LABORATORY REFERENCE DOCUMENT NUMBER 83-03

THE EFFECT OF WATER RESIDENCE TIME ON THE PLANKTON POPULATION LEVELS ON GEORGES BANK

by

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APPROVED FOR DISTRIBUTION

(APPROVING OFFICIAL)

(DATE)

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MARMAP Contribution MED/NEFC 83-04

June 1983

1. Introduction

Georges Bank exhibits a very high rate of primary production and supports a large commercial fishery involving a number of fish species. A biological energy budget developed for the bank by Cohen et al. (1982), however, concludes that the production at the higher trophic levels is not as high as might be expected given the magnitude of the primary production. Specifically they show that Georges Bank is much less efficient than the North Sea at passing energy from the primary producers to the higher levels. They suggest one explanation for this lower efficiency may be the advection of organisms off of the bank. Table 1 shows the production values at different trophic levels for Georges Bank and the North Sea (from Cohen et al., 1982). The third column in the table gives the relative efficiency of Georges Bank compared to the North Sea. For each unit of primary production, the bank exhibits only about one third the zooplankton production and only one sixth the pelagic fish production as the North Sea. For the benthos and demersal fish, Georges Bank is about half as efficient.

The motion of water around and off of Georges Bank is highly variable. Recent measurements have established that the mean circulation pattern throughout the year is a "leaky" clockwise gyre (Butman et al., 1982) and that the mean residence time on the bank for a water parcel in the upper ten meters of the water column is 2-3 months (Flagg et al., 1982). The residence time is comparable to the generation time for larger zooplankton species and to the planktonic stage for the larvae of most commercially important fish species.

The purpose of this study is to quantitatively evaluate the effect this short residence time of water could have on the plankton population levels on Georges Bank. A simple model for doing this is presented in section 2; it is applied to Georges Bank in section 3, and the implications of the results are discussed in the last section.

2. The Models

To assess the influence of water residence time on plankton population levels, a simple model is used in which population growth is balanced against loss by advection. The growth of a plankton population is modeled by assuming a density dependent logistic growth relationship. For a population of initial level N_0, its growth with time is given by:

$$N(t) = K * [1 + (\frac{K-No}{No})e^{-rt}]^{-1} \qquad (1)$$

and illustrated in Figure 1. N is the population level at time t. Initially, the population increases rapidly, but then slows to assymtotically approach the value K termed the system's carrying capacity. This upper limit on population size reflects the limitation imposed by food or light availability or some other unspecified factor. In all cases considered, K will be set equal to 1. The calculated population levels, therefore, will express results as percentages of the carrying capacity for that population. The r in equation (1) is a growth rate parameter.

For convenience in considering plankton populations, r may be related to the characteristic generation time of the population. G will be defined as the time required for a population starting at a level 0.1K to reach 0.2K, i.e. a doubling time in an uninhibited environment. Then:

$$r = 0.81/G$$

and is substituted into equation (1).

To model the loss of organisms due to exchange or flushing of water off of Georges Bank, a portion of the water and the organisms it contains is periodically removed. The compensating replacement of water is assumed to contain no organisms. The amount and frequency of each removal is balanced to exchange a full system volume in a period equal to the system's residence time. For example (Figure 2), if the residence time on the bank is one year, one third of the water and plankton population could be removed every four months (one third of a year). The population continues growing according to equation (1) after each flushing event. The number of events can be increased with the limit of infinitely many infinitesimal events representing a continuous loss. Continuous loss can be analytically combined with logistic growth [see Appendix A] to yield:

$$N = (r-w)\ [(\frac{r-w}{No} - \frac{r}{k})e^{-(r-w)t} + \frac{r}{k}]^{-1} \qquad (2)$$

where w is the inverse of the mean water residence time T. For w equal to zero (no loss occurring from the system) equation 2 reduces to equation 1.

The simple model described has many inherent limitations. The logistic growth formulation models only the growth of a single plankton population - that characterized by K, No, and G or r. It also assumes that these parameters are constant. No interaction or interdependence between populations is considered. The approach used to model the loss of water and organisms assumes that the plankton population is uniformly distributed over Georges Bank, that the system is well-mixed between flushing events, and that no organisms are contained in the compensating inflow to the system. The physical processes that induce the exchange of water off of the bank or determine the water residence time are not considered. The physical aspects of the system are characterized only by the residence time, T, and the number of flushing events within that period, E.

The effect of the removal of water on a growing plankton population may be investigated by varying the different parameters that characterize the population and the physical system. For all combinations of parameters, a general pattern is found that results in a stable plankton population. Generally, if a low value of N_0 is used, the population grows over time, while if a high value is used, it exhibits a decrease (Figure 3). This occurs because at low levels, the population has a high growth rate and may increase more rapidly than it is removed by flushing. At a value near the carrying capacity the growth rate

is greatly reduced and the population is removed more quickly than it grows. An intermediate initial value exists where the growth and loss processes are in balance and at the end of a residence time period the population value is still equal to N_0 (Figure 3). This value of N_0 is termed the equilibrium population level, N_{eq}. It is the level a population will ultimately approach and remain at through successive residence time periods.

For the continuous-loss environment after a long period of time equation 2 indicates that

$$N_{eq} = k[1-1.24\frac{G}{T}] \qquad (3)$$

where the substitutions for r and w have been made. The equilbrium population level is a linear function of the ratio of the generation time to the water residence time. For discrete flushing events, the model results also appear linear in the same ratio, with a progressively more negative slope as the number of events is decreased (Figure 4). For low values of the ratio G/T, the generation time is short compared to the residence time and the population can be maintained at nearly the carrying capacity applicable in the absence of flushing. For larger values of G/T the effect of the residence time and the associated loss of organisms becomes greater and N_{eq} decreases linearly. When the generation time of the population approaches the residence time of the water ($G/T \rightarrow 0.8$), N_{eq} goes to zero, indicating that the population cannot be sustained in that environment at any level.

The assumption that the water entering the system contains no organisms may not be valid in all cases. The model results in Figure 4 would be modified if this water did contain organisms that acted as a source for the population within the system. With a source that is some constant proportion of the system population, the effective rate of removal of organisms is reduced by that proportion. This is equivalent to a proportionately longer residence time for the system. For example, if the source population was one third of the system population, for every three organisms removed, one would be added; the net rate of removal would be only two thirds (2/3) of what it had been; to remove any given number of organisms would require 1.5 times as long (3/2, the inverse of the effective removal rate). The resulting equilibrium population still could be obtained from Equation 3 by using a residence time that is one and one half times the actual water residence time for the system.

To consider a source that is instead a constant proportion of the system's carrying capacity, the model was modified to input the appropriate level of population after each flushing event. The results are shown in Figure 5 and indicate an increase in the equilibrium population above that given in Equation 3 by an amount dependent upon the ratio G/T. At low values of G/T, where N_{eq} would be high with no source input, the addition of organisms yields only a small increase in N_{eq}. The increase is less than the population level added by the source. As G/T increases, the increase in N_{eq} also gets larger. At G/T = 0.8, where the population would not be self-sustaining (N_{eq} = 0

in Equation 3), the increase in N_{eq} is a maximum, being two to three times the source population level.

Three aspects of the results summarized in Figures 4 and 5 are noteworthy. First, for a given physical system (T and E fixed) the effect on plankton populations at different trophic levels would vary due to their different characteristic generation times. Second, for realistic values of the critical ratio G/T, the reduction in population level below the normal system carrying capacity can be significant. Third, a source of organisms in the inflowing water would be relatively unimportant at low values of G/T, but would be critical to the existence of populations with G/T values approaching 0.8.

The model described is formulated for reproducing plankton populations. The ichthyoplankton population is set initially at the time of spawning, and is then susceptible to loss by advective processes throughout the larval period. The effect of residence time on ichthyoplankton will be modeled with no growth in population size (r=0), and with loss by periodic removal occurring for a period equal to the time from spawning to the post-larval stage, when the fish are free-swimming. For the continuous loss case with r=o, equation 2 indicates exponential decay with an e-folding time equal to the residence time of the system. The results for ichthyoplankton will be expressed as the proportion of the spawned population remaining at the post-larval stage. No other mortality mechanisms are acting on the larval population.

3. Application to Georges Bank

The model results can be applied to the characteristic plankton communities on Georges Bank to estimate the influence of the water residence time on their mean population levels. The residence time is assumed to be 2-3 months (Flagg et al., 1982). A continuous loss environment ($E \to \infty$) is also assumed since this provides a minimum estimate of the reduction in population level due to the water residence time.

Phytoplankton have a generation time of about one day and as a result, would have an equilibrium population level of 98-99% of the system's carrying capacity (Figure 6). The zooplankton on Georges Bank range from species (e.g. Centropages and Paracalanus) with generation times of about three weeks to larger species (e.g. Calanus finmarchicus) with generation times of about two months. The small faster growing species would have equilibrium levels of 50-70% of the carrying capacity. For the larger species, the level would range from zero (non-sustainable) for a two month residence time, up to 17% for the three month residence time. Ichthyoplankton for the important fish species on Georges Bank become free-swimming at an age of about 4 months. The removal of water from the bank would leave from 8 to 26% of the fish larvae at that time. While the phytoplankton are not affected by the residence time of the water on the bank, the higher trophic levels could suffer significant reductions in their sustainable population values.

The possible input of organisms to Georges Bank would not effect the equilibrium population of the phytoplankton since it

is already essentially at the carrying capacity of the system. Similarly, the ichthyoplankton would not likely be effected since the spawning of the important fish species is concentrated on the bank itself. The zooplankton population level could be effected by an input of organisms. The source of water for Georges Bank is primarily from the Gulf of Maine (Hopkins and Garfield, 1981). The population densities (numbers/m^3) in the gulf for the dominant zooplankton species are about 40% of that on Georges Bank (from data presented in Sherman et al., 1982). Given this source of zooplankton, the net removal rate from the bank would be only 60% of the rate with no input of organisms. As discussed above, this source may be considered by using an effective residence time that is 1.67 times (1/0.6) the actual value. The faster growing zooplankton species then have equilibrium levels of 70-80% of the carrying capacity, and the slow growing species have levels of 25-50%. These values are also included in Figure 6.

The North Sea has a residence time of water of about 1.5-2.0 years (Ursin and Andersen, 1978). The modeling results would indicate that the North Sea is an ecosystem where residence time would exert little influence on the plankton populations. If the dominant difference between the North Sea and Georges Bank plankton populations is due to the effect of water residence time, the reduction in population levels calculated for Georges Bank should be comparable to the reduced efficiencies given in Table 1. The circles in Figure 6 show the observed efficiencies of Georges Bank relative to the North Sea presented in Table 1.

For phytoplankton the relative efficiency is one by definition since each system was referenced to its own level of primary production. The zooplankton production value for Georges Bank in Table 1 was derived using a productivity to biomass ratio with a biomass dominated by the larger, slower growing species (Cohen et al., 1982). The appropriate model results for comparison with the observed zooplankton efficiency would be most closely represented by the results for the slower growng species shown in Figure 5. For both zooplankton and ichthyoplankton, the average anticipated reductions in population levels attributable to removal of water from Georges Bank are comparable to the observed lower efficiencies relative to the North Sea. This comparison of population and production levels assumed that a similar relation between production and biomass exists in both areas. This assumption is reasonable due to the similarity in species composition and temperature regimes. The implication of the comparison in Figure 6 is that the major difference between the North Sea and Georges Bank effecting ecosystem efficiency is the additional mortality on Georges Bank due to advective loss.

4. Discussion

The residence time values used for Georges Bank were derived from observations in only the upper 10 m of the water column. While a large portion of the bank is vertically well-mixed year round, the deeper waters probably have a longer mean residence time. Hopkins and Garfield (1981) calculated a range of 2-5 months from winter to summer for the bank as a whole based on

hydrographic data. The longer residence time for subsurface waters is consistent with the efficiency of Georges Bank for benthos and demersal fish production being more nearly equal to that of the North Sea (Table 1).

The large, slow growing zooplankton species (G approximately 2 months) would not have self-sustaining populations on Georges Bank according to Equation 3 because the ratio G/T is close to unity. Pseudocalanus sp. and Calanus finmarchicus are two, slow growing zooplankton that are dominant on Georges Bank during part of the year (Sherman et al., 1982). The model results suggest that an input of organisms from the Gulf of Maine would be critical for the maintenance of these populations on Georges Bank. Davis (1982) modeled the population of Pseudocalanus sp. (G approximately 2 months) and could match observed distributions only by having a continuous input of adults from the Gulf of Maine along the northern edge of the bank. A similar dependence likely exists for Calanus finmarchicus as well.

The simple model presented is not an attempt to model the complexities of the Georges Bank ecosystem or to accurately model the bank's plankton populations. Instead it is an investigation of what is believed to be a dominant relationship for the system - the balance between growth and advective loss. The specific values plotted in Figures 4 and 5 are not critical. The important result is that the predicted reductions in population levels are large. That they are similar to the results from the North Sea comparison suggests that they are realistic. Our conclusion is that in the mean, the advective loss of water and

organisms from Georges Bank is an important mechanism for controlling the plankton population levels on the bank, and that the physical environment has an important role in determining the mean biological efficiency between the trophic levels in the Georges Bank ecosystem.

The residence time of water on Georges Bank is not due to either a continuous loss or to uniform discrete events as modeled. Instead it results from the accumulation of various temporally and spatially varying processes. Among these are the entrainment of water by warm core Gulf Stream rings, the response to major wind events, and dynamic instability in the shelf/slope frontal region. The actual time a water parcel remains on the bank varies considerably depending upon the processes acting during that period. For example, the satellite-tracked drifters deployed by Flagg et al. (1982) remained on the bank for periods of from 3 to 113 days.

The zooplankton and ichthyoplankton on Georges Bank also are not uniformly distributed as assumed in the model. Instead their distributions are often characterized as patchy with areas of very high concentrations (e.g. Sherman et al., 1982 and Smith et al., 1980). The interaction of biological distributions and physical processes that are both spatially and temporally varying will result in a loss rate of organisms from the bank that is highly variable. Therefore, the advective loss of water may be important for not only controlling the mean plankton population levels on Georges Bank, as suggested by the model results, but also for determining variations in these levels from year to year or season to season.

Application of the results of this modeling effort to future research strategy is clear. To understand the mean and variations in the production of the Georges Bank ecosystem, an understanding of the physical processes that control the removal of water from the bank and the recirculation of water around the bank will be required.

Acknowledgements

Discussions with Cabell Davis and comments by Michael Sissenwine on an earlier draft of the manuscript were very helpful and gratefully acknowledged.

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APPENDIX A

LOGISTIC GROWTH IN A CONTINUOUS LOSS ENVIRONMENT

For a population exhibiting logistic growth as in equation 1 the rate of change in the population size is:

$$\frac{dN}{dt} = N\, r(1-\frac{N}{k})$$

where r is a growth rate parameter and k is the system carrying capacity. In the well-mixed continous loss environment the removal of water results in a rate of loss for a population of particles that is proportional to the number of particles present at that time:

$$\frac{dN}{dt} = -wN$$

where the proportionality constant w is the inverse of the water residence time, T:

$$w = \frac{1}{T}$$

Combining the growth and the loss rates

$$\frac{dN}{dt} = Nr(1-\frac{N}{k}) - wN \qquad \text{(A1)}$$

For the initial condition that:

$$N = N_o \quad \text{at } t = 0$$

equation A1 has a solution:

$$N = (r-w)\ [(\frac{r-w}{N_o} - \frac{r}{K})\ e^{-(r-w)t} + \frac{r}{K}]^{-1} \qquad (A2)$$

As time increases the exponential term in equaion A2 ultimately goes to zero. The equilibrium population level that results is:

$$N_{eq} = (r-w)\ \frac{K}{r}$$

Substituting for r and w yields equation 3:

$$N_{eq} = K(1-1.24\ \frac{G}{T})$$

	PRODUCTION ($x10^4$ Jm^{-2} yr^{-1})		
	GEORGES BANK	NORTH SEA	RATIO (GB/NS)
Phytoplankton	2,470	549	1.00
Zooplankton	146	99.6	0.34
Benthos	83.7	37.7	0.49
Pelagic	2.38	3.35	0.16
Demersal	2.93	1.05	0.62

Table I. Comparison of the production at different trophic levels for Georges Bank and the North Sea (values from Cohen et al., 1982). The third column is the ratio of the efficiencies of Georges Bank and the North Sea at passing energy from the primary producers to the higher trophic levels.

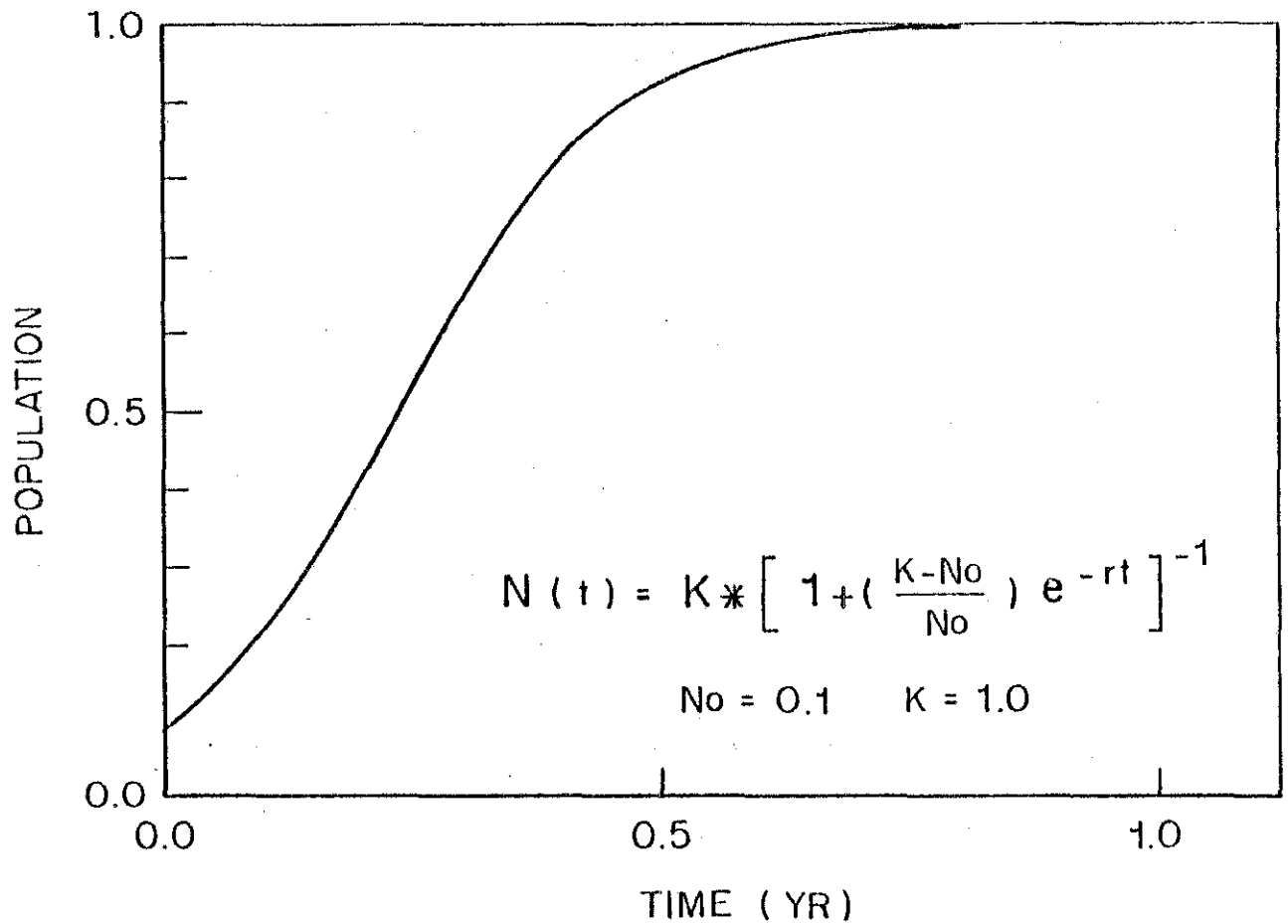

Figure 1. Population level versus time for logistic growth given in equation 1.

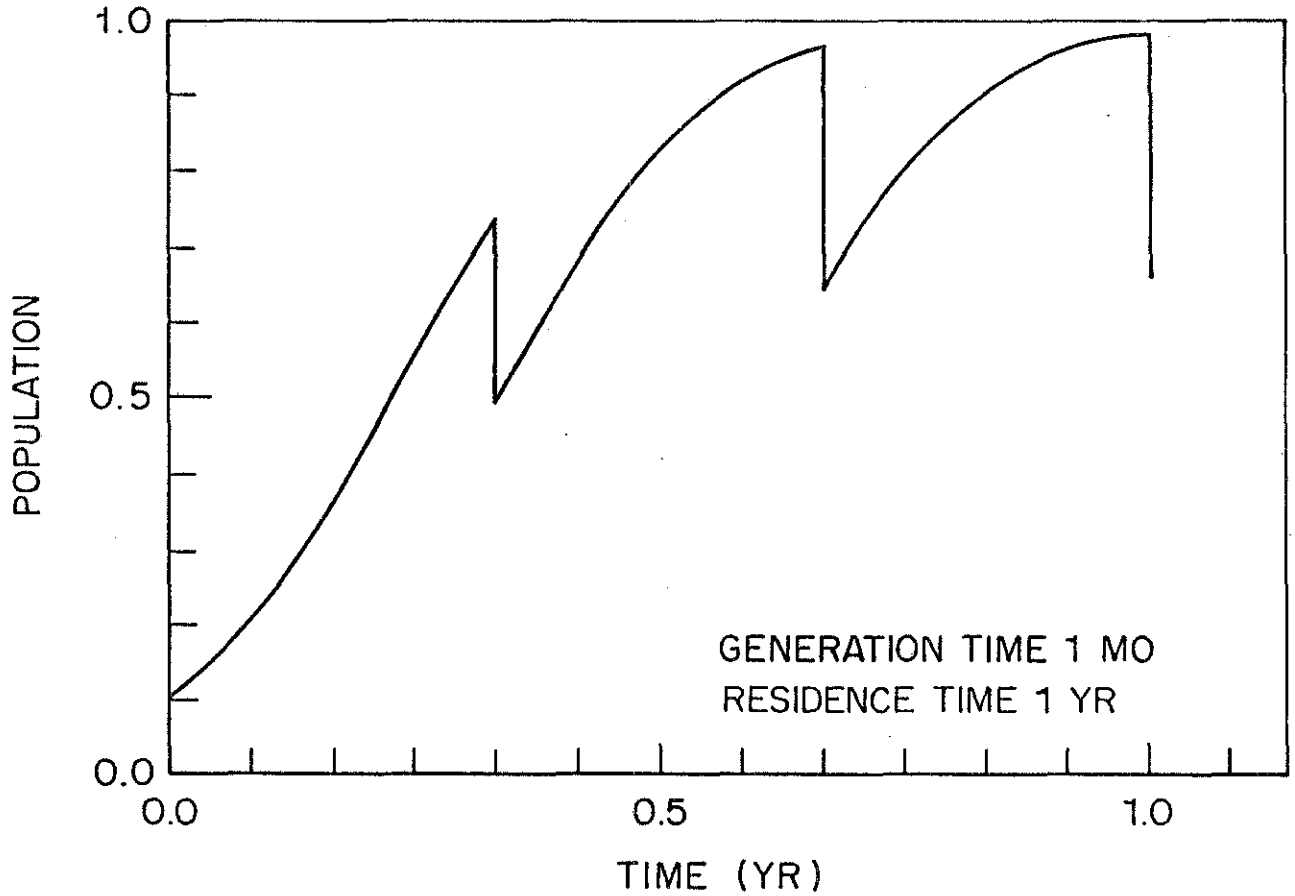

Figure 2. Population level versus time for logistic growth coupled with episodic loss. One third of the population is removed on three occasions, spaced evenly through the water residence time.

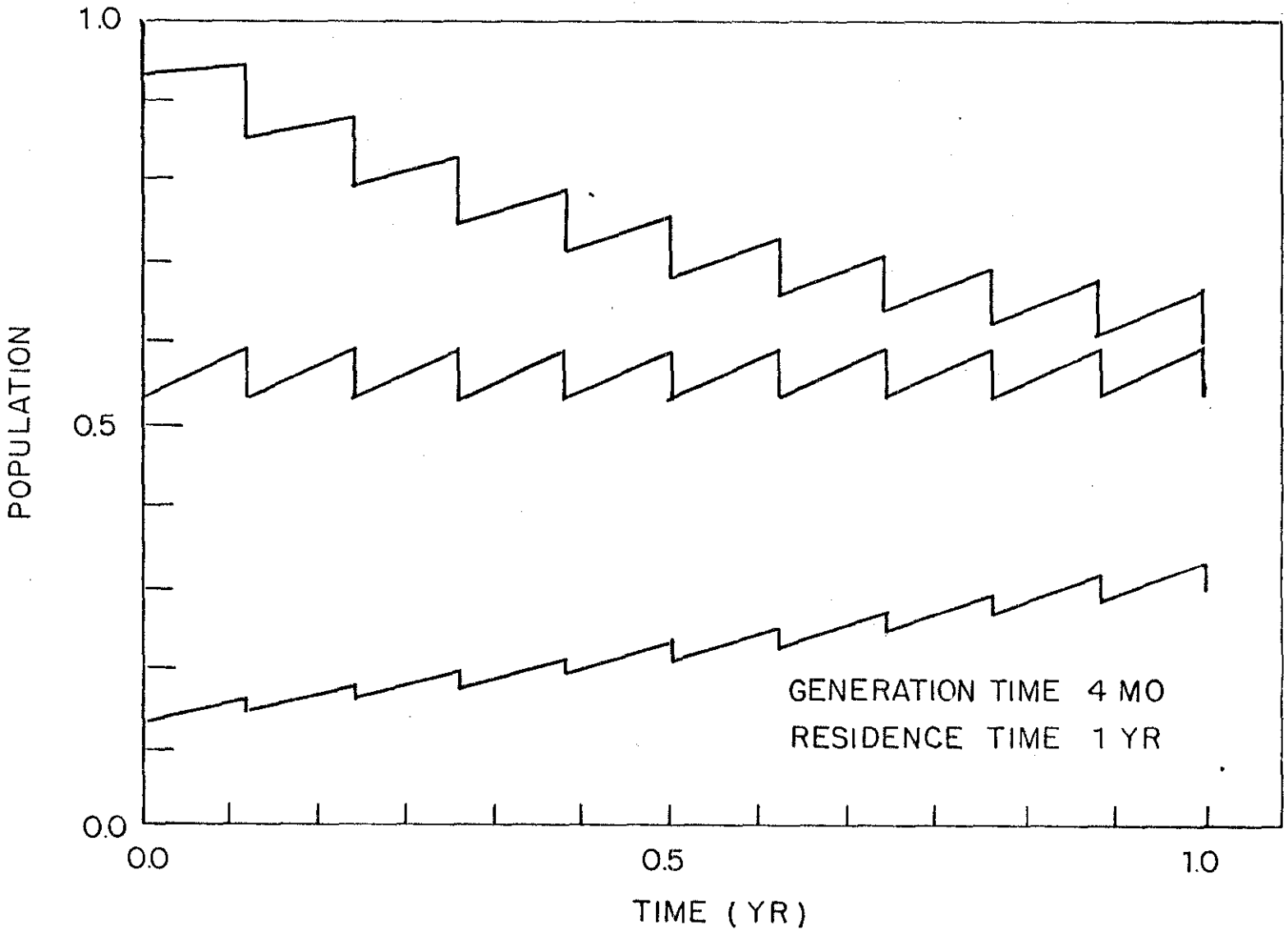

Figure 3. The effect of different values of the initial population level, N_0. For a high value the population decreases, for a low value it increases and for a particular intermediate value, the population at the end of one residence time is still equal to N_0.

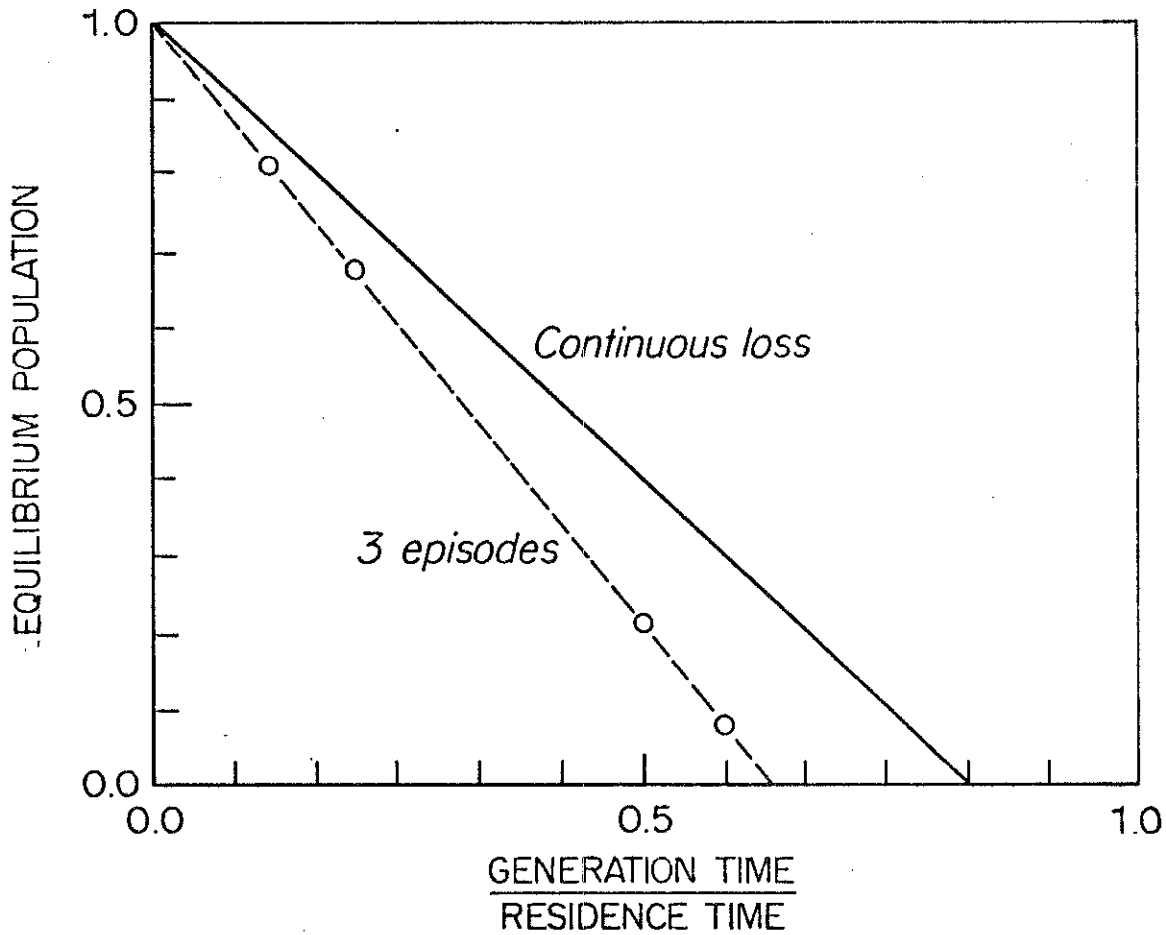

Figure 4. Equilibrium population value as a function of the population generation time to water residence time ratio. The solid curve is for a continuous loss environment (see Appendix A). The dashed curve is for an environment with three loss episodes per residence time (E=3). The appropriate curves for increasing values of E progressively approach the continuous loss curve.

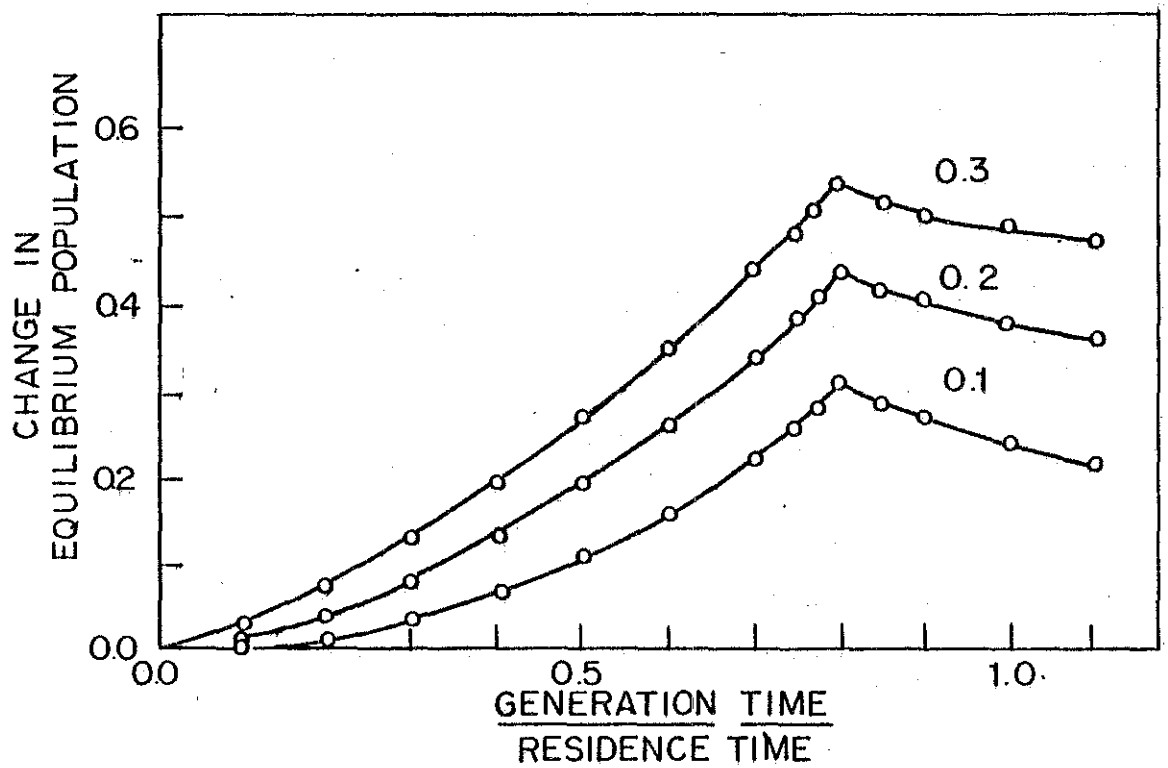

Figure 5. Increase in equilibrium population level (N_{eq}) above that predicted by equation (3) for a constant source population with a density of 0.1 to 0.3 of the system carrying capacity. Twenty flushing events per residence time (E=20) were used in all cases to closely approximate a continuous loss environment.

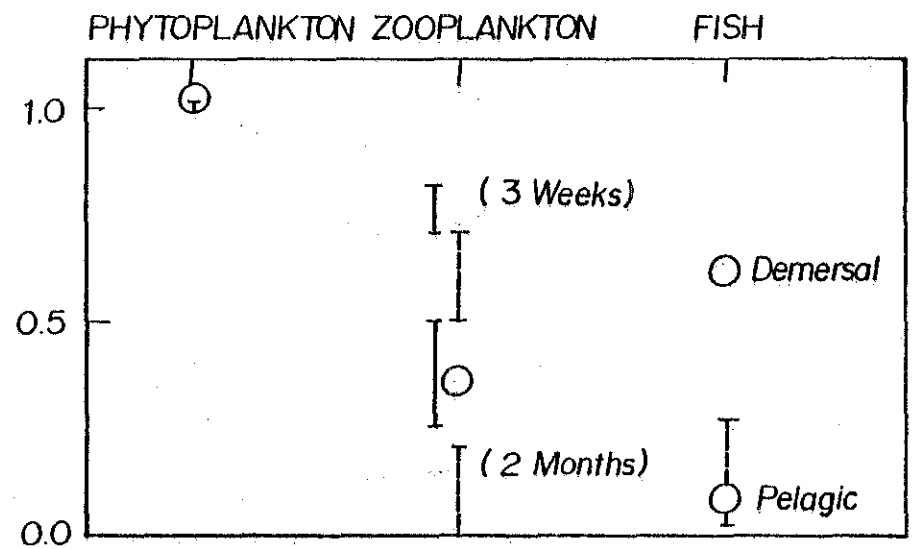

Figure 6. Equilibrium populations values (dashed bars) for phytoplankton, zooplankton, and ichthyoplankton on Georges Bank assuming a residence time of 2 to 3 months and a continuous loss environment. For zooplankton, results are shown for small species with generation times of 3 weeks and for large species with generation times of 2.0 months. The circles indicate the efficiency of Georges Bank relative to the North Sea from Table 1. The solid bars are the results of zooplankton when a 40% source population is included.