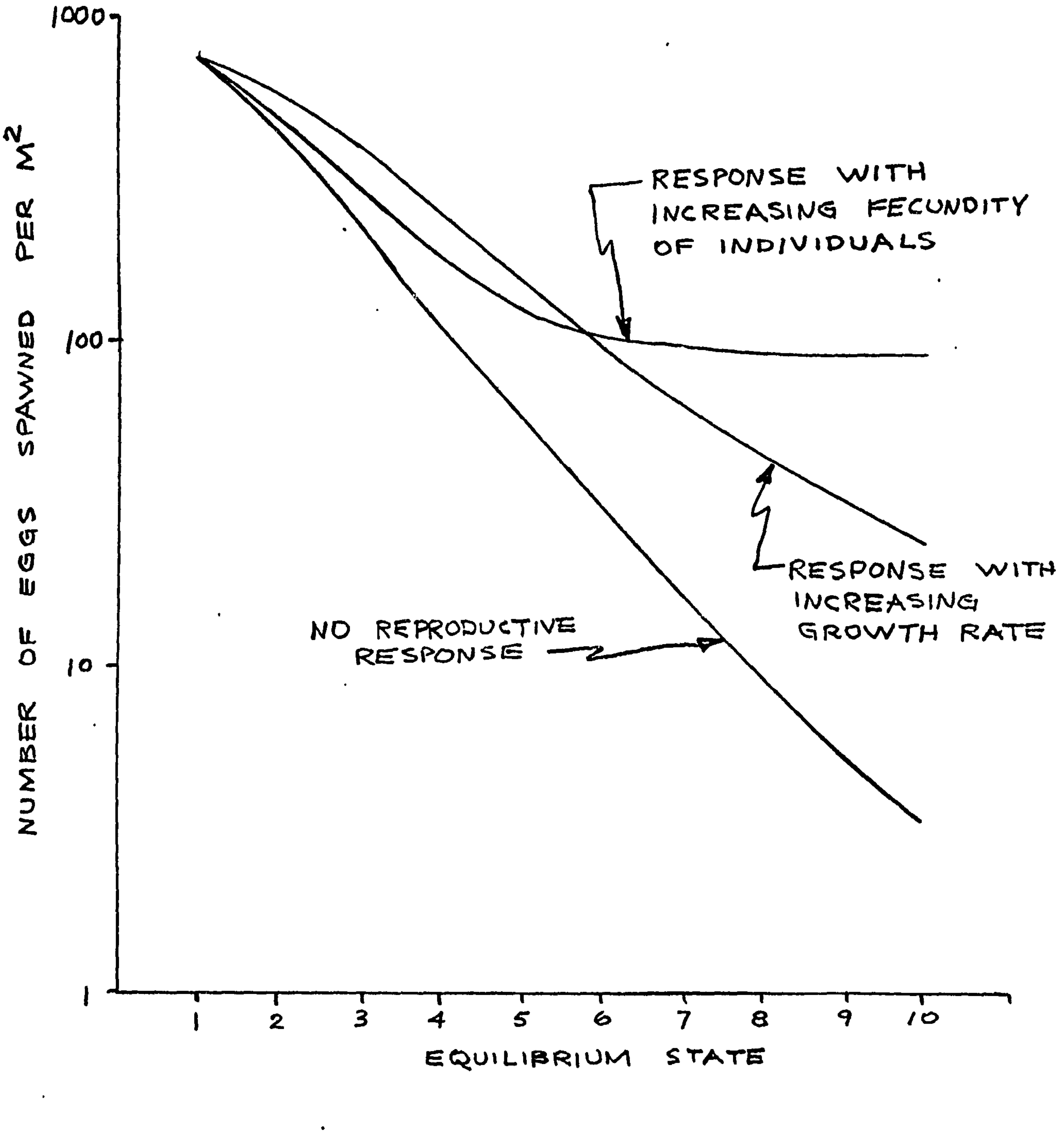


Figure 9. Variation of population reproduction parameters for the postulated sequence of states resulting from fishing.

B. Variation in number of eggs released. Population is assumed to respond in three different ways as described in the text.

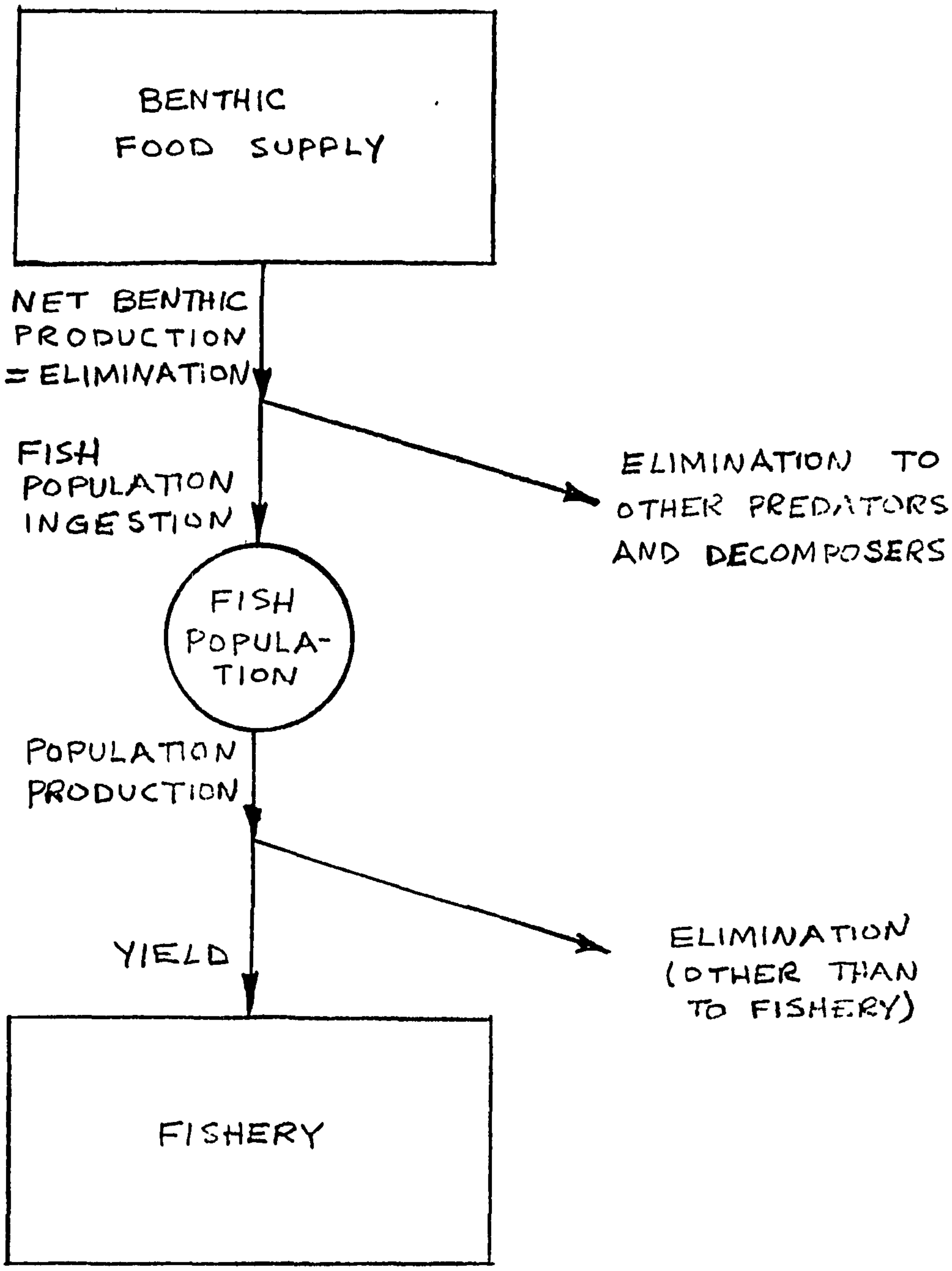


Figure 10. Food chain representation of energy flows for a demersal fish population.

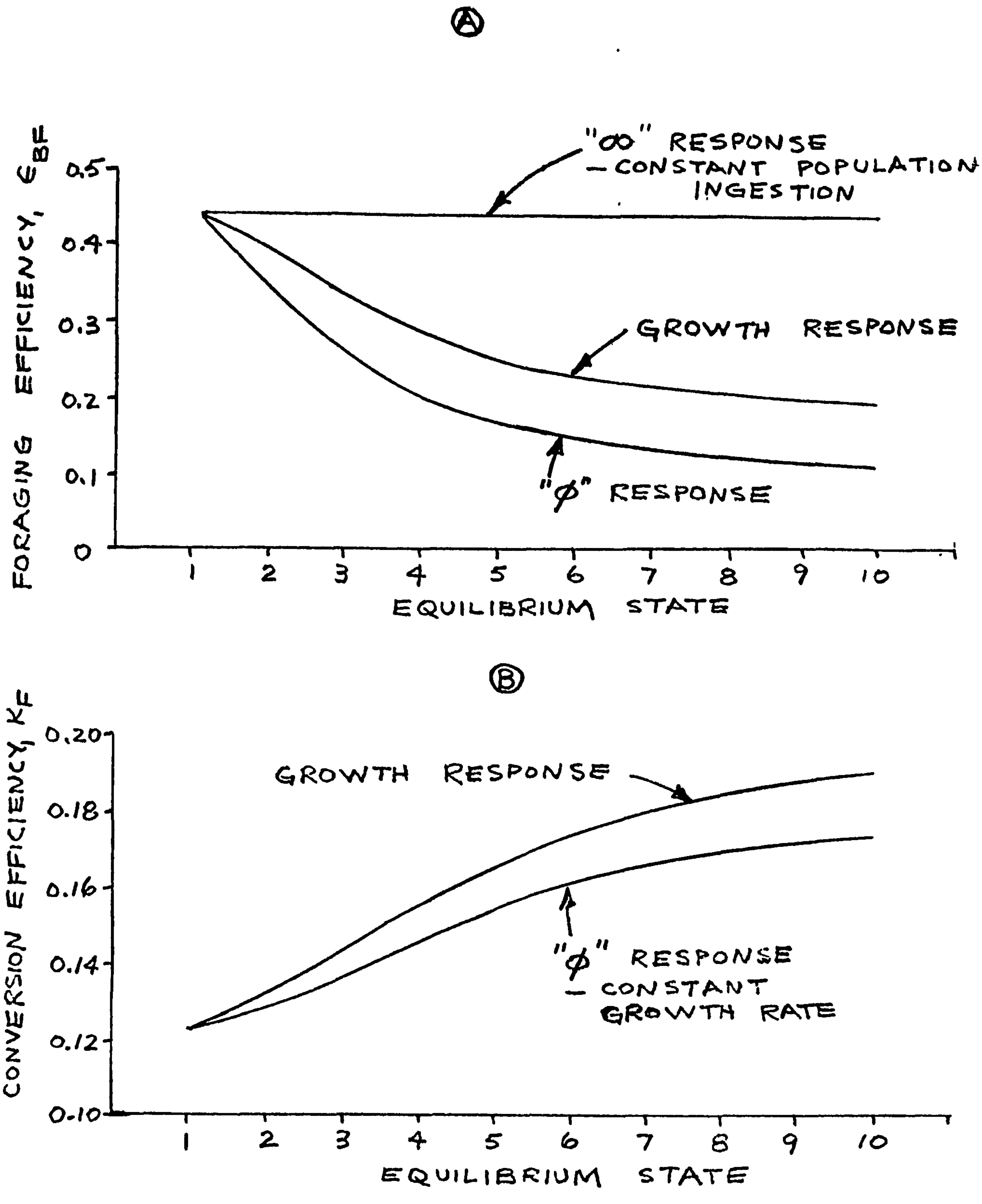


Figure 11. Variation of food chain model parameters for the postulated sequence of states resulting from fishing.

A. Variation in foraging efficiency.

B. Variation in conversion efficiency.

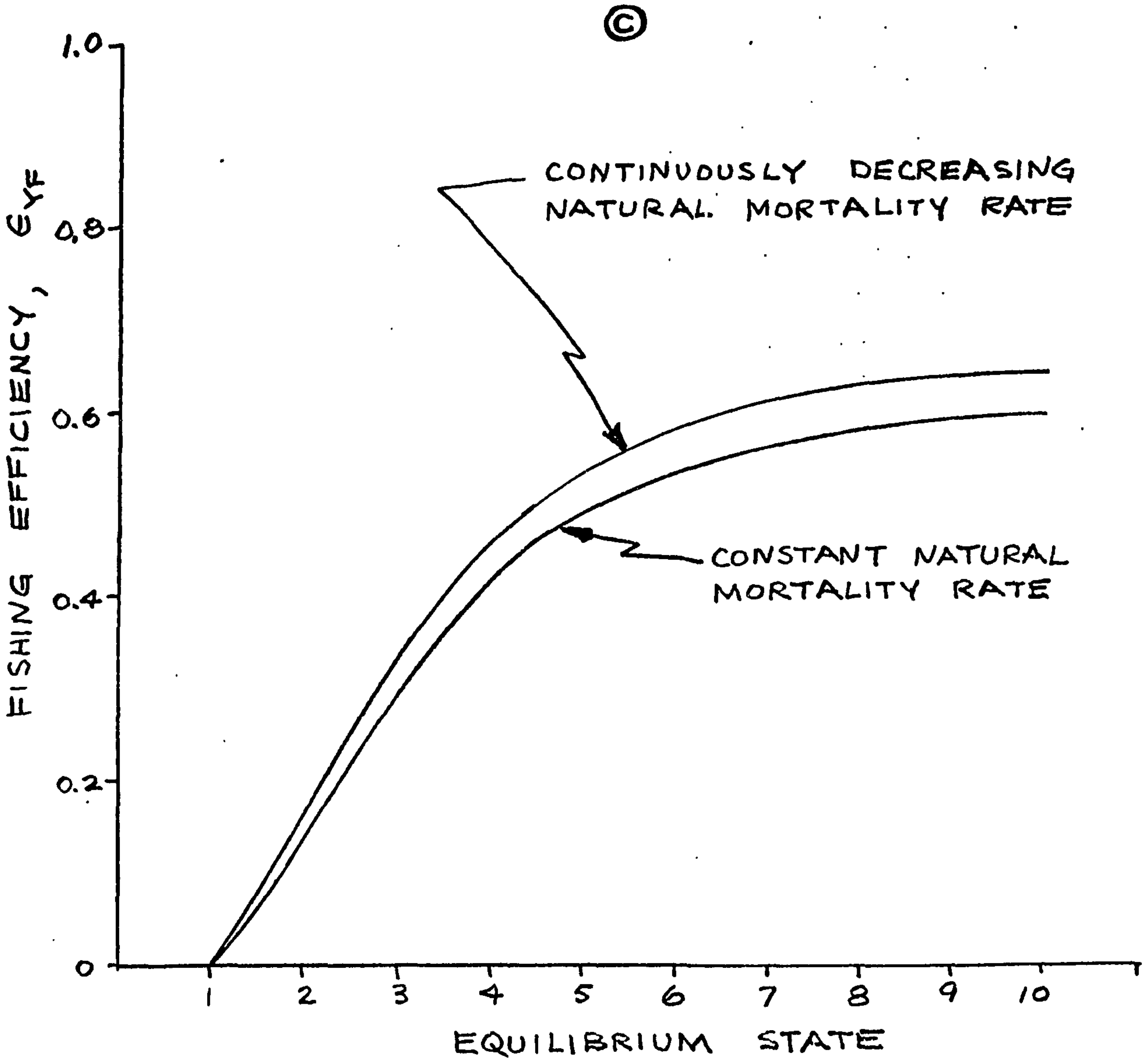


Figure 11. Variation of food chain model parameters for the postulated sequence of states resulting from fishing.

C. Variation in fishing efficiency.

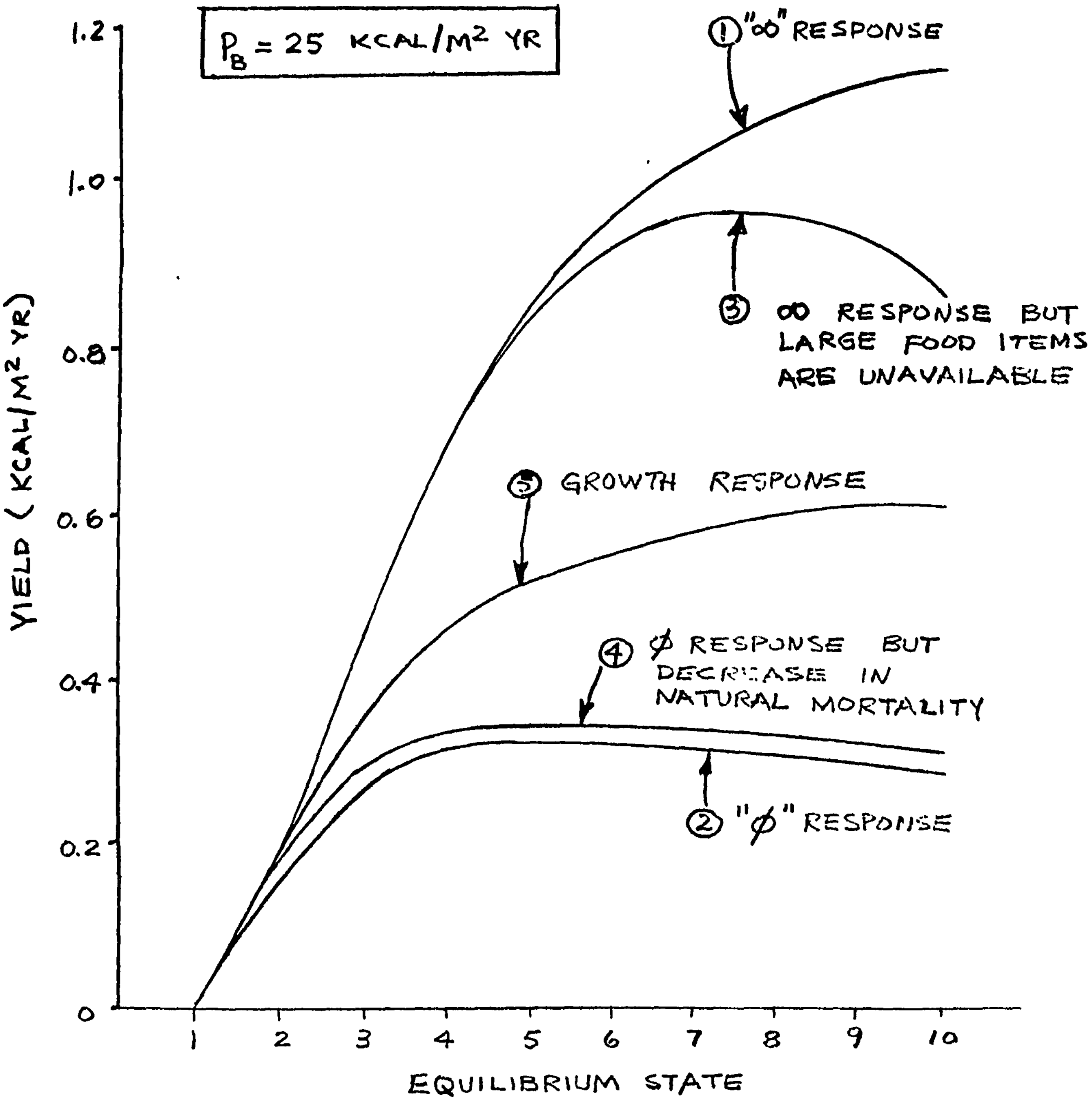


Figure 12. Equilibrium yields for the postulated sequence of states resulting from fishing. The various types of population response are discussed in the text.

SECTION B

Summer Storage of Energy and Its Use for Winter Metabolism and Gonad Maturation in American Plaice

by

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INTRODUCTION

During the summer American plaice (*Hippoglossoides platessoides*) not only feed intensively and increase in weight and length but they also accumulate sotres of energy which are drawn upon in winter and early spring for metabolism and gonad maturation. As a consequence, the energy content of an individual fish increases yearly with development and growth but also has a cyclic variation with season. This energy storage cycle is associated with the annual cycle of events comprising migration, overwintering, spawning and feeding which are characteristic of temperate marine fishes (Nikolsky, 1963). Changes in condition are related to these events (LeCren, 1951; Bagenal, 1957), as are changes in chemical composition (Love, 1970).

Although temperatures of water inhabited by American plaice differ by only a few degrees between winter and summer months, these fish virtually cease feeding during the winter (Powles, 1965; Bakken, 1972). Similar observations have been reported for other flatfishes (Wimpenny, 1953; Rae, 1965) and for temperate water fish in general (Nikolsky, 1963). It is often assumed, tacitly or explicitly, that this phenomenon is a response to low temperature. However, this cannot be the case in St. Margaret's Bay, N. S., for example, where maximum annual bottom water temperatures occur during November and December while mid-summer temperatures are close to the annual mean.

The periods of summer feeding and winter fasting in American plaice are directly associated with the annual cycle of energy storage. This paper documents the cycle observed in plaice of St. Margaret's Bay and considers the adaptive significance of this strategy as compared to an alternative involving year-round feeding.

MATERIALS AND METHODS

American plaice were taken by otter trawl in St. Margaret's Bay, N. S., on nine occasions between March 1970 and February 1971. Fish were selected from the catch and sorted into samples defined by size, sex and state of maturity.

Sampling Scheme

Female plaice in St. Margaret's Bay grow to approximately 55 cm in 25 years while males seldom exceed 40 cm and 16 years of age. In order to give reasonable representation of this population three sample categories were established: (1) mature females, 30-40 cm; (2)

of the year. These times were chosen so that relatively more effort was devoted to sampling during late spring and early summer when gonad maturation and spawning, accompanied by major changes in energy storage, take place.

Sample Processing

Fish for each sample category were selected from the trawl catch, packed on ice and transported to the lab; processing was begun immediately and was usually completed the next day.

Overall length from snout to tip of mid caudal ray was measured to 0.1 cm. Gross body weights were determined to within 0.1 gm. Gonads and viscera were removed and gutted weight recorded. Gonad weights were measured to 0.01 gm. Viscera samples were prepared by removing stomach and intestinal contents and blotting on paper. Body samples were taken by cutting a section across the fish behind the visceral cavity.

Samples of body and gonads of fish in all sample categories were taken routinely. Viscera samples were taken on only two occasions during the year, spring and autumn. Samples of heads from males and females were obtained once.

Drying Methods

All sample materials were oven dried at 60°C for 4 to 5 days. Preliminary tests were carried out to determine adequate drying times to contstant weight. As a check on the dry/wet weight ratios determined by drying at this temperature, equivalent samples were freeze dried and the results compared with those for oven drying. Ovaries of mature females were divided and one half was freeze dried for 5 days while the other half was oven dried at 60°C for the same length of time. The dry/wet weight ratio for freeze drying was 0.272 ± 0.006 versus 0.267 ± 0.006 for oven drying.

Whole gonad and viscera samples were dried whereas body sections constituting about 15% of gutted weight were assumed to be representative of body materials. On one occasion 14 body sections and 13 whole bodies less head were dried. The dry/wet weight ratio for body sections was 0.185 ± 0.006 versus 0.186 ± 0.006 for whole bodies.

After drying the materials were weighed and then ground into a fine powder with a Krups coffee grinder. The samples were placed in separate vials and stored in a desiccator.

Calorimetry

A Phillipson micro-bomb calorimeter was used for determination of energy content of all materials

(Phillipson, 1964). Although the accuracy of this calorimeter is less than those which take larger samples, the time required to analysis of one sample is relatively short. In this investigation it was considered to be more important to analyze samples from several different fish rather than to determine calorific values for a few fish with greater accuracy. Also, use of the micro-bomb calorimeter permitted analysis of all materials with the same apparatus.

The calorific value of freeze dried materials was compared with oven dried materials and no significant difference was found. On the occasion that two methods of drying mature ovaries were compared, samples of the materials were analyzed for energy content. The freeze dried materials contained 5387 ± 306 cal/gm while the oven dried materials had 5288 ± 136 cal/gm.

Energy content of body sections was not found to differ significantly from whole body material. At the time the dry/wet weight ratios of these materials were compared samples were analyzed for calorific value; energy content of body sections was 4734 ± 297 cal/gm versus 4500 ± 90 cal/gm for whole bodies.

RESULTS

Seasonal Changes in Condition

The exponent of the weight-length regression for American plaice from St. Margaret's Bay varied among sample categories and between sampling times but the variation was not consistent and the exponent never differed significantly from 3.0. During the 1970-71 sampling series, exponents for the different sample categories ranged from 2.6 to 3.3; the restricted range of weights in each sample probably had as much influence on exponent variation as did seasonal effects. In 1967 Bakken (1972) measured weights and lengths of 612 plaice from the Bay, covering both sexes and a complete size range, and found an exponent of 3.099, which was not significantly different ($P < 0.05$) from 3.0.

Because of this erratic but not significant variation in exponent of the weight-length regressions it is not satisfactory to represent seasonal changes in condition or weight relative to length by the intercept values of these regressions. Instead gutted weights at median length were computed from the weight-length regressions for each sample category and the results for samples taken between March 1970 and February 1971 are given in Table 1.

For all three sample categories the general trend of weight at median length versus time indicates a minimum weight and condition in April and a maximum in September. The variation in weight at median length is largest and most regular in mature females. Weights of fish captured in November were somewhat lower than the general trend would suggest; percent dry weight and energy per unit dry weight of these materials were also lower than suggested by overall trends. In general the times of minimum and maximum condition coincide with corresponding extreme values of percent dry weight and energy per unit dry weight of body materials.

Annual Gonad Weight Cycle

The ovary weight of a 35 cm mature female varied from 1.6% of body weight after spawning to about 10% of body weight prior to spawning whereas the ovaries of immature fish of similar length weighed close to 0.8% of body weight throughout the year. The trend in mature ovary weights is very consistent and suggests a gradual development throughout the year, with very significant changes during the overwintering months (Table 1). The data provide some evidence for a seasonal cycle in immature ovary weight but the variations appear to be more closely correlated with changes in overall body condition than with the reproduction cycle.

Testes weight of 25 cm males varied from 1% to 2% of body weight during the year, with a maximum in late March prior to spawning and a minimum from June to September. The gradual decrease in testes weight during the spawning months (Table 1) is partly due to the fact that immature and spent testes were not distinguished from mature testes so that the computed testes weight for the sample category would decrease as spent fish became relatively more frequent in the sample. It should also be noted that the testes weight of mature males of this length would be slightly larger than the sample average; most samples of males of this size range from St. Margaret's Bay would contain at least 80% mature fish.

Spawning in 1970 occurred from April to June, with a probable peak late in May. Ovary weights of mature females reached a maximum in May and testes weights decreased progressively during this three month period. Examination of the complete trawl catch at the end of June showed that the percentage of sample category size fish with ripening (stage IIIA) ovaries (Powles, 1965; Pitt, 1966) was less than half that of previous months. Furthermore the relative number of females with very ripe (stage IIIC) ovaries was considerably larger than in previous months. The catch in July contained almost no females with stage IIIA or IIIC ovaries.

Ovary weights of mature American plaice at spawning are relatively larger in big fish. In May 1970 the ovaries of 50 fish were examined and ovary weight w_{ov} (grams) was found to be related to gutted weight w (grams) by the regression

$$w_{ov} = 0.252\, w^{1.261}$$

The exponent is significantly different ($p < 0.05$) from 1.0. The ovary weight of a fish weighing 150 grams constitutes 9.3% of the gutted weight whereas the ovary of a 500 gram fish amounts to 12.7% of the weight.

Dry Weight of Materials

Percent dry weight of body materials for all three sample categories attained a minimum value in April and a maximum in September. Values for each sample category at various times of year are given in Table 2. Both mature and immature female body materials varied from 18 to 22% dry weight. Values for male body materials ranged from 20 to 23% dry weight.

The percentage dry weight of mature female ovary materials is closely related to stage of development in the annual reproductive cycle. Spent ovaries in July contained 15% dry weight of material and the percent dry material increased gradually as the ovaries recovered and began to ripen. By February the percent dry weight was 27% and the ovaries could clearly be classified as ripening (stage IIIA). The value of 27% dry weight is maintained while further ripening takes place in the remaining few months before spawning.

During the final stages of ovary maturation prior to spawning the percent dry material decreases and the ovary wet weight increases considerably. In the sample of June 1970 comparable numbers of fish with ripening (stage IIIA) and very ripe (stage IIIC) ovaries were obtained. The ovary wet weights at median length given in Table 1 were 28.0 and 35.9 grams respectively. The corresponding values for percent dry material were 25.6 and 17.6% (Table 2).

The percent dry weight of immature ovary material during the year was within the range 15 ± 1% while the percent dry weight of testes material was 12 ± 2%.

On two occasions head samples amounting to about 25% of gutted weight were obtained and the percent dry weight for 35 cm females was 17.4 ± 0.4% while the corresponding value for 25 cm males was 19.6 ± 0.5%.

Dry weights of viscera materials which constituted about 4% of gutted weight were determined on occasions during summer and winter for both males and females. Percentage dry weight of female viscera in May was 18.5 ± 0.5% and in November was 19.5 ± 0.9%. Values for males in July were 23.3 ± 1.2% and in February were 19.2 ± 0.5%.

Energy Content of Materials

The seasonal patterns of energy per unit dry weight of all materials were similar to the patterns for percent dry weight of these materials but energy content values in most cases did not vary beyond ±5% of the annual average value for each type of material. Energy per unit dry weight values for body and gonad materials are given in Table 3.

The calorific value of head materials was 4088 ± 224 cal/gm dry weight for females and 4430 ± 332 cal/gm dry weight for males.

Viscera material from females contained 5055 ± 264 cal/gm in May and 5105 ± 152 cal/gm in November while material from males contained 5313 ± 392 cal/gm in July and 5105 ± 159 cal/gm in February.

Seasonal Energy Storage Patterns

In following the seasonal pattern of energy storage it is convenient to subdivide the total energy content of a fish into components such as those defined by the following expression

$$E = E_h + E_b + E_v + E_g$$

where E_h = energy stored in the head, E_b = energy stored in the body less gonads, E_v = energy in viscera, and E_g = energy in the gonad. Evaluation of seasonal changes in these components of energy storage allows one to assess the main sources of energy storage variation and to detect possible transfers of energy among the parts of the fish. Since significant amounts of energy are diverted to reproduction, especially in mature females, it is convenient to consider gonads as a separate component. Changes in energy content are associated with the deposition and subsequent use of fat around the intestine and with annual variations in liver weight; it is therefore useful to consider viscera as a separate component of energy storage. The energy per unit weight of head is expected to remain relatively constant during the year but considerable changes in energy of body muscle may occur during the periods of gonad maturation and overwintering; a somewhat arbitrary division of the gutted body into head and body components is therefore valuable.

Total energy content of fish of median length in the three sample categories was computed from the data on energy in each component of the fish. Results for an annual cycle in mature females are shown in Figure 1.

Head samples from 15 females were found to constitute 27% of gutted weight including gonads while heads from 20 males amounted to 24% of gutted weight. Since 25 cm females weigh about 300 grams while 25 cm males weigh 100 grams it is reasonable to assume head component weights of 75 and 25 grams and energy contents of 53.4 and 21.8 kcal respectively. Energy per unit dry weight and percent dry weight values for head materials were given previously.

Energy content of viscera throughout the year was computed from data on viscera energy for samples taken on occasions in summer and winter together with assumptions concerning the seasonal pattern of variation. The mean ratio of viscera weight to gutted weight for a total of 40 females on the two sampling occasions was 0.042. Assuming an average body weight of 290 grams for a 35 cm fish the viscera weight is 12.3 grams. The mean energy content of the viscera examined was 975 cal/gm wet weight and so the mean viscera energy of a 35 cm female can be taken as 12.0 kcal. Variation in viscera energy from this mean value is due largely to seasonal changes in liver weight. Observations on liver weight variation of plaice (J. Smith, personal communication) indicate that during the year the range in liver weight amounts to about 1% of gutted weight. For a 35 cm female fish this would mean a liver weight change of 3 grams during the year. As a conservative estimate it will be assumed that energy per unit liver weight is the same as that for viscera in general; this indicates a change of 3.0 kcal in the viscera energy of a 35 cm female during the year. The observed pattern of liver weight variation coincides in general with the pattern of body condition; it is assumed that the viscera energy reaches a maximum on 1 November, a minimum on 1 May and that the variation in between is linear. Similar considerations apply to the calculation of viscera energy for males; observations on 35 fish gave a mean ratio of viscera to gutted body weight of 3.6% and an energy content of 1110 cal/gm.

The energy storage in body components was computed by subtracting the estimated head weight from the gutted body weights (Table 1) and multiplying the remainder by corresponding values of percent dry weight and energy per unit dry weight (Tables 2 and 3).

Energy of gonad components was computed from gonad weights (Table 1) by the procedure described above for body components.

In general, the seasonal pattern of total body energy storage is similar to the pattern of condition defined by body weight at median sample length, but the magnitude of variation is relatively greater in the energy storage pattern. A standard 35 cm mature female, for example, experiences an annual body weight variation of 35 grams relative to an average weight of 290 grams while the energy storage variation is 100 kcal and the average total energy is 275 kcal. Immature females and males exhibit similar patterns but the ranges of variation are not quite as large because much less energy is diverted to reproduction.

DISCUSSION

Energy Content of American Plaice Materials

The energy per unit dry weight values for all American plaice materials were within the range 5000 cal/gm ± 8%; these values are therefore consistent with the range 5000 cal/gm ± 20% given by Winberg (1956) for all fish species. American plaice contain relatively little fat and it is, therefore, not surprising that the mean calorific value is close to that of protein and that the seasonal variation is relatively small. The energy values for plaice are low relative to recently published values for fish with significant fat cycles. Lasker (1970) gives 1400 cal/gm wet weight as the calorific value for body material of the sardine (*Sardinops caerulea*). Assuming a percent dry weight of 25%, this would give a value of 5600 cal/gm dry weight. Sandercock (1969) found average values of 5740 cal/gm dry weight for body material of kokanee (*Oncorhynchus nerka*) and 5600 cal/gm for trout (*Salmo gairdneri*).

The annual variation in energy per unit wet weight of plaice is comparable with that reported for other species. Observed mean and extreme values for energy content of plaice materials are summarized in Table 4. The largest changes in energy content occur in mature females; the range of variation was 39% of the mean energy per unit weight for body material, while the variation was 58% of the mean value for ovary material. Body materials of immature females and males displayed similar seasonal variations in energy content while variation was least for immature ovaries but almost as large in testes as in mature ovaries. Mann (1972) reported changes in energy from 850 cal/gm to 1150 cal/gm during the year for roach (*Rutilus rutilus*) and 870-1450 cal/gm for bleak (*Alburnus alburnus*). Sandercock (1969) found annual variations of 870-1360 cal/gm in mature trout (*Salmo gandneri*) and 725-1490 cal/gm in mature kokanee (*Oncorhynchus nerka*) while seasonal changes in energy content of immature fish were somewhat less.

Energy Storage and Conversion Processes

Energetics principles provide a basis for relating the seasonal patterns of energy storage to the processes of energy transfer and conversion in fishes. This analysis depends upon evidence concerning periods of feeding and growth, timing of events in the reproductive cycle, rates of metabolism and certain energetics efficiencies together with the conservation of energy equation

$$\frac{dE}{dt} = A - R$$

where dE = change in energy content of an individual fish during a time interval dt, A = net energy intake as assimilated food less energy loss as excretion during the interval, and R = net energy expenditure for metabolism (respiration).

American plaice in the Northwest Atlantic feed very little during the winter months of December to April and increases in length occur mainly from May to November; for approximate calculations it is reasonable to postulate that feeding and growth in length occurs only during the period from May 1 to November 30. Powles (1965) examined stomachs of plaice from the Gulf of St. Lawrence during January and February and found that 93% were empty; in the stomachs with food present the mean volume of food was less than that observed during the summer and the fall. Observations on stomachs of plaice from St. Margaret's Bay indicated that they were generally empty during the winter months. Pitt (1967) studied the seasonal pattern of length changes of plaice in St. Mary's Bay and concluded that during 1957 most growth in length occurred from April to August but that in 1958 growth continued until November.

Mature ovaries increase continuously in weight and energy from the time of recovery from spawning in the summer months until spawning in the following spring; in the absence of winter feeding there must be transfer of energy from the body to the ovary. Biochemical considerations suggest that an energetic efficiency of perhaps 90% for this transfer process would be reasonable (Blaxter, 1967).

American plaice are not very active fish and during winter months especially, when little feeding occurs, the level of metabolism may be close to standard metabolism values measured in the laboratory whereas during the summer routine metabolism would be somewhat higher than standard metabolism. Values for standard metabolism of plaice at temperatures representative of St. Margaret's

Bay are reported in MacKinnon (1972).

Analysis of the seasonal energy storage patterns (Fig. 1) shows that the net decrease in energy during the winter months is approximately sufficient to meet energy requirements for gonad maturation and metabolic maintenance. For 35 cm mature females the decrease in total energy, excluding ovaries, between December 1 and April 30 is 92 kcal. The increase in ovary energy during this period was 18 kcal and, assuming an efficiency of 90%, the decrease in body energy required to meet this requirement was 18/0.90 = 20 kcal. Energy available for maintenance requirements is therefore 92-20 = 72 kcal or 72/5 = 14.4 kcal/month. Calculations based on plaice respiration measurements indicated that about 14.3 kcal/month were consumed in standard metabolism processes.

Of the energy assimilated and stored by a mature American plaice female of 35 cm a proportion is used for growth associated with an increase in body length, but there is also storage of energy in a form which can be withdrawn and used for gonad maturation and winter metabolism. A female plaice of this size in St. Margaret's Bay increases in length by 2 cm and in weight by about 18% during one year (Bakken, 1971); the corresponding amount of energy storage, assuming an average weight of 290 grams, during the annual cycle and an average energy content of 980 cal/gm, is

290 × 0.980 = 51.2 kcal. During the feeding season a total of 20.7 kcal is produced and stored directly in the ovary; prior to spawning 12.3 kcal is added to the ripening ovary and during recovery 8.4 kcal is added before December. The net increase in energy of the body excluding gonads, which is not associated with growth in length, is 91.5 kcal; as noted above 20 kcal of this amount is used during winter for ovary maturation and hence a total of 40.7 kcal per year is devoted to egg production. The total production of materials by a 35 cm female during the feeding period can then be computed as follows:

Energy storage associated with growth in length = 51.2 kcal

Energy stored in the ovary
- before spawning (1 May-30 May) 12.3 kcal
- after spawning (1 June-30 June) 8.4 kcal

total = 20.7 kcal

Energy storage for winter metabolism and gonad maturation = 91.5 kcal

TOTAL =163.4 kcal

Averaging over the 7 month feeding period this gives a production of 23.3 kcal/month.

The average monthly production values given above are consistent with information reported in the literature on food conversion of flatfish (Pandian, 1970; Edwards *et al*, 1969). These studies indicate that it is reasonable to assume an overall growth efficiency of 30% for a 290 gram plaice; this would give a monthly ingestion rate of 23.3/0.30 = 77.5 kcal. Winberg (1956) has shown that assimilation efficiencies of 80% are appropriate for fish and Kerr (1971) has reviewed evidence that indicates approximately 30% of ingested energy is lost as heat during food processing. The average amount of energy per month for metabolism can then be estimated as follows:

		kcal/month
Energy ingested as food, C =		77.5
Less losses due to egestion and excretion, F + U =		15.5
Energy assimilated, A =		62.0
Less energy losses during food processing (specific dynamic action), 0.30 C =		23.2
Energy remaining for growth, standard metabolism, and activity =		38.8
Growth and summer gonad production	10.2	23.3
Energy storage for winter metabolism and gonad maturation	13.1	
Energy for summer standard metabolism and activity - by difference =		15.5

Estimated energy expenditure for standard metabolism of a fish this size at temperatures characteristic of St. Margaret's Bay in summer is 14.3 kcal/month according to laboratory respirometer measurements (Mackinnon, 1972). In these experiments, no significant difference between standard respiration rates of plaice during summer and winter months was detected.

The reasonable agreement between estimates for metabolic expenditures computed from observed changes in energy storage and the laboratory measurements of standard metabolism is support for the essential features of the analysis outlined above. During winter months, energy expenditures for activity are probably minimal since little foraging occurs; accordingly, the maintenance metabolism computed from energy storage changes is approximately equal to standard metabolism computed from respiration measurements. For the summer months, the energy for standard metabolism and activity estimated above from energy changes, 15.5 kcal/month, exceeds the estimate of 14.3 kcal/month for standard metabolism according to respirometer measurements. The difference of 1.2 kcal/month for activity seems reasonable in view of the foraging behavior of plaice but this value must be considered only a rough estimate because of the number of assumptions involved in its calculation.

Energy Storage and Reproduction

Analysis of the energy changes in mature plaice females suggests that accumulation of energy in the ovary occurs partly during the feeding season and partly during the overwintering period by transfer of energy from other parts of the body. Love (1970) has suggested that the buildup of gonads is often, perhaps always, accomplished at the expense of body proteins. In American plaice it appears that about 50% of gonad energy increase occurs during the winter months when there is essentially no feeding and continuous decrease in body energy; the absence of feeding makes it necessary to postulate transfer of energy from body to gonad. During the summer months it is conceivable that energy would first be stored in the body and then transferred to the gonad but it would seem improbable in view of the relative inefficiency of such a process.

Prior to spawning the ovary appears to swell considerably due to incorporation of water. During June 1970, 15 ripening and 12 very ripe ovaries were examined (Tables 1, 2 and 3). The energy per unit dry weight was approximately the same in each type of ovary. However, the very ripe ovaries had a relatively higher wet weight and a lower percentage dry material by comparison with the ripening ovaries. The computed dry weight of material in the ovaries of a 35 cm fish at this time is 7.2 grams when in a ripening state and 6.3 grams when very ripe. Since the percent dry weight values for the very ripe ovaries ranged from 10 to 23% it is reasonable to suppose that some eggs were released from the ovaries with the lowest percent dry material and to conclude that there is no significant difference between the dry weights of ripening and ripe ovaries although the latter have a higher wet weight.

The above explanation of energy changes associated with spawning in American plaice differs from the interpretation by Sandercock (1969) of spawning energetics of salmon and trout. Sandercock rejected the hypothesis that energy was transferred from body to gonad prior to spawning and postulated that the observed decrease in body energy resulted in part from the demands of migration but was largely due to the metabolic processes associated with significant changes in physiological state which take place near spawning time. It would appear that the complex of energetics processes during the spawning period of American plaice is quite different from that for salmon or trout. Furthermore it seems clear that the suggestion by Lova (1970) concerning build-up of gonads cannot be considered a general proposition.

The amount of energy diverted to egg production in American plaice is relatively greater in larger and older fish, thus supporting the expectation of Williams (1966) that in species which spawn repeatedly the intensity of reproductive effort should increase with age. Ovary weight of plaice at spawning time was found to be proportional to body weight raised to a power of 1.26 and, when the energy content of plaice material is considered, the energy in ripe gonads of 150 and 500 gram fish constitutes 13% and 17% of total body energy respectively. The fact that the ripe gonads of fish may constitute a relatively larger proportion of body weight as age increases has been considered earlier, e. g. Orton (1929), but, in the absence of energetics data it was not possible to show that this involved a relative increase in energy expenditure for reproduction.

Production and storage of materials for spawning and overwintering maintenance of mature American plaice is at least equal to production of materials for overall body growth; in larger fish, production for growth tends to become a minor component of total production while egg production assumes increasing importance. An estimate of this change in production pattern with size can be made by considering the body and gonad growth data for fish of 30 and 40 cm, the extremes of size in the sample category of this study. Production for overwintering can be estimated from the value for a 35 cm fish by assuming a variation with weight raised to the 0.8 power; although this assumption cannot be proved with the present data it seems reasonable in view of the fact that metabolic expenditures vary in this manner. The estimated annual production quantities for 30, 35 and 40 cm mature plaice females are given below:

Fish length (cm)	30	35	40
Gutted weight (grams)	180	290	440
Body growth production (kcal)	40.6	51.2	60.4
Egg production (kcal)	21.0	38.7	65.8
Production for overwintering maintenance (kcal)	48.8	71.5	99.8
TOTAL Production (kcal)	110.4	161.4	226.0

These calculations indicate that production for body growth decreases from 37% of total production in the 30 cm fish to 27% in the 40 cm fish. However egg production increases from 19% of total production in a 30 cm fish to 29% in a 40 cm fish.

An important conclusion regarding fishing strategy that emerges from the above production calculations is that a significantly greater yield would be obtained from the same number of fish by fishing intensively at the end of the summer period rather than distributing effort throughout the year. This conclusion follows from a distinction between "summer production" which occurs during the feeding period and "net annual production" which amounts to the difference between summer production and the energy expenditures required for overwintering maintenance. At the end of the feeding period, the summer production (excluding gonads) of a 35 cm female, 142.7 kcal, could be harvested by removal at that time whereas only the net annual production, 142.7 - 91.5 = 51.2 kcal, could be obtained by taking the same fish at the end of the overwintering period.

The increased energy requirement for gonad maturation in large, old plaice may give rise to the jellied condition of flesh, involving high water content,as proposed by Templeman and Andrews (1956) and ultimately may be a contributing factor to death as Gerking (1959) suggested. Estimated annual egg production in a large plaice weighing 2000 grams is 500 kcal. If one assumes that about 50% of this energy is transferred from body to gonad during a 5 month overwintering period with an efficiency of 90% the resultant transfer is 55.5 kcal/month. This is a large amount relative to an estimated standard metabolic requirement of 66 kcal/month and, if the total energy storage prior to overwintering was not quite adequate or if unfavourable feeding conditions were encountered following spawning, the fish might encounter very severe depletion in body energy and a consequent increase in moisture content leading to a jellied conditon. Sandercock (1969) found very high water content and corresponding low energy content in ripe kokanee females which died following spawning. Love (1970) observed that larger cod had relatively higher water content and were physically weak when landed. It is therefore possible that larger plaice which undergo greater than average depletion at spawning may have an increased probability of death.

The Strategy of Summer Feeding

Evidence presented in this paper establishes the existence of an energy storage cycle associated with the annual feeding-overwintering-spawning events in American plaice but no direct information is provided concerning the factors which control this cycle. It appears, however, that there is no simple dependence upon environmental variables such as temperature and light. The standard metabolism of plaice is independent of temperature within the range normally experienced by the species in St. Margaret's Bay (MacKinnon, 1972). Feeding rates of plaice, as well as migratory movements, are not consistently related to temperature; Powles (1965) observed that fish in the Gulf of St. Lawrence move inshore to feed in the spring when temperatures are very cold (-1.8 - 0 C) while overwintering occurs at temperatures of 2 - 3 C which are high relative to the annual average. Spawning time of plaice has been found to be uncorrelated with water temperature (Pitt, 1967). Light intensity in the environment inhabited by plaice has a relatively larger and more regular annual variation than temperature. In view of the postulated widespread occurrence of circannual clocks in organisms (Pengelley and Asmundson, 1971), it is possible that such a cycle is present in plaice, with light intensity providing the main environmental cue.

The strategy of summer feeding plus an energy storage cycle probably has some advantage to American plaice as a species since it is generally accepted (Nikolsky, 1963) that the seasonal cycle of events in the mode of life of fishes has adaptive significance. An assessment of the relative advantages of various feeding strategies can be made by computing the annual energy intake needed for a specified amount of annual growth; better strategies should be more conservative of energy.

When food has a constant availability throughout the year, calculations with a simple metabolism/growth model show that there appears to be no energy conservation advantage in adopting a cyclic strategy with feeding in summer only. In an earlier section, it was shown that estimated energy intake of a 35 cm plaice for a seven month feeding period is 77.5 kcal/month, giving an annual intake of 542.5 kcal. A comparable estimate can be made for year-round feeding by assuming that standard and average activity metabolism requirements per month are unchanged, food processing efficiency is constant, and the energy stored for growth in length and gonads is the same. With these assumptions, the energy intake for year-round feeding is 45.2 kcal/month. Gross growth efficiency with the cyclic feeding strategy is 30% in summer and 0% in winter whereas with year-round feeding, the efficiency is 16% during every month. On an annual basis, however, both strategies result in the same energy intake and growth efficiency.

In situations where there is a significant seasonal variation in the availability of prey which constitute the food resource, there is an energy conservation advantage to a fish in employing a cyclic feeding strategy. Food availability may vary seasonally with changes in productivity arising from the annual pulse of primary production which is characteristic of temperate waters. Further amplification may be provided by changes in vulnerability to predation. Ware (1971) found that, even when abundance was relatively constant, a ten-fold variation in vulnerability to predation occurred during the year as a result of changes in behavioral and physical characteristics of the prey. These experiments concerned animals living in an environment with relatively large annual temperature variations which may have had a major influence on prey availability. However, it is reasonable to postulate that seasonal variations in vulnerability are of general occurrence and that suitable mechanisms exist to produce these variations in a constant temperature environment such as that inhabited by plaice. Foraging costs to an individual fish per unit energy intake may be significantly higher during winter months when food availability is relatively low. This additional energy expenditure for winter foraging would make the annual energy intake greater than in the previous case of year-round feeding and constant food availability. It follows that a strategy involving summer feeding only has an energy conservation advantage when food availability varies and has a summer maximum.

An alternative explanation of the cycle is that it evolved in an environment where cyclic operation was imposed and that, in the present relatively constant temperature environment, the mechanism has been retained but the adaptive significance has been lost. This alternative, however, seems less probably than that of a cycle caused by seasonal variation in food availability.

In addition to possible increases in efficiency of energy use, a biological system with a cyclic mode of operation attains greater stability in situations where there are fluctuations in the energy (food) supply (Sollberger, 1965). An organism without an energy storage capacity is constantly dependent upon energy flow from its food resource for its survival; any significant interruption in this flow will result in death. When energy can be stored, the organism attains increased homeostatic capacity, i.e. stability, which allows it to survive periods of interruption in energy flow from its food supply. This homeostatic capacity would be of considerable value to a fish in an environment where the food supply varied seasonally to such an extent that during winter months availability would very probably attain levels equal to or less than the fish's maintenance requirements. Under these circumstances, a storage capacity would be necessary to survive periods of several months when the mean level of food availability is below maintenance as well as shorter periods of very low food abundance which might randomly occur.

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Table 1 . Seasonal Changes in Body and Gonad Weight for Fish Of Median Length In Three Sample Categories.

Month	Mature Females		Immature Females		Mature and Immature Males	
	Body Weight (d)	Ovary Weight (e)	Body Weight (d)	Ovary Weight (f)	Body Weight (d)	Testes Weight (f)
March	281.7 (29)	16.9 (29)	284.8 (30)	2.4 (20)	104.4 (18)	2.0 (18)
April	265.7 (33)	20.9 (33)	271.8 (31)	2.0 (22)	96.8 (30)	1.3 (20)
May	272.2 (50)	29.6 (50)	296.0 (37)	2.5 (20)	104.6 (30)	1.2 (20)
June	273.8 (27)	28.0 (15)	286.5 (35)	2.4 (15)	99.7 (30)	0.9 (15)
		35.9 (b) (12)				
July	299.9 (c) (30)	4.9 (15)			104.0 (30)	1.0 (20)
Sept.	300.1 (29)	5.3 (20)	301.2 (30)	2.8 (15)	106.2 (30)	1.1 (15)
Nov.	285.5 (30)	6.5 (30)	288.5 (30)	3.0 (15)	102.2 (30)	1.4 (15)
Dec.	297.9 (30)	10.7 (30)	308.9 (30)	2.5 (15)	103.1 (30)	1.6 (15)
Feb.	294.2 (30)	15.0 (30)	287.3 (30)	2.1 (15)	101.1 (30)	2.1 (15)

Notes: (a) Median Length for female categories is 35 cm and for males is 25 cm.; number of fish examined is given by figures in brackets.

(b) Ovaries with this mean weight were in an advanced stage of ripeness.

(c) Sample might include some immature females due to difficulty in distinguishing spent from immature ovaries.

(d) Confidence limits (95%) for body weights are approximately ±3% of the value given.

(e) Confidence limits (95%) for mature ovary weights are approximately ± % of the value given.

(f) Confidence limits (95%) for immature ovaries and testes are approximately ± % of the value given.

Table 2. Percent Dry Weight of Body and Gonad Materials From Fish In Three Sample Categories[a].

Month	Mature Females		Immature Females		Males	
	Body	Ovary	Body	ovary	Body	Testes
March	18.5 ± 0.6 (15)	27.0 ± 0.7 (19)	18.2 ± 0.4 (19)	14.0 ± 0.4 (18)	...	11.1 ± 0.5 (17)
April	17.7 ± 0.6 (23)	27.7 ± 0.5 (23)	18.3 ± 0.5 (22)	14.9 ± 0.6 (22)	20.2 ± 0.5 (20)	10.1 ±0.5 (20)
May	18.4 ± 0.3 (17)	27.0 ± 0.4 (17)	19.4 ± 0.5 (20)	13.9 ± 0.6 (10)	20.2 ± 0.6 (20)	12.1 ± 0.5 (20)
June	19.3 ± 0.6 (20)	25.6 ± 0.4 (15)	20.0 ± 0.4 (15)	15.6 ± 0.3 (15)	20.5 ± 0.6 (15)	11.9 ± 0.7 (15)
		17.6 ± 2.8[b] (12)				
July	20.4 ± 0.4 (15)	15.2 ± 0.6 (15)			22.0 ± 0.7 (20)	11.4 ± 0.9 (20)
September	22.6 ± 0.5 (15)	17.0 ± 1.4 (15)	21.8 ± 0.6 (15)	15.0 ± 0.7 (15)	23.4 ± 0.5 (15)	14.0 ± 0.7 (15)
Nov.	21.1 ± 0.5 (15)	19.8 ± 1.4 (15)	20.1 ± 0.7 (15)	14.6 ± 0.6 (15)	21.2 ± 0.5 (15)	14.8 ± 0.7 (15)
Dec.	21.7 ± 0.5 (15)	22.4 ± 1.3 (15)	21.4 ± 0.7 (15)	14.5 ± 0.4 (15)	22.6 ± 0.5 (15)	11.8 ± 0.6 (15)
Feb.	20.7 ± 0.3 (20)	27.0 ± 0.9 (20)	20.4 ± 0.5 (15)	15.0 ± 0.5 (15)	21.2 ± 0.5 (15)	12.0 ± 0.3 (15)

Notes: a Figures are sample means with 95% confidence intervals. Number of replicates is given in brackets.

b These ovaries were in an advanced stage of ripeness.

Table 3 Energy Per Unit Dry Weight of Body and Gonad Materials From Fish In Three Sample Categories.[a]

Month	Mature Females		Immature Females		Males	
	Body	Ovary	Body	Ovary	Body	Testes
March	4734 ±297 (6)	5272 ± 233 (6)	4843 ± 614 (4)	4656 ± 265 (3)	....	5160 ± 306 (4)
April	4662 ± 167 (6)	5190 ± 300 (6)	4816 ± 549 (4)	4448 ± 330 (3)	4617 ± 261 (4)	4707 ± 383 (4)
May	4812 ± 153 (6)	5288 ± 136 (6)	5044 ± 306 (4)	4651 ± 147 (3)	4960 ± 87 (6)	5139 ± 228 (4)
June	4997 ± 161 (6)	5358 ± 125 (6)	4880 ± 234 (6)	4567 ± 271 (3)	4983 ± 403 (4)	5163 ± 274 (4)
		5272 ± 267 (6)				
July	5016 ± 243 (6)	4909 ± 289 (4)	...	...	4915 ± 287 (7)	4970 ± 195 (4)
Sept.	5342 ± 334 (6)	4980 ± 247 (6)	5278 ± 453 (4)	4767 ± 285 (3)	5263 ± 196 (4)	4901 ± 336 (3)
Nov.	4743 ± 316 (6)	4986 ± 228 (6)	4647 ± 285 (4)	4579 ± 597 (3)	4576 ± 138 (4)	4743 ± 420 (3)
Dec.	4914 ± 470 (6)	5043 ± 219 (6)	5129 ± 469 (4)	4892 ± 447 (3)	4902 ± 410 (4)	5020 ± 106 (3)
Feb.	4883 ± 422 (6)	5417 ± 333 (6)	4913 ± 358 (4)	4630 ± 921 (3)	5392 ± 508 (4)	5386 ± 502 (3)
Annual Mean	4900 (54)	5160 (52)	4944 (34)	4649 (24)	4951 (37)	5021 (32)

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[a] Figures are sample means with 95% confidence intervals. Number of replicates is given in brackets.

Table 4. Mean and Extreme Values for Energy Content of American Plaice Materials.

	Mature Females		Immature Females		Males	
	Body	Ovary	Body	Ovary	Body	Testes
Mean Cal/gm dry weight	4900	5160	4944	4649	4951	5021
Mean.percent dry weight	20.0	22.7	19.9	14.6	21.4	12.2
Mean cal/gm wet weight	980	1171	984	679	1060	613
Maximum cal/gm wet weight	1207	1428	1150	715	1232	720
Minimum cal/gm wet weight	825	746	881	647	933	475
Range in cal/gm wet weight	382	682	269	68	299	245
Range in Mean cal/gm wet weight	39%	58%	27%	10%	28%	40%

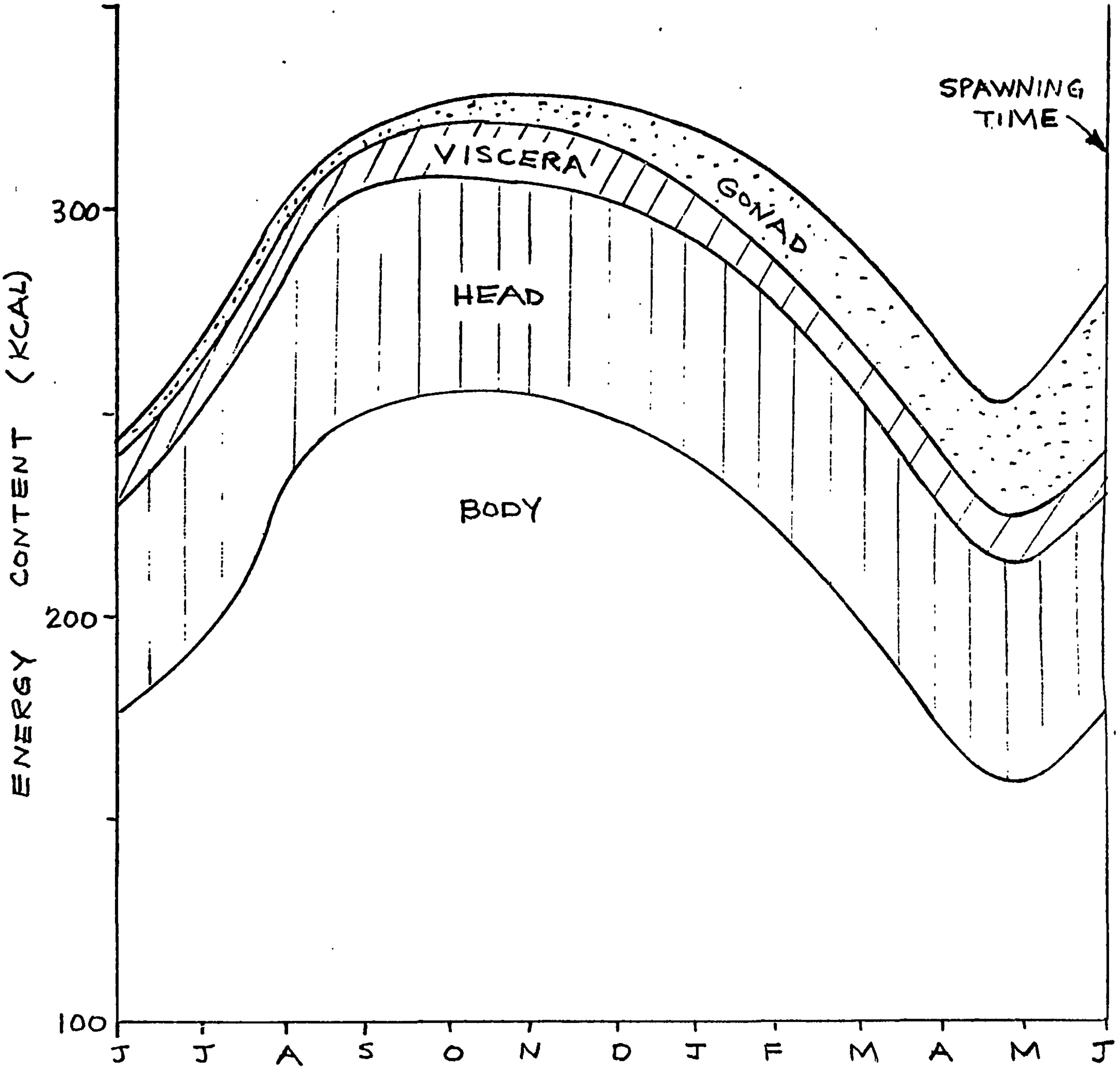

Figure 1. The seasonal energy storage pattern for a mature 35.cm. female American plaice from St. Margaret's Bay, N. S.

SECTION C

Relationship between metabolism and growth rate of American Plaice

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INTRODUCTION

Rates of metabolism and growth of animals are closely inter-related. Beamish and Dickie (1967) have reviewed the consequences of this relationship for fish production processes and Winberg (1968) developed general equations describing the metabolism/growth rate interaction. In applying these principles to a particular species it is important to consider that metabolic and growth processes reflect an animal's response to a complex of ecological and physiological factors which may change during the course of its life-history (Parker and Larkin, 1959).

This paper presents measurements of the low routine oxygen consumption rate (Fry, 1971) of American plaice (*Hippoglossoides platessoides*) and an analysis of the relationship between the rate of metabolism and the growth rate observed in different populations of this species. An attempt is made to consider all stages of development from egg to adult even though metabolic data were obtained for a limited size range and information on the growth and environmental conditions of plaice larvae and small fish is limited.

The measurements of plaice metabolism were obtained as part of an energetics study of a population in St. Margaret's Bay, N. S. It was recognized that respiration rates of fish are significantly affected by a variety of environmental factors (Fry, 1971) and considerable care was taken to ensure that laboratory conditions approximated those currently prevailing in the natural environment from which the fish were taken. However, the choice of experimental conditions was influenced by the requirements of an ecological energetics viewpoint. A detailed study of the respiratory metabolism of American plaice, comparable with those available for other fish (e.g. Brett, 1964), was not attempted.

Adaptation of poikilotherms to low temperatures has been much discussed in the literature (Scholander *et al*, 1953); the evidence suggests that rates of metabolism at low temperatures may be elevated relative to values predicted with temperature correction curves (Winberg, 1956) such as that of Krogh. If this metabolic adaptation is of general occurrence one can conclude that growth rate and productivity of fish in northern regions will not be reduced to the full extent predicted by temperature "correction" relationships. Since American plaice is a common north temperate species it is of some interest to consider whether there is evidence for adaptation of its metabolic rate.

The data on respiration rate of American plaice are a contribution to the small amount of published information on the metabolism of flatfish species. Edwards *et al* (1969) measured the respiratory rate of European plaice (*Pleuronectes platessa*) and common dabs (*Limanda limanda*) weighing 0.05 to 10.0 grams at temperatures of 5 to 20°C. In later work, using similar techniques, Edwards *et al* (1971) reported respiration rates for tropical flatfish (*Cynoglossus*, *Brachirus* and

Synaptura) of approximately 1 to 100 grams at temperatures close to 28°C. Hempel (1964) gave respiration values for European plaice with a mean weight of 142 grams for a temperature of 10°C. Data for winter flounder (*Pseudopleuronectes americanus*) weighing 4 to 50 grams for temperatures of 10 and 20°C were reported by Voyer and Morrison (1972). Hickman (1959) obtained metabolic rates for starry flounder (*Platichthys stellatus*) of 4 to 300 grams at temperatures of 10 and 15°C and also reported some data for sole (*Parophrys vetulus*) and sand dab (*Citharichthys stigmaeus*).

MATERIALS AND METHODS

Specimens of American plaice were caught by otter trawl in St. Margaret's Bay, Nova Scotia, on several occasions during 1970 and 1971. Short tows were made in order to minimize injuries to the fish. After a short period in tanks on deck, where temperatures approached those of surface water in the Bay, the fish were transported to the laboratory and were placed in tanks with water at a temperature approximating the prevailing temperature of bottom water in the Bay. The entire operation took about three hours from the time of capture. During the first two or three days about 50% mortality was observed, but after this period the mortality rate was generally very low.

Metabolic rates were determined from measurements of oxygen consumption rate at a time of day (around noon) when the fish displayed minimal spontaneous activity (Fry, 1967) and were therefore considered to be low routine values, approximating standard metabolism. In laboratory tanks American plaice display a marked diurnal activity pattern involving active swimming throughout the tank during the night and resting on the bottom, covered with sand if available, during the daytime (D. Ware, personal communication). This pattern of behaviour is very similar to that reported by Verheijen and Groot (1967) for *Pleuronectes platessa*. When plaice are confined in respirometer boxes the rate of oxygen consumption varies erratically during the night with rates which are sometimes twice the steady daytime value. On one occasion the oxygen consumption rates of three fish were monitored at regular intervals during the period from 24 to 48 hours after being placed in the respirometer. The metabolic rates during the day at 24 and 48 hours agreed within 4% but the nighttime values for the period between were 20% higher. This observation is in accord with Hempel (1964) who found that respiration rates of *Pleuronectes platessa* averaged 26% higher at night. Hickman (1959) observed similar diurnal variations in metabolic rate of *Platichthys stellatus*.

Fish were acclimated to laboratory conditions for one to two weeks after capture. Small quantities of food were provided during this period but not during winter months because plaice do not feed at this time under natural conditions. Each experimental fish was denied food for at least 24 hours before being put in the respirometer.

Oxygen consumption rates were measured with a continuous flow respirometer. Each fish was placed in a rectangular clear plastic box fitted with a removable top (Fig. 1). Boxes of five different sizes were used so that the ratio of box volume to fish volume would be approximately 30:1. Eight small holes were bored in the front end of each box to allow an even inflow distribution. Water was siphoned out of the back of the box through two larger holes and flow rates were adjusted so that water in the box was completely changed about once every hour.

The respirometer boxes were placed in a large rectangular tank with water temperature maintained within ±0.5°C of the St. Margaret's Bay bottom water temperature for the time of year. The area was enclosed and light of appropriate duration and low intensity was provided. Oxygen concentration of water in the tank was close to saturation and outflow water from the respirometer boxes was greater than 80% saturation.

Experiments were begun and terminated around noon and the oxygen consumption rates for each fish were computed from the average measurements of flow rate and oxygen concentration which were obtained on separate occasions, 2 to 4 hours apart, at times close to 24 hours from the start of the experiment. Two or three fish in separate boxes were tested on each occasion. Flow rate through the respirometer boxes was measured by a graduated cylinder and watch. Dissolved oxygen concentration was found by the Winkler method and the procedure of Carpenter (1965). Empty boxes were used as controls.

RESULTS

Data were obtained for low routine oxygen consumption rate of American plaice captured on four occasions and tested at temperatures corresponding to those of St. Margaret's Bay (Fig. 2). In accordance with the usual assumption that oxygen consumption rate and wet weight are related by a power law relationship a log-log transformation of the data was made prior to statistical calculations (Table 1).

A slope of 0.8 for the standard metabolism versus weight relationship is appropriate for American plaice. When all respiration rate data for the year are pooled the slope, with 95% confidence limits, is 0.794 ± 0.082. The slope determined from data for each test series did not differ significantly ($p < 0.05$) from 0.8.

No evidence was found for a significant seasonal influence on respiration rate independent of temperature. Oxygen consumption rates calculated for a 300 gram fish from the regressions for the August, April and June data at 3°C are given in Table 1. The 300 gram fish was chosen for comparison because this weight is close to the mean weight of all fish tested and the 95% confidence limits for prediction of oxygen consumption rate from the various regressions are close to minimal at a weight of approximately 300 grams. There is no significant difference ($p < 0.05$) between the respiration rates calculated for a 300 gram fish at 3°C in August, April and June.

Temperature did not have a significant influence on oxygen consumption rate, given no demonstrated effect of season. Calculated respiration rates of a 300 gram fish at 1, 3 and 6°C did not differ significantly ($p < 0.05$) from one another (Table 1). Since metabolic processes in poikilotherms must be temperature dependent, it follows that the fish were compensating for temperature changes in the environment.

Sex, state of maturity and stage of gonad ripeness did not have a significant influence on respiration rate. When all data for males and females are pooled, there is no significant difference ($P < 0.05$) between the respiration rate of a 300 gram fish of either sex. Also no difference is found when pooled data for mature and immature females are compared. Ovaries of the mature females tested in June were considerably larger than those of fish examined in February and April, in accord with field observations on gonad development (MacKinnon, 1972). Spawning of St. Margaret's Bay plaice appears to occur from April to June and, judging by ovary size and appearance plus occasional observations of eggs in the laboratory tanks, these fish tested in June must have been very close to spawning. However, no significant differences ($P < 0.05$) in respiration rates were detected between the mature females examined in February, April and June.

DISCUSSION

Metabolic Adaptation of American Plaice

American plaice in St. Margaret's Bay inhabit an environment whose temperature generally varies from 1 to 6°C but there appears to be little evolutionary adaptation (Somero and Hochachka, 1971; Fry, 1967) of metabolic rate to these low temperatures although there is a significant compensation for seasonal fluctuations in temperature.

When observed values for the low routine metabolic level of American plaice are compared with predictions of the general equation by Winberg (1956) for the metabolism of all fishes, there is essentially no relative elevation of metabolic rate, suggesting that evolutionary adaptation has not occurred in this species. The pooled data for respiration rate of St. Margaret's Bay plaice at a temperature of 3°C are represented by the equation

$$R = 0.0582\ W^{0.8}\ \text{mg}\ O_2/\text{hr}$$

According to this equation, the respiration rate of a 300 gram fish is 5.6 mg/hr. The corresponding prediction by Winberg's equation, corrected with Krogh's curve to 3°C, is 5.2 mg/hr.

This apparent lack of significant metabolic adaptation in American plaice at low temperatures is in contrast to observations on some other poikilotherms. Scholander *et al* (1953) found evidence that a variety of arctic species maintained a much higher resting metabolic rate than tropical species at the same temperature and concluded that physiological adaptation of poikilotherms to cold lies in displacement to the left of the metabolism-temperature curve. A particularly good example of cold adaptation is found in the Antarctic fish *Trematomus bernacchii* whose normal habitat temperature is -1.9°C; respiratory rates of both whole organisms and tissues were roughly the same as the rates characteristic of temperate zone species at much higher environmental temperatures (Somero *et al*, 1968). However, Bullock (1955) reviewed the evidence for temperature adaptation of poikilotherms and concluded that there was great variation among species in the extent and manifestation of this adaptation.

The degree of metabolic compensation for seasonal temperature fluctuations appears to be very significant in American plaice, suggesting that there might be a considerable amount of biochemical restructuring (Somero and Hochachka, 1971) on a seasonal basis. No significant differences were found among respiration rates of plaice tested at temperatures ranging from 1 to 6°C at selected times of the year (Table 1). The extent of the metabolic compensation implied by these results is indicated by comparison with the variation in metabolic rate predicted by Winberg's (1956) general equation using seasonal temperature fluctuations in St. Margaret's Bay from Sharaf-el -Din *et al* (1971)(Fig. 3). Although there is esentially no seasonal change in the respiration rate of plaice, the variation predicted by Winberg's equation is from 3.6 mg/hr to 9.0 mg/hr, a factor of 2.5. Miller (see Miller *et al*, 1971) found that the temperature correction curve of Krogh which is used by Winberg overestimates the change in respiration rate at low temperatures for cold-water species. The seasonal variation in respiration rate predicted with the temperature correction factor of Miller is less than that predicted by Winberg's equation but would produce a variation of from 4.6 to 6.8 mg/hr (Fig. 3).

Further evidence concerning the degree of metabolic adaptation in American plaice is provided by a comparison of respiration rates of temperate and tropical flatfish species at their normal environmental temperature and at a reference temperature (Fig. 4). In order to make these comparisons, it is necessary to correct respiration rates to temperatures other than those of the original measurements and, occasionally, to estimate rates for temperatures that a particular species could not normally tolerate. Krogh's curve is commonly used for making these temperature corrections (Winberg, 1956) but Miller (personal communication) concluded from a review of the data on respiration rates of cold-water marine poikilotherms that a correction using $Q_{10} = 2.06$ was more appropriate for species whose normal habitat temperature averages 5 to 10°C.

At a temperature of 10°C, the standard metabolic rate of a 10 gram American plaice, 0.61 mg/hr, is comparable with that of winter flounder (0.55 mg/hr), starry flounder (0.57 mg/hr), and *Cynoglossus* species (0.42 mg/hr) but lower than the value of 1.61 mg/hr reported for European plaice (Table 2). According to the general equation of Winberg (1956), the respiration rate of a 10 gram fish at 10°C is 1.01 mg/hr so that only European plaice has a relatively high metabolic rate and significant adaptation to temperature.

At their normal environmental temperatures, there is a five-fold difference between respiration rates of 10 gram flatfishes of various species (Table 2). A *Cynoglossus* specimen living at 28°C consumes 2.02 mg/hr while an American plaice of the same size consumes 0.37 mg/hr at 3°C. The oxygen consumption rate of a 10 gram European plaice at 10°C is 1.61 mg/hr and Edwards *et al* (1970) concluded that, by comparison with the rate for the *Cynoglossus* species, there is a considerable degree of temperature adaptation in European plaice. By contrast, the respiration rate of a 10 gram winter flounder which normally inhabits water of a similar temperature is 0.55

mg/hr suggesting almost no adaptation.

In view of the preceding comparisons of flatfish respiration rates, one must conclude that temperature adaptation is not a general phenomenon. Furthermore, both methods of assessing the extent of temperature adaptation, viz. comparison of respiration rates of temperate and tropical species at normal temperatures and comparison of rates at a reference temperature, are not very satisfactory. Inherent differences between species as well as differences in response to experimental conditions and problems arising from temperature correction make it very difficult to conclusively demonstrate the presence or absence of temperate adaptation.

Relationship Between Metabolism and Growth

Winberg (1968) discussed the relationship between intensity of metabolism and rate of growth in animals and presented equations describing this relationship. If one combines the definition of net growth efficiency (growth rate/assimilated food) with Winberg's energy equation relating growth rate, food ingestion and metabolism the following equation is obtained:

$$\frac{dw}{dt} = \frac{K}{1 - K} R \qquad (1)$$

where dw/dt = change in weight per unit time, K = net growth efficiency, and R = rate of metabolism. Winberg found that the assimilation efficiency of fish is approximated by a constant value of 0.8 so that there is a simple relationship between ingested and assimilated food and between net and gross growth efficiency. For many animals, including fish, the rate of metabolism is related to body weight by an expression of the form

$$R = aw^{b} \qquad (2)$$

It is convenient to express the total metabolism in terms of standard or routine metabolism as measured in the laboratory and a parameter c which is an estimate of the relationship between laboratory and field metabolism. The standard or routine metabolism can be described by an equation similar to (2) with an appropriate parameter a so that equation 1 can be written as

$$\frac{dw}{dt} = \frac{K}{1 - K} \; c \; a \; w^{b} \qquad (3)$$

If the growth efficiency K and the other parameters are assumed constant during a given period of growth this equation can be integrated to give

$$w(t) = \left(\frac{K}{1 - K} \, c \; a \; (1-b)(t-t_0) + w_0^{\,1-b} \right)^{1/(1-b)} \qquad (4)$$

where w_0 is the weight at time t_0 and $w(t)$ is the weight at any time t.

The parameters K, c, b and a in equation 4 are not constant during all stages of growth in the life history of a fish (Winberg, 1956). Growth experiments indicate that the efficiency K is highest during the earliest stages of development. Values of a obtained for resting fish may not be strictly comparable between large and small fish because of differences in response to experimental conditions. Furthermore, the natural environmental conditions for small and large fish may not be comparable; the pelagic larvae of American plaice in St. Margaret's Bay develop in surface waters with temperatures of 10-18°C whereas older fish live in bottom water with temperatures of 1-6°C. The appropriate value of c is very difficult to define; Winberg (1956) suggested that a value of 2 might be a reasonable approximation. In the present work it was found that $b = 0.75$ to 0.80 is appropriate for larger flatfish whereas Edwards *et al* (1969) found values for b of 0.70 to 0.75.

Parker and Larkin (1959) presented a concept of growth in fishes in which growth rate was assumed to be related to weight by an expression of the form $dw/dt = k\ w^x$, with appropriate values for k and x determined for separate life history stages. This relationship is similar to equation 3 except that in equation 3 the various parameters are operationally defined in terms of energetics concepts.

Calculations of the growth of female American plaice were made with equation 4, using appropriate values for K, c, a and b (Table 3) and the following "idealized" stages in life history development of the plaice:

(1) egg/larva (0-3 months);
(2) very small (0+) fish (4-12 months);
(3) small immature fish (1-5 years);
(4) maturing fish (6-15 years);
(5) large mature fish (16-25 years).

The computed weights at age of American plaice were compared with the values observed by Bakken (1972) (Table 4). Computed weights tend to be lower than the observed weights throughout most of each stage but towards the end of the stage the computed weights are higher; this is the inevitable result of the assumption that growth efficiency K is constant throughout the stage and the difference could be reduced by postulating a continuously decreasing value for K.

The agreement between observed and computed weights at age in Table 4 indicates that equation 4 can adequately represent data on the growth of fish. Parker and Larkin (1959) have pointed out the importance of visualizing growth rates in relationship to life history stages and that a method of depicting growth should have parameters reflecting both ecological and physiological factors and be consistent with the observation that change in size is a function of size achieved. Parameters a and b in equation 4 are essentially physiological variables defining standard metabolism although a is also dependent upon environmental temperature. The parameter c reflects a complex of ecological factors affecting rate of food ingestion and the resultant level of metabolism relative to standard. Growth efficiency K describes the relative amount of energy diverted to body growth and is known to generally decrease with fish size. It is to be admitted that there is some latitude in fitting equation 4 to the data for American plaice since the values for c and K are somewhat arbitrary. However, equation 4 is derived from well established principles, values for a and b were established in this investigation, the value for c is close to that found suitable for other fish, and values chosen for K are comparable with those reported for growth experiments with flatfish (Pandian, 1970).

Comparisons of growth characteristics of different populations of a species can conveniently be made with the method outlined above if growth efficiency is related to relative size. Size appears to be an approximate index of life-history development but the maximum size attained by a species varies considerably among populations. For comparisons between populations it is therefore convenient to define relative size as the ratio of size to maximum size attained in the particular population. As an index of relative stage of development in a population relative size can be expected to be related to the growth efficiency, a parameter which is known to vary throughout the course of life-history development.

A computer program incorporating the relationships described above was written to calculate net growth efficiency versus relative size from metabolism and growth data for various plaice populations. The parameters used in this program include constants for weight/length, length/age, and standard metabolism/weight regressions as well as estimates of maximum age in the population and the ratio of field metabolism to standard metabolism.

This program was used to study the effects of parameter variation on the computed growth efficiency at different relative sizes. For details see Figure 5. Variations in the ratio of field to standard metabolism (c) and the intercept value (a) for the standard metabolism/weight relationship, as by changing the temperature, had the most significant influence on magnitude of the net growth efficiency. Small changes in constants of the weight/length relationship or in the maximum size attained had little effect. A decrease in the slope (b) of the metabolism/weight relationship results in somewhat lower growth efficiencies at small relative sizes.

Calculations of net growth efficiency versus relative size were also made for other American plaice populations (Fig. 6). Populations with features which contrasted with those of the St. Margaret's Bay population were chosen. The following stocks were considered:

1. Gulf of St. Lawrence and the Grand Banks off Newfoundland where temperatures are similar to St. Margaret's Bay but fish grow slightly faster and reach larger final sizes (Powles, 1965; Pitt, 1967);
2. Cape Cod where temperatures are higher and growth is much more rapid than in St. Margaret's Bay although final sizes are comparable (Lux, 1970);
3. The Firth of Clyde where temperatures are higher and growth is faster but the final size attained is about half that of St. Margaret's Bay plaice (Bagenal, 1955).

Metabolism data reported in the present paper were used in calculations for all populations; a value of $c = 2$

in equation 4 was assumed in all cases. It was necessary to make approximate estimates of the representative environmental temperature and the size at maximum age and to correct in some cases for the inadequacy of the length/age equations at smaller fish sizes. The final results must therefore be considered only as reasonable estimates.

Values for the net growth efficiency and the pattern of decrease with relative size are similar in the various plaice stocks in spite of differences in environmental temperature and population structure. Plaice in St. Margaret's Bay, however, appear to have consistently lower growth efficiencies relative to fish in the Gulf of St. Lawrence and the Grand Banks even though the environmental temperatures are very similar. Differences in species composition and quantity of the food supply were considered by Rae (1965) to constitute the major basis for large variations in growth of lemon sole (*Microstomus kitt*) in different areas. Food supply characteristics probably constitute the major influence on the low growth efficiency of St. Margaret's Bay plaice but evidence is not sufficient to define the underlying mechanisms. Diet is known to differ from that of fish in other areas (Ardill, 1968; Yanulov, 1962; Powles, 1965) and a significant feature in this respect is a relative scarcity of larger epifauna in the Bay. Some of the difference in net growth efficiency between areas may be due to difference in the length of the feeding season since the calculations are based on annual growth data. It is also possible that the density of the St. Margaret's Bay stock is high relative to a limited food supply since the stock is unfished.

Relatively less energy is diverted to body growth in older fish but the efficiency with which materials are synthesized and stored in the body does not decline to values as low as the growth efficiencies in Figure 6 for relatively larger fish would suggest. MacKinnon (1972) found that large plaice put relatively more energy into gonads and that as size increased the storage of energy as body growth constituted a progressively smaller proportion of the total energy storage. Onset of maturity in plaice populations is spread over a range of sizes, with 50% of fish becoming mature at 60-70% of the maximum length attained in a particular population. Much of the decline in growth efficiency from a relative size of about 0.5 onwards is therefore compensated by an increase in synthesis of materials for reproduction.

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Table 1 Observations on standard oxygen consumption rate of American plaice at temperatures corresponding to those of St. Margaret's Bay

DATE	August	November	February	April	June	Annual
TEMPERATURE (°C)	3	6	1	3	3	-
NUMBER OF FISH	11	24	11	27	27	100
- mature females	-	-	4	9	16	(29)
- immature females	-	20	5	13	6	(44)
- males	-	4	2	5	5	(16)
MEAN WEIGHT OF FISH IN SAMPLE (gm)	267.8	230.7	389.5	294.1	344.1	295.5
SLOPE OF REGRESSION EQUATION*	1.096±0.369	0.784±0.086	0.492±0.408	0.834±0.158	0.876±0.257	0.794±0.082
LN ESTIMATED OXYGEN CONSUMPTION RATE (mg/hr) OF 300 gm FISH*	1.892±0.164	1.770±0.062	1.733±0.153	1.642±0.085	1.650±0.010	1.703±0.044
LN OXYGEN CONSUMPTION RATE (mg/hr) AT SAMPLE MEAN WEIGHT*	1.767±0.158	1.564±0.058	1.862±0.110	1.635±0.085	1.770±0.094	1.691±0.044

*numbers are shown with 95% confidence limits

Table 2. Respiration Rates of Various Flatfishes Weighing 10 Grams

Species	Temperature of Experiment	Respiration Rate at 10°C (mg/hr)	Respiration Rate at other Temperatures (mg/hr)	Source
Pleuronectes platessa	10	1.61		data: Edwards *et al* (1969)
Pseudopleuronectes americanus	10	0.55		data: Voyer and Morrison (1972)
Platichthys stellatus	15		1.10	data: Hickman (1959)
	10	0.57		
Hippoglossoides platessoides	3		0.37	data: this paper
	10	0.61		temperature corrected: Miller (personal communication)
	10	1.09		temperature corrected: Winberg (1956)
Cynoglossus sp.	10	0.42		temperature corrected: data Edwards *et al* (1970)
	10	0.39		temperature corrected: Winberg (1956)
	28		2.02	data: Edwards *et al* (1971)
All Fish	3		0.34	equation of Winberg (1956)
	10	1.01		equation of Winberg (1956)

Table 3 Parameters of the metabolism/growth equation for American plaice[2]

Life History Stage	1	2	3	4	5
Initial weight, w_o(gm)	0.001	0.075	2.4	44.9	491.3
Environment temperature (°C)	14	8	3	3	3
Metabolic parameters:					
a (mgO_2/gm hr)[1]	0.117	0.083	0.058	0.058	0.058
b	0.75	0.75	0.8	0.8	0.8
c	1.9	1.9	2.0	2.0	2.0
K	0.50	0.45	0.27	0.17	0.11

[1] Conversion of *a* to suitable units is made as in the following example; *a* = 0.0582 mgO_2/gm hr x 3.38 cal/mgO_2 x 24 hr/day x 7 day/week ÷ 1000 cal/gm = 0.0330 gm/gm week.

[2] Example equation for *a* stage 3 fish :

$$w(t) = \left(\frac{0.3}{1-0.3} \times 2 \times 0.0330\ t + 2.4^{0.2}\right)^{1/0.2}$$

$$w(t) = (0.330\ t + 2.4^{0.2})^{5} \text{ grams}$$

Table 4. Comparison of growth of American plaice in St. Margaret's Bay with computed values from the metabolism/growth equation.

Age	Length (cm)	Growth Stage	Computed Weight (gm.)	Observed Weight (gm.)
0 weeks	0.001	1	0.001	(0.001)
4			0.009	
8			0.034	
12		2	0.096	(0.075)
40			1.29	
1 year	7.3	3	2.85	2.36
2	10.4		6.21	7.0
3	13.0		14.0	15.2
4	16.1		28.1	27.7
5	18.9	4	51.8	44.9
7	24.0		83.1	94.5
9	28.7		143.9	165.0
11	33.7		236.0	255.9
13	37.1		370.0	365.4
15	40.8	5	559.1	491.3
18	45.9		700.9	705.3
21	50.4		976.5	941.4
24	54.3		1332.7	1191.2

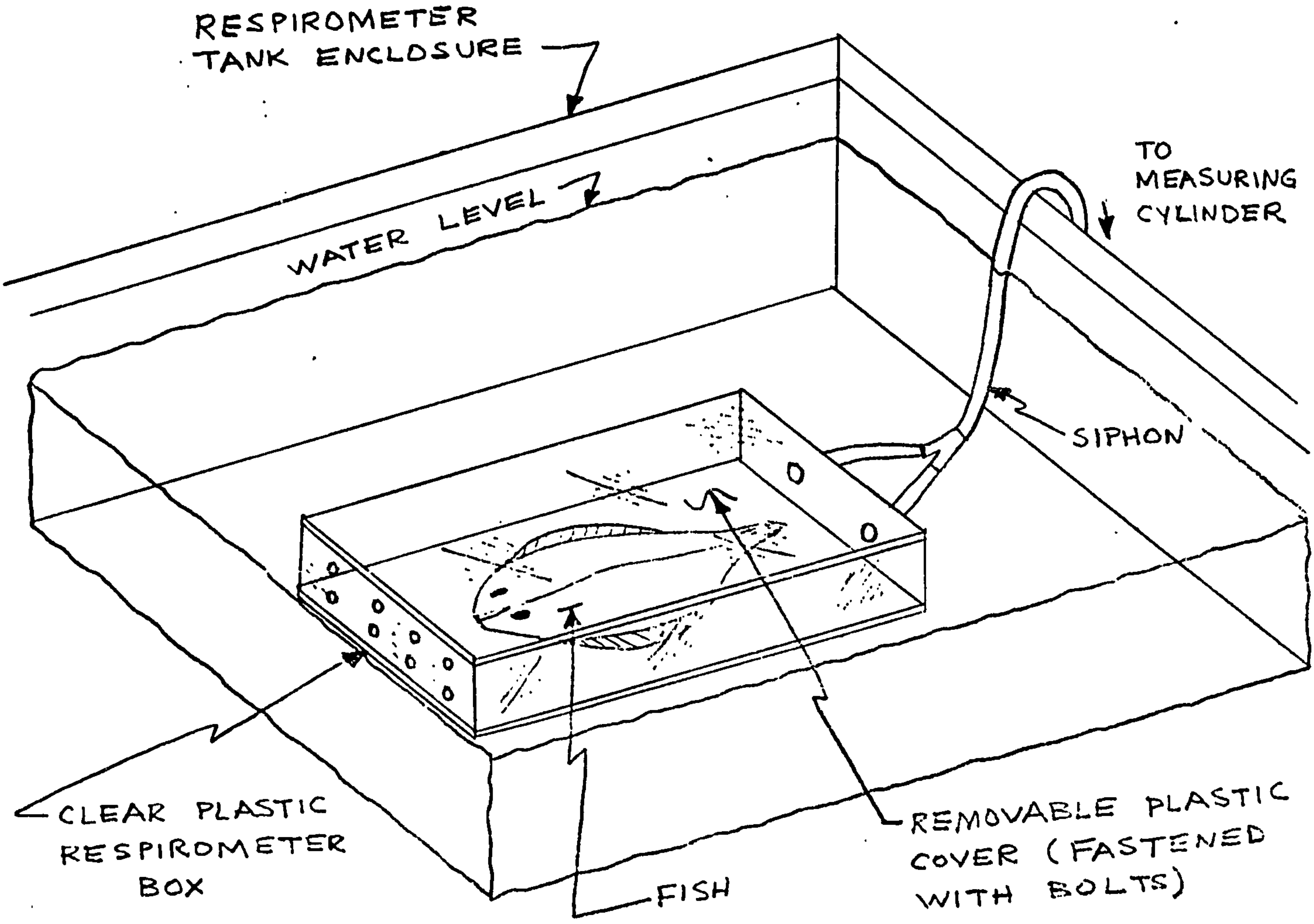

Figure 1. Respirometer for experiments with flatfish.

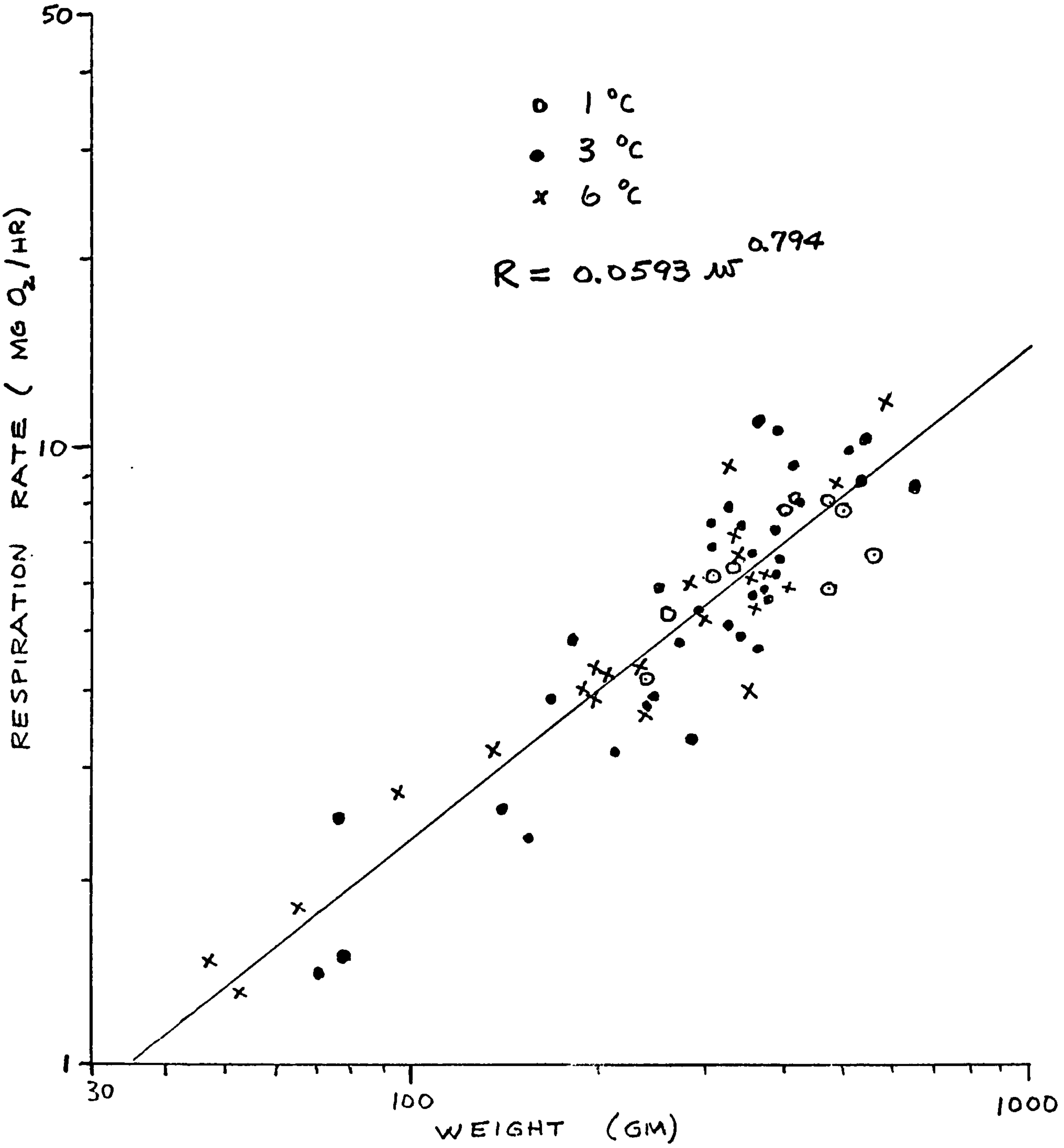

Figure 2. Low routine respiration rates for American plaice of both sexes at temperatures of 1-6°C.

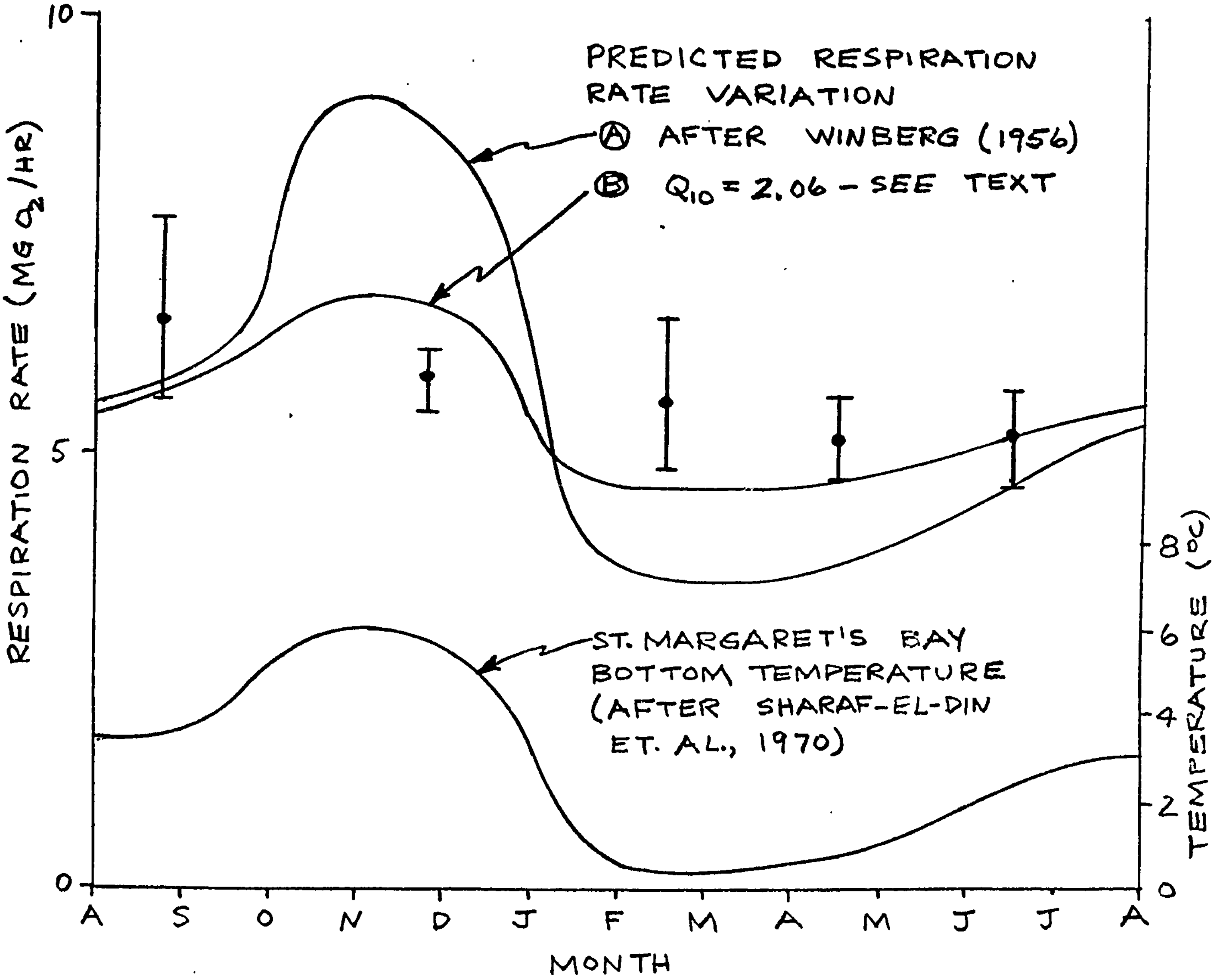

Figure 3. Comparison of observed respiration rates of a 300 gram American plaice with variations predicted for seasonal temperatures of St. Margaret's Bay, N. S.

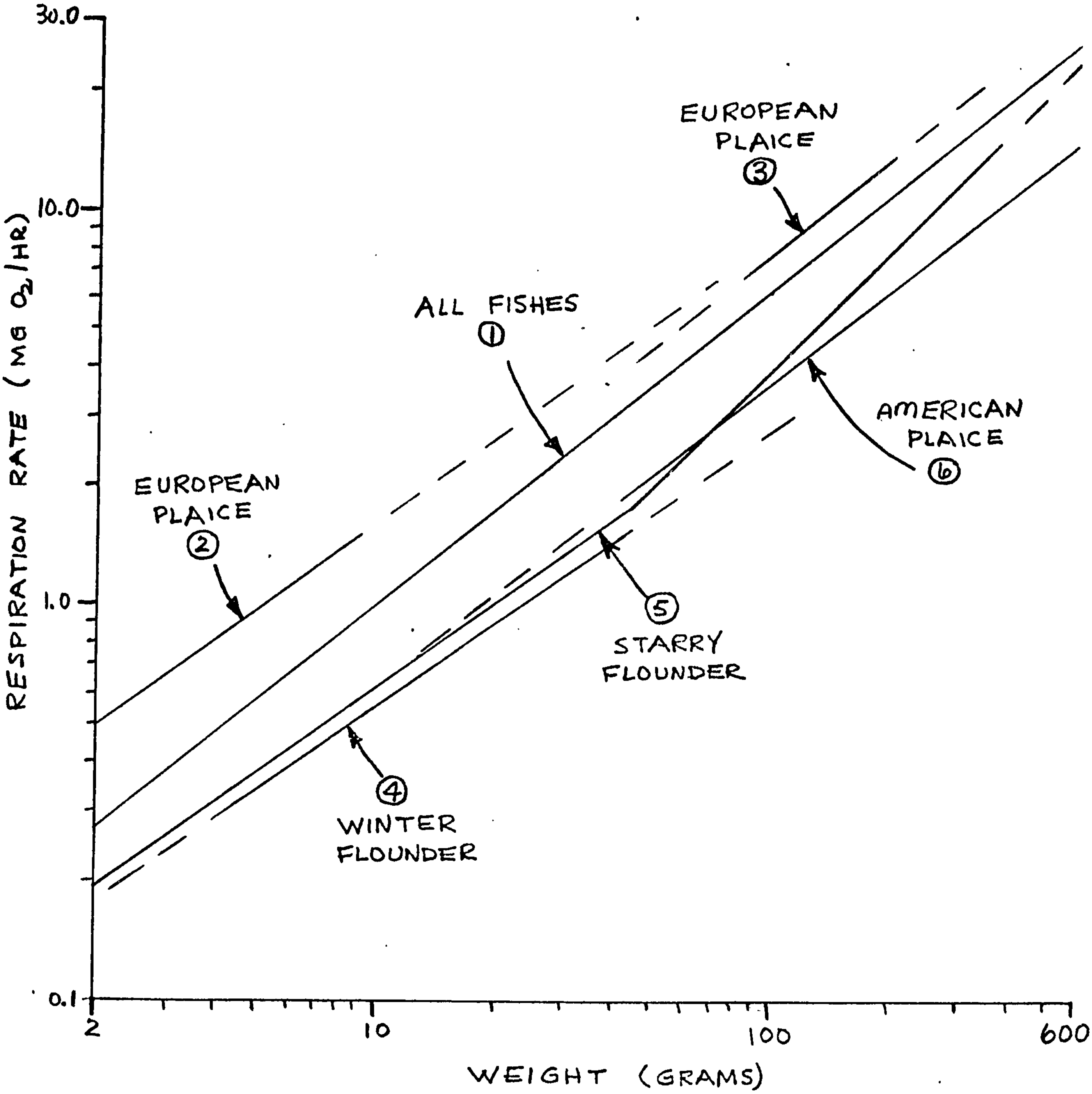

Figure 4. Low routine respiration rates of flatfish species at 10°C.

1. equation for all fishes (Winberg, 1956);
2. European plaice, *Pleuronectes platessa* (Edwards *et al*, 1969);
3. European plaice (Hempel, 1964);
4. winter flounder, *Pseudopleuronectes americanus* (Voyer and Morrison, 1972);
5. starry flounder, *Platichthys stellatus* (Hickman, 1959);
6. American plaice, *Hippoglossoides platessoides* - temperature corrected with Q_{10} = 2.06 (this paper).

The solid lines indicate the weight range of observations for each species.

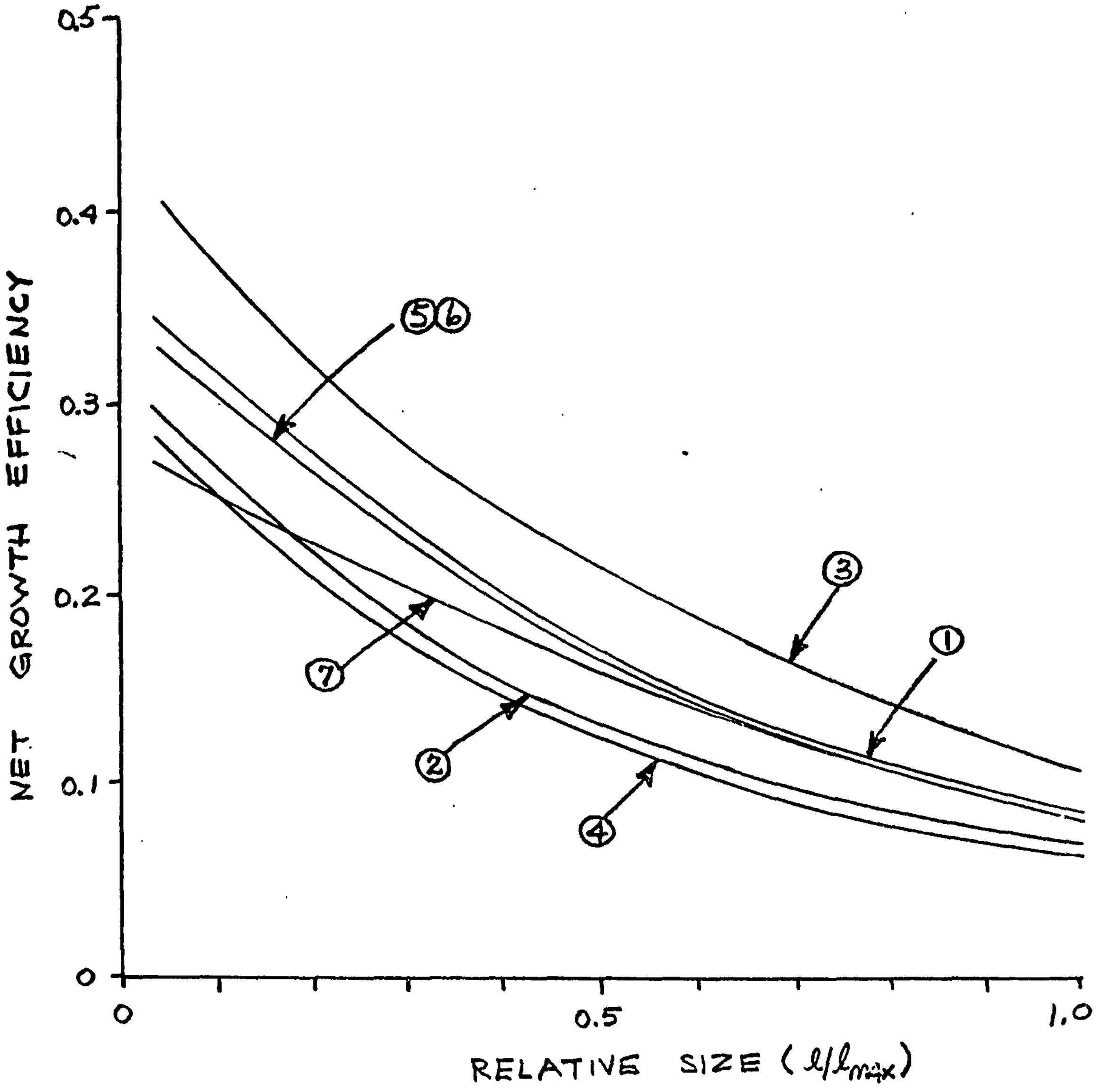

Figure 5. Effect of parameter variation on the net growth efficiency of American plaice, computed with the metabolic growth equation.

1. reference data for the St. Margaret's Bay population;
2. increase in C to 2.5;
3. decrease in C to 1.5;
4. change in mean temperature to 6°C;
5. use of weight/length regression for Grand Banks plaice;
6. increase in absolute value of l_{MAX} by 30%;
7. decrease in b to 0.7.

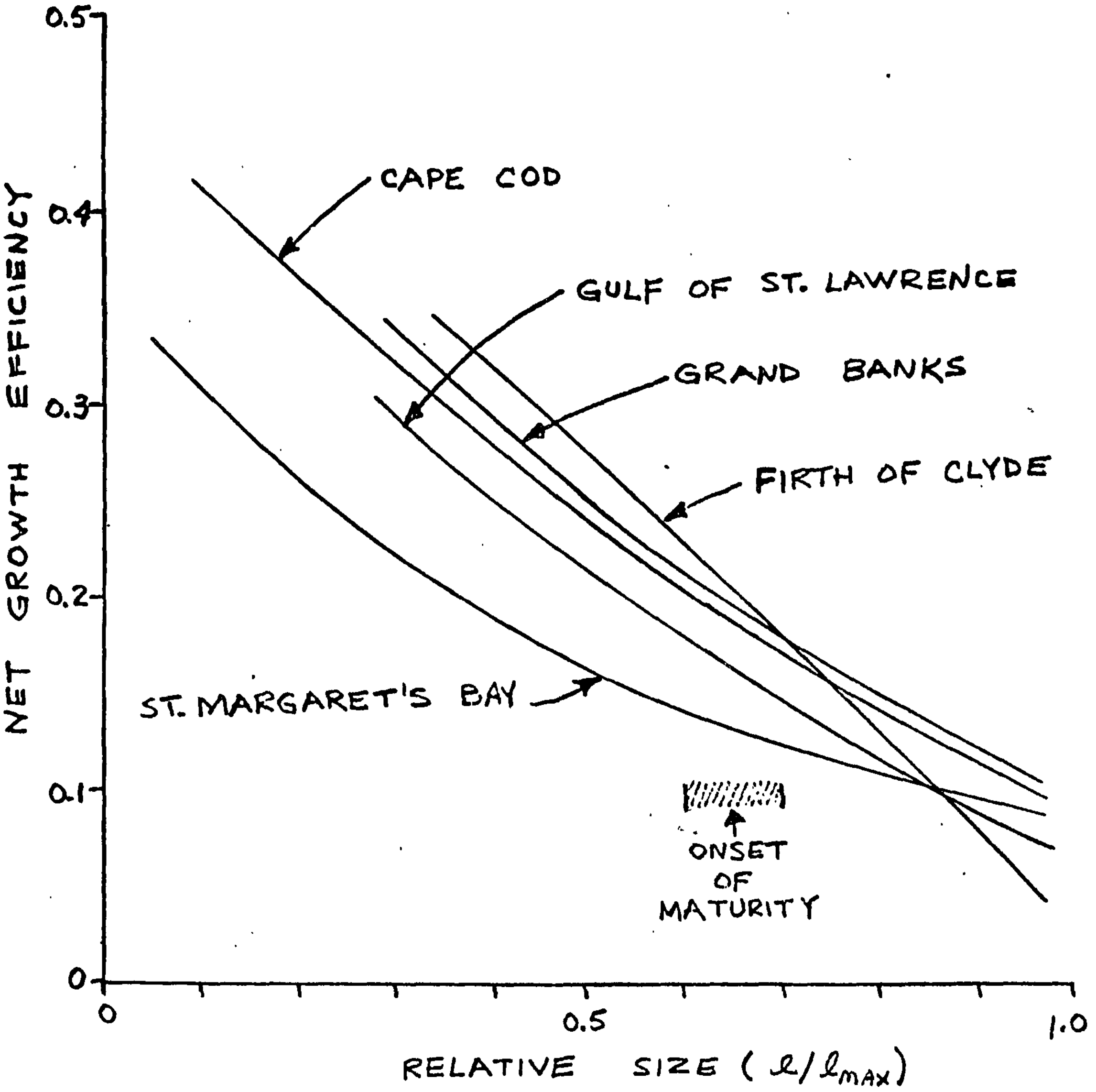

Figure 6. Net growth efficiency versus relative size for different American plaice populations, computed from growth data reported in the literature and the metabolic data of this paper.

APPENDIX

Main Features of the Production Model and of Beverton-Holt Yield Models: A Comparison

	Yield Model (Beverton-Holt)	Production Model (this thesis)
Objectives Emphasized	-analysis of the fish population/fishery interaction; evaluation of yields and other catch properties (e.g. mean weight and length of captured fish) in relation to fishing activity	-analysis of the production process of the fish population in its ecological context; evaluation of population energy flows, including production and yield, and the changes caused by exploitation.
Basic Assumptions	-population assumes states of dynamic equilibrium, with a stable age structure	-population assumes states of dynamic equilibrium, with a stable age structure
	-changes with time are not treated explicitly; year-to-year changes are analyzed as a series of equilibrium states	-changes with time on a seasonal basis are considered; year-to-year changes are analyzed as a series of equilibrium states
	-only an arbitrary "recruited" phase of the population is considered	-all life history stages (eggs, larvae, immature/mature fish) are considered
	-in general the population is assumed to respond passively to exploitation but density dependence of some parameters is considered	-in general the population is assumed to respond actively to exploitation by regulatory mechanisms which tend to match population numbers to the food supply; this response is simulated by making simultaneous changes in various population parameters

Natural Mortality Assumptions	-natural mortality is represented by a variable M derived from an exponential numbers/age function appropriate to an unexploited population	-natural mortality of fish is represented by a variable M derived from an exponential numbers/age function appropriate to an unexploited population; mortality of eggs and larvae is represented by survival probabilities with corresponding time intervals
	-in "simple" models M is constant but in "extended" models M is a linear function of either age or density	-constant values of M are used for various groups of male and female age classes
Fishing Mortality Assumptions	-fishing mortality is represented by a variable F derived from an exponential numbers/age function appropriate to an exploited population and by a function defining age at first capture	-fishing mortality is represented by a variable F derived from an exponential numbers/age function appropriate to an exploited population; age at first capture is constant but could easily be varied
	-the value of F is found by subtracting a constant value of M from the total mortality rate for the exploited population	-the value of F is found by subtracting a constant value of M from the total mortality rate for the exploited population
	-in "simple" models F is constant but in "extended" models F varies with either (1) age, (2) density, (3) year-to-year changes in fishing intensity, (4) season,or (5) space	-constant values of F are used for various groups of male and female age classes

Growth Assumptions	-net annual growth is defined by vonBertalanffy length/age expression plus weight/length regression	-net annual growth is defined by length/age and weight/length regression
	-seasonal growth pattern is not considered	-seasonal growth pattern is described by expressions for (1) change in weight relative to length, i.e. condition, versus time, and (2) the variation in length during the year
	-energy content of materials is not considered	-seasonal variation in energy content of component body materials is described as a function of time
	-food requirements are estimated from growth/maintenance coefficients obtained in feeding experiments	-food requirements and metabolic expenditures are evaluated with an analytical energy metabolism model based upon laboratory-derived parameters
	-in "simple" models parameters of the length/age expression are constant but in "extended" models these vary with: (1) age and (2) population density according to expressions (a) derived empirically, and (b) deduced from theoretical considerations involving food requirements and limitations	-changes in growth rate due to decrease in density (such as are caused by fishing) are described empirically by varying parameters of the length/age expression

Reproduction Assumptions	-seasonal pattern of gonad growth and associated energy requirements are not considered	-seasonal pattern of gonad development is described by expressions for gonad weight and energy content as functions of time
	-in "simple" models the number of eggs is not considered but in "extended" models egg production is derived from data on (1) population numbers and sex ratio, (2) fecundity, (3) age at maturity	-numbers, weight and energy of eggs are computed from data on (1) numbers per age class and sex ratio, (2) fecundity versus individual weight, (3) percent individuals mature at age
	-in "simple" models recruitment R is constant but in "extended" models R is described by an empirical function of egg numbers	-compensatory mortality of eggs/larvae/0^+ fish is assumed when changes in number of eggs spawned occur -the numbers of age 1 fish are then constant; probable, high and low estimates for mortality rate of each stage are considered
	-in "self-regenerating" models R is varied in responde to changes in (1) annual egg production of the spawning stock and (2) year-to-year changes in larval mortality	-no variation in R is considered in view of the compensatory mortality assumption above

Major Model Output Parameters	1. yield per recruit 2. catch and population properties: a. catch per unit effort b. mean population numbers/biomass c. mean length/weight age of fish in catch	1. annual population energy flows per unit area a. ingestion b. metabolism c. body/gonad production d. elimination and spawn e. faeces and urine 2. initial/final state parameters--eg. numbers/biomass/energy per unit area, number of eggs spawned, etc. 3. seasonal variations in energy flow for a. individuals b. various age classes c. the population 4. energy "efficiency" parameters (annual and "instantaneous" time scales) for individuals, age classes and the population