

DYNAMICS OF THE
GEORGES BANK SCALLOP FISHERY

by

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ABSTRACT

The cyclical dynamics of the Georges Bank sea scallop fishery are investigated by time series and spatial data analysis, modelling, and dynamical hypothesis testing.

Surveys of Placopecten magellanicus, on Georges Bank, provided size-frequency distributions of the population from 1977 to 1988. Commercial time series of effort and catch, extending to 1944, corroborate the surveys. Population reproduction, early life history survival, and stock-recruitment interactions, within and between subareas along the clockwise direction of current flow, are computed.

Recruitment and egg production on the Northern Edge and Northeast Peak are correlated, suggesting a reproductively self-sustaining population. Large increases in stock-recruitment correlations were observed when the egg contribution of newly fecund scallops ages 3 and 4 was omitted from yearly totals which, together with physiological studies, suggests that scallops age 3 and 4 are not yet fully mature. Recruitment could be substantially enhanced by raising age of first capture.

Hypotheses for the 15-year cycle of Georges Bank scallops are threefold: periodic environmental forcing, Schaefer predator-prey, or Ricker density dependence. The fishery closely matches assumptions and mathematical features of the age-structured, stochastic-recruitment Schaefer model, comparing auto- and cross-correlations of recruitment, effort and stocksize from model and data. Population cycle hypothesis testing criteria are applied that are qualitative, and therefore robust.

Density dependence is implicated from age structure before compared with under exploitation. Due to a greatly shortened lifespan in the fishery, egg survivorship to age 2 is 300 times greater, estimated from survey, compared with a natural population, whose egg to recruit survival is deduced as the reciprocal of mean lifetime egg production.

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INTRODUCTION

Population cycles played an important role since the inception of ecology beginning with Lotka (1925) and Volterra (1927) who independently showed that the simplest set of equations describing the interaction of a predator population and its prey result in closed, neutrally stable oscillations. The investigations of Gause (1935), Elton (1942) and Nicholson (1957), and more recently May (1973), Krebs and Meyers (1974), Nisbet and Gurney (1983) and others, established the cycle as a principal subject of theoretical, field and laboratory population biology. Cycles are a valuable subject of study for these reasons: ecologists study dynamics to understand why populations change, to determine which population processes are acting and to determine which of many factors predominate. The existence of cycles presupposes certain regularities in the processes of population change, thus making them more amenable to analysis. The question of steady states, why many populations do not change, is also one of dynamics--how the various dynamical processes affecting population size, including the tendency to exponential increase, are balanced.

By contrast, observations and measurements of a steady state population inform us little about its dynamics. Many combinations of these processes can all yield basically the same outcome, namely a time series which fluctuates about a mean value. If, however, that balance is perturbed, the

response of population size affords a better look at the main factors causing the population to change. The resulting time series may then yield a long-term trend with an amplitude of variation which is greater than the random fluctuations observed in most real populations. A population oscillation, whether stable or decaying to the steady state, is the next step upward in complexity. The information that it conveys about dynamics is richer, inspiring the historical interest in cycles of classical ecology.

May (1974, 1976) showed that the non-linear nature of population interactions, in particular strong density dependence, creates dynamical behavior which is far richer still, namely chaos. In a fisheries context, Ricker (1954) observed cycles and what was effectively chaos in discrete single-species models similar to May's. However observations of and experiments with real populations suggest, perhaps counter-intuitively, that single-species populations cycle very rarely (Thomas et al. 1980, Mueller and Ayala 1981, Stokes et al. 1988). By (non-group) selective evolutionary processes (Mani 1984, Nisbet et al. 1989), the form of density dependence usually yields stability. Furthermore, the cycles which Ricker and May observed in discrete-time models were shown to be far less likely in continuous time and do not occur, for example, with logistic density dependence. However, with more than two species, chaos is common in the parameter space of many

models because, just as with the 3-body problem of classical mechanics, 3 continuously, non-linearly reacting elements often yields mathematics which is neither steady nor periodic. And whether a steady state or chaos (or perhaps, most likely, a highly complex, multi-periodic movement about a steady state), dynamics which involve three variables yield an outcome, even from a purely theoretical perspective, which is very difficult to determine with our present analytical tools. Finding the cause of a real population cycle is the often more difficult inverse process of finding the rate equations from their solution, impossible if the equations cannot be solved. Although with computers there has been rapid progress, it is evident that even if the dynamics are governed by known and deterministic equations, the great sensitivity of chaotic solutions makes them unpredictable, even in models over long times, and certainly in real populations where noise is present.

A cycle thus appears as a compromise between the two extremes of a steady state and chaos, including the relative benefits of both. It moves, but in a pattern which is simple and relatively steady, so it can be studied and its properties identified.

This perspective serves to impart a format on the organization of this thesis.

Chapter 1 presents estimates of density, egg production and natural mortality describing the steady state of the Georges Bank scallop (Placopecten magellanicus) population

from survey data averaged over time. A spatial partition of Georges Bank into five subregions, employed in Chapter 1, forms the basis of Chapter 2, in which yearly changes in recruitment and egg production and their relationships are considered. Recruitment success and the spatial distribution of adults is strongly determined by the fate of larvae, which float freely in the water column during their first month of life. Georges Bank water flows in a semi-closed gyre, and the retention of larvae above the Bank is thought to be an important reason why half of the world's production of this species is sustained there. The subpopulations spaced along the direction of current flow may, by larval transport, be reproductively linked, a possibility investigated in Chapter 2.

Both the catch and effort time series of the Georges Bank scallop fishery, presented in Chapter 3, give evidence of a cycle. Three population dynamical mechanisms are hypothesized to explain this periodic variation: environmental forcing, a Ricker cycle driven by density dependence within the population, and a Schaefer predator-prey cycle, involving 0, 1 and 2 variables of species interaction respectively.

Theoretical population biologists have sought to determine how robust these three classes of cycle-inducing mechanism are by solving a wide range of models. Most population models have a range of solutions that yield an oscillation, depending on the parameters. If a model

predicts qualitatively new dynamical states in response to small changes in either the equations or parameters, it is "structurally unstable", and is an unlikely candidate for explaining a real, stable population cycle. The elements of the real system represented by its parameters, namely the external influence of environment and biology not explicit in the model equations, fluctuate considerably in most real populations. Population parameters may often be taken as constants only when interpreted as means averaged over a number of years. Likewise, the rate equations, expressing the dependence of population growth on the sizes of interacting populations, are certain to be inexact. If this modification of the simple model eliminates cyclical behavior (or transforms it, by bifurcation into some other form of dynamical solution), that cause of population cycle embodied in the model would be unlikely in reality. For persistent population cycles, structurally unstable mechanisms may be excluded, a priori.

It was for this lack of robustness that the pure Lotka-Volterra model was deemed unlikely to occur in real populations, its neutrally stable form being a structurally unstable artifact. However, for the more general class of predator-prey models, of which Lotka-Volterra is effectively a subset of measure zero in the space of possible models, the situation is reversed. The theorem of Kolmogorov (1936), rediscovered in the 1960's (Rescigno and Richardson 1967, Waltman 1964, Scudo 1971) proved under realistic

general assumptions, which express the most likely population growth responses for two species interacting as predator and prey (May 1973), that some form of cycling about the steady state is mathematically very difficult to avoid. Analyzing variants of the basic Lotka-Volterra model, notably the 4 or 5 likely non-linearities in the population rate equations typical of predators and prey, May (1973) found that the steady state can be stable or unstable with equal realism, but that predator-prey oscillations (counterclockwise about the steady state in the x-as-prey, y-as-predator phase plane) are invariably the dynamical response of the two model populations in the neighborhood of the steady state and, for the majority of models, globally in the state space. Among all of these, the most likely solution is a deterministically stable, predator-prey oscillating spiral.

Schaefer extended the study of predator-prey dynamics to fisheries when he proposed a 2-variable model of fisheries economics (1954), unifying the population biology of the stock and the economics of the fishermen. The principal contribution (published in the same year as Gordon's (1954) seminal work in the theory of fisheries economics), was the second of his two equations for the rate of change of effort. The economic response of fishermen as predators, entering the fishery when stocks were abundant enough to make fishing profitable, and leaving when money, on average, is being lost, yields the same equation for the

rate of predator population change that Lotka and Volterra derived. Applying a method of Lotka (1923), Schaefer (1954) solved the model analytically and graphically, and showed that its solution is a damped stable focus, fishing effort and stocksize stabilizing in an oscillatory manner to their steady states, fishing effort following stocksize by a quarter cycle. Schaefer (1954) showed, in numerical examples, that when the population growth coefficient, r , of the stock was of the same order of magnitude as the response rate of the fishermen to profit, that damped predator-prey cycles ensue, but when the prey are modelled to respond 15 times more quickly than fishing effort, the solution is a non-oscillatory decay to steady state. Clark (1976a, 1985), citing Smith (1969), noted the oscillatory nature of the Schaefer model solution near its steady state and globally, and recast the model in a form where profit is explicit, employing the fundamental economic parameters of price of landed fish and cost of unit fishing effort. In its equilibrium form, the Schaefer model has served as the theoretical basis of classical fisheries economics (e.g. Anderson 1977).

The model has three fundamental assumptions: First, effort should track fishstock abundance, rising and falling at a rate proportional to total profit. When real costs are fixed, profit is directly related to fishstock abundance; specifically, how far stock density lies above or below open access equilibrium where the total cost of pulling a net

through the water just equals the average revenue from fish captured. The rate of increase or decrease of fishing effort is also directly related to the level of effort itself. The two additional assumptions are that fish population grow logistically and that catch rate should be linearly proportional to both stocksize and effort. These specific assumptions of the classical Schaefer model will be assessed for the case of the Georges Bank scallop fishery in Chapter 3. With these assumptions, Schaefer wrote the model rate equations, for the stocksize variable, S , and effort, E , as

$$\frac{dS}{dt} = k_1 S (K - S) - q S E \quad (0.1)$$

$$\frac{dE}{dt} = k_3 E (S - S_0)$$

where K is the fish population's natural carrying capacity and k_1 its intrinsic growth rate; q is the catchability; k_3 the response coefficient of effort to profit, and S_0 is the bionomic equilibrium level of stocksize, representing the steady state value of fishstock in the model where resource density is just sufficient to pay the cost of fishing, leaving profit at 0. Expressing the model in the form of a single second-order differential equation, Schaefer derived

an approximate analytic solution using a method analogous to solving for the linearized steady state of the original 2-variable model (Clark 1976a). By showing where the roots of the characteristic equation pass from real to imaginary, Schaefer (1954) delineated the boundary in parameter space separating oscillatory from non-oscillatory solutions. In the majority of fisheries where the bionomic equilibrium level of stocksize is at or below MSY, one may summarize this criterion by saying that stable predator-prey cycles are the solution as long as the time scales of change of the two levels of interaction, economic and biological are of a similar magnitude. Cycling is also predicted if effort changes more quickly than fishstock abundance, but not if effort changes an order of magnitude more slowly.

Because the open access steady state is stable, the pure Schaefer model does not represent a hypothesis for long-term cycles, but in evolving towards equilibrium, a pure deterministic Schaefer fishery would be expected to oscillate with decreasing amplitude as the populations of fishermen and stock stabilized. Schaefer (1954) identified two examples, California sardine and Pacific halibut, which evolved in a predator-prey manner in the effort-fishstock phase plane and, "... appear to be consistent with the hypothesis that one of the major causes of the changes has been the associated changes in the intensity of fishing." Wilen (1976) noted the example of the North Pacific fur seal fishery in its development phase, which also appeared to

respond cyclically as a Schaefer model would predict, spiralling counterclockwise toward the steady state in the predator-prey phase plane.

Because it is mathematically the same model, the theory of Lotka, Volterra, Kolmogorov, May and others, which was developed to investigate the qualitative dynamics of the predator-prey interaction in an ecological context, may be adapted directly to the question of whether or not the Schaefer model is robust. For many modifications of the basic Schaefer model, the effect on stability of the steady state, and thus on cyclicity, can be inferred. Five improvements to the model, in particular, are worth consideration, chosen because they should often be expected to characterize real fisheries:

(1) The type II predator response of Holling (1959) occurs when 'handling time' is an important limitation on harvest rate, presumably when fishstock are so abundant that the time spent trawling is significantly reduced and is taken up instead in handling, storing and unloading the unusually large catch, or, in a scallop fishery, in shucking the meats from their shell. The effect of this modification is to destabilize the steady state, increasing the tendency to cycle. For most fisheries, however, including Georges Bank scallops, the case of too many fish is not a region of the state or parameter space of particular concern.

(2) The pure Lotka-Volterra model is neutrally stable. The addition of density-dependence to fishstock

reproduction, for instance logistic growth in a Schaefer model, stabilizes the cycling populations at their steady state. As average fishing pressure increases, the level of fishstock is driven farther below the carrying capacity where density dependence is less important. Thus, increased average fishing pressure is a destabilizing factor.

(3) Fishstock refuges, including areas inaccessible to fishing gear or simply where concentrations of fish are unknown to fishermen, create a type III response. The same effect of reducing the relative rate of fishing at low stock levels, results from switching to an alternative species when the targeted fishstock is reduced to unprofitable levels. A type III predator response is a stabilizing factor.

In a multi-species fishery, therefore, predator-prey cycles would be expected only if all species were fished to low levels at the same times and if they each responded with a similar growth rate. This synchrony would allow the stock-variable in the Schaefer model to include all species as a single resource. Nevertheless, multi-species fisheries would, in general, be less likely to cycle in a simple predator-prey manner.

(4) Clark (1976a) investigated the dynamical effect of compensatory fishstock growth at low population levels, most common in the case of schooling fishstocks such as herring. Clark demonstrated that its effect is destabilizing and under more extreme circumstances can result in catastrophic

fishstock collapse when the population density is driven below some critical level where population reproduction is hindered.

(5) The range of predator-prey models which cycle has recently been enlarged to include some which are deterministically stable. Nisbet and Gurney (1982) showed that predator-prey systems which have inward spiralling foci as deterministic solutions, are excited by yearly random variation in the growth rate coefficient, r . Long-term irregular predator-prey cycles are the outcome. Since substantial recruitment variation is the rule in marine fishstocks, and since the most widely accepted basic models of fishery dynamics, such as the pure Schaefer model, are deterministically stable, this may be a likely scenario.

In general, the application of the Kolmogorov theorem, which predicts either stable predator-prey oscillations or limit cycles about the steady state, to the general class of Schaefer models (which includes the basic model (0.1) and most of its modifications) suggest that the interaction of an unregulated fishing fleet with a single species fishstock will generally induce predator-prey cyclicity, either stable or unstable. One important exception is when effort returns much more slowly to its steady state than does the fishstock population. Likewise, if processes or influences other than the unregulated Schaefer interaction have a greater influence on the fishstock or the fishermen, most particularly, rigorous fisheries management, then a

predator-prey interaction would be difficult to discern or absent.

To investigate the effect of modifications of the pure Schaefer model on its predictions, a discrete simulation model of the Georges Bank scallop fishery is constructed in Chapter 4, incorporating the predominant factors likely to be significant in the dynamics of this population. A density dependent stock-recruitment relationship, yearly random variation in recruitment success, and age-structure are combined with the classic Schaefer mechanism determining the effort response to changing stock abundance. A method of parametrizing this model is formalized and its fundamental assumption, namely that the steady state values of the variables in the model are well approximated by the mean values of these same variables in real data, is assessed in a Monte Carlo investigation employing the model itself.

One example of a cycle in a fishstock driven by the predator-prey interaction of fishing effort and stocksize is the whitefish population of Lesser Slave Lake (Bell et al. 1977). This interaction was also considered, and rejected as the primary cycle-inducing factor in the Dungeness crab cycle (Botsford et al. 1983, Methot and Botsford 1982) and Digby scallops (Caddy 1979), although in both cases the interaction with effort was considered likely to represent an additional process exacerbating the tendency to instability and cycling.

However, predator-prey cycles in nature have been rarely been fully demonstrated, and more frequently population cycles have been ascribed to environmental forcing. Periodicity in the flux of sunlight is a universal cause of environmental forcing, notably the diurnal and annual motions of the earth with respect to the sun which resonate in virtually every level of life, from biochemistry to biosphere. Forcing of periods greater than one year, while not as strong, may nevertheless be significant due, conceivably, to the sunspot cycle of 11 years, oscillations in solar flux of 12, 22 and 76 years (Gilliland 1982), or perhaps, most importantly for coastal marine populations, the 18.6 year lunar nodal tidal cycle (Loder and Garrett 1978, Currie 1981).

The environmental forcing hypothesis in North Atlantic fishstocks was advanced in comprehensive studies by Sutcliffe (1972, 1973) and Sutcliffe et al. (1977, 1976), who proposed that yearly variation in St. Lawrence River discharge affects total primary production in Gulf of St. Lawrence waters, which is then carried south by the Labrador Current thus affecting fish production of the Scotia Shelf, Gulf of Maine and Georges Bank. Sutcliffe et al. (1983) later expanded this hypothesis to consider stratification and mixing effects from freshwater discharge into Hudson Bay and the Gulf of Maine. To assess the effect of these environmental factors on fishstock production, the correlations of St. Lawrence River discharge and Gulf of

Maine sea-surface temperature (SST) with 17 fishstocks were calculated. Of these, Sutcliffe et al. (1977) identified 10 which yielded significant correlations. In addition, they checked for evidence of periodicity in the environmental signal, calculating the autocorrelations of Gulf of Maine SST and St. Lawrence River discharge, which all yielded clear peaks in the neighborhood of 22 years. This corresponds with the 22-year Northern Hemispheric temperature periodicity identified independently by Gilliland (1982), and assumed to represent the effect of variation in solar radiation flux associated with the 22-year Hale solar magnetic cycle. Their conclusions were strengthened by a good agreement between the correlation lag between fishstock (measured as yearly harvest) and environment (measured as SST) and the approximate age of entry of each species into the fishery, comporting with the belief that yearly variation in early life history stages plays an important role in fishstock abundance.

However, Sinclair et al. (1986) and Koslow et al. (1986) questioned the importance of river discharge in affecting marine biological oceanographic processes and, in particular, those in the Gulf of Maine, hundreds of miles to the south.

More recently, Drinkwater (1987) reexamined the 10 fishstocks in the Gulf of Maine which yielded significant correlations. He extended the data sets for landings of each species and SST, calculating the prediction of catch as

a function of Gulf of Maine SST (but not St. Lawrence runoff) based on the years of Sutcliffe's study, up to 1977, and compared these predictions with reported landings in recent years. Agreement for 7 of the 10 species was poor. For only two, redfish and scallops, did prediction roughly agree. In contrast, for fishstocks within the Gulf of St. Lawrence, correlations with St. Lawrence river flow were also reexamined by Drinkwater and shown to be significant, substantiating Sutcliffe's predictions for the Gulf of St. Lawrence, but not for the open sea.

Sutcliffe et al. (1977) also noted a striking improvement in correlation when variation in fishing effort was explicitly considered, in all fishstocks where effort data were available. Compared to correlations of landings with SST only, they reported increases from $r = 0.85$ to $r = 0.896$ in ICNAF Area 5 cod, for Area 5 haddock from 0.5 to 0.776 and for Atlantic menhaden from 0.76 to 0.924.

Extending the Sutcliffe hypothesis, Cabilio et al. (1987) proposed that an important periodic forcing could result from the lunar nodal cycle of 18.6 years, shown by Loder and Garrett (1978) to entrain mean SST by a few tenths of a degree Celsius or more over the course of one cycle. Selecting the landings data for 19 fishstocks, mainly in the Gulf of Maine and Bay of Fundy, where tidal influences on production and temperature are likely to be strongest, Cabilio et al. (1987) undertook an analysis of 4 steps: (1) The data were smoothed by a seven-point Cartwright filter.

(2) The cross-correlations of the smoothed catch time series with a synthetic 18.6 year period were calculated. (3) Data sets which did not yield a peak in the cross-correlation function were not considered further. (4) A linear model was constructed to assess the level of significance of the peak in cross-correlation observed. A number of stocks did yield significant or nearly significant correlations. Cabilio et al. conclude that these populations are strongly affected by the lunar tidal cycle. Among the species considered were New England scallops, the updated time series of US landings from Georges Bank and the Gulf of Maine employed by Sutcliffe et al. (1977) and Drinkwater (1987).

However, the study of Cabilio et al. (1987) may be criticized on a number of grounds. First unlike the studies by Sutcliffe, no clear phase relationship is postulated between the 18.6 year temperature variation and landings. Among the various stocks, the peak lag of cross-correlation varies widely among species. Cabilio et al. postulate two important environmental processes that could significantly enhance marine populations, namely decreased stratification which results in increased mixing and thus increased primary productivity and secondly higher temperatures which are hypothesized to improve the chance of larval survival by accelerating their growth. But because these would act at precisely opposite phases along the tidal cycle, productivity peaking when temperatures due to greater mixing

are lowest, phase of peak recruitment along the cycle cannot be predicted.

Secondly, once phase is neglected, the only remaining information obtained from the cross-correlations of catch data with the 18.6 year sine wave they describe as "synthetic" is the period of the cycle. If fishstock landings undergo a cycle with a period of about 18.6 years then, whatever the cause, it should yield a positive peak of cross-correlation at some unspecified lag. Indeed, the majority of fishstocks did yield such a peak, varying in peak cross-correlation coefficient from 0.2 to 0.4. Among those species that were not discarded, New England scallop landings were relatively weakly identified, yielding a peak correlation of approximately 0.2 at lag +1.

Thirdly, the "Slutzky-Yule effect" (Slutzky 1927, Yule 1927) warns against subjecting data to smoothing precisely when a cycle is the hypothesis being tested, since it will create the false appearance of a cycle by introducing false autocorrelation among neighboring values. Even a 3-point filter would render the subsequent tests for cyclicity biased. A 7-point filter would certainly make this line of analysis worth reinvestigating further.

It is conceivable that such low correlations (0.2 to 0.4), and in particular, a correlation of 0.2 to 0.24 for scallops, could occur with observable probability in a randomly generated time series. Since the Georges Bank scallop stock, in particular, does exhibit a clear cycle in

landings of ~16-17 years, once smoothed, a mild cross-correlation with an 18.6 year sine wave at some unspecified lag would be expected. Thus, the method of Cabilio et al. (1987) appears likely to yield positive results for any cycling population with a period lying near 18.6 years, whatever its dynamical cause.

The hypothesis of 18.6 year tidal forcing in the Georges Bank scallop population is one of three closely analyzed in Chapter 3.

A number of other cycles in fishstocks have been reported. A 9-year cycle in the Digby scallop fishery (Dickie 1955, Caddy 1979) is well explained by an environmental forcing hypothesis mediated by temperature or larval circulation, in turn driven by the strong tidal currents in the Bay of Fundy. Vasil'kov et al. (1981) postulate a link between saffron cod (Eleginus gracilis) and a 13 year solar periodicity. Baleares hake (Caddy and Gulland 1983) undergo a 13 year oscillation.

Less likely than predator-prey and exogenous forcing, as mentioned above, are single-species cycle-inducing mechanisms, since it appears that single populations evolve away from the extreme density dependence needed for Ricker cycles.

Taking the work of Nicholson (1933) as a starting point, Ricker (1954) observed that all populations must exhibit self-limitation of their growth or they would increase without end, and noted that these density dependent constraints may assume a wide variety of forms but must in general be biological, i.e. endogenous, precisely because they do depend on population density. He observed that any curve lying wholly above the 45 degree line in a stock-recruitment graph results in a population that increases without bound, and that any curve lying wholly below leads to extinction. Thus, each stock-recruitment curve must rise along its "left limb" to the left of the 45 degree line and decline to the right. The point where it passes through the 45 degree line is the population equilibrium. For curves having a right limb steeper than -45 degrees (i.e. a slope less than -1), the equilibrium point is unstable and a limit cycle ensues. For discrete generations, where each recruited year class dies off after spawning and is succeeded the following year by their offspring, the period of this oscillation is 2. The population level jumps up and down, above and below the equilibrium value. For multi-age spawning populations where generations overlap, Ricker observed that the period of oscillation is simply twice the mean age of maturity, and is effectively independent (for his discrete time analysis) of the exact shape of the reproduction curve and of the number of generations in the spawning stock. The amplitude of the oscillation, on the

other hand, is strongly determined by the steepness of the peak; the steeper the curve, the greater the amplitude of the Ricker cycle. The amplitude is small for a multi-age population breeding for four successive years beginning at age 1. The amplitude then increases with the time it takes an egg to mature because of the increase in delay between the spawning of a generation and its eventual recruitment to the parent stock.

Time delay is thus identified in single species populations as a fundamental cause of cyclicity. The Hutchinson (1948) cycle, which has a different mathematical form is, in this way, closely linked to a Ricker cycle. Both have at their basis, a time delay in the response mechanism which pulls the population back to equilibrium. (In a sense the same is true of predator-prey oscillations, where cycles result from the delay in response of one species to change in abundance of the other.)

Ricker (1954) was also the first to examine the effect of stochasticity induced by environmental variability on these density dependent cycles. Model simulations allowed the size of each recruitment cohort to vary in a gaussian multiplicative way. Stochasticity enhanced the amplitude and made the periodicity less regular. Ricker also examined the effect of a steady harvest which removes a fixed fraction of the mature population each year, reducing density dependence. Dramatic decline in amplitude of the oscillation became a virtual steady state when exploitation

reached 20% in his simulated population. The damping effect is even more evident for multi-age spawning populations. Also, the period is reduced slightly with exploitation because the average age at maturity is lowered. These qualities that characterize Ricker cycles may serve as a key to identifying this dynamical mechanism in real cycling populations.

Ricker examined eight natural populations but was able to identify only one with a right limb in its stock-recruitment curve whose slope was steeper than -1. This fishstock, Georges Bank haddock from 1912 to 1929, did oscillate quite plainly and two qualities of this oscillation imply that it probably is an example of a Ricker cycle. The period was 8-9 years, as predicted, since average age-at-maturity for haddock is about 3.5-4.5 years. Second, when the rate of exploitation increased around 1930, the oscillation was effectively eliminated which is precisely what the Ricker model predicts. Cushing (1971) surveyed a number of common fishstocks and found no examples where the steepness of the right limb would be sufficient to generate oscillations, as noted by Goh and Agnew (1978).

May et al. (1974) and Levin and May (1976) illustrated the importance of time delay in causing a large class of single variable population models to oscillate. They formulated a set of very general criteria for determining when a time lag becomes sufficiently long that the stable (but oscillatory) steady state bifurcates into a limit cycle

oscillation. They then apply these criteria to demonstrate that a vast array of widely used continuous and discrete single population models will cycle when the time delay becomes longer than the natural population response time. The time delay is therefore a destabilizing force. Among exploited marine populations this destabilizing effect was shown for the example of baleen whales, where the maturation time lag is particularly long (Clark 1976b).

In a series of recent papers summarized by Nisbet and Gurney (1983, 1984), a rigorous and straightforward mathematical technique is developed to model laboratory insect population cycles, particularly Nicholson's blowflies (1954, 1957) and Lawton's more recent experiments with Indian meal moth (Plodia interpunctella). A full age-structured description is simplified to just two stages for the insect population, adults and larvae. In this "stage-structure" model, the time lag, from egg to maturity is analytically derived from the more intuitively clear but mathematically unwieldy age-structure form. The time lag becomes an additional variable. Stage-structure models are the most successful class of population cycle models proposed thus far and demonstrate their value in describing Nicholson's blowflies and Lawton's meal moth which are distinguished by their periods of "two-and-a-bit" and "one-and-a-bit" multiples of the maturation time. Incorporating the differences in life history between the two laboratory populations, the model successfully predicts the correct

form of cycle observed in each experiment, in particular, distinguishing the cycles by their period length expressed in maturation times, and correctly describing the notch which is observed, a brief decline in abundance which punctuates each peak.

The question of density dependence in the Georges Bank scallop population, is investigated in Chapter 5, even if not the principal cause, can strongly affect the population dynamics. The biology of the scallop, particularly reproduction, is also considered in Chapter 5, drawing on the extensive scientific literature. A link is sought between the organismic levels of physiology, behavior, and life history strategy, and the population-level dynamics of the previous chapters. In particular, I consider, in Chapter 5, the hypothesis that in an unfished scallop population, density dependence is strong and plays a fundamental role in population stability.

Among oscillating populations, two taxa have attracted the most intensive investigation: the Dungeness crab and northern mammals.

The fishery for the northern California Dungeness crab (Cancer magister) is restricted to males of carapace width 159 mm and greater, annually removing as much as 90% of recruited stock. The cycle in yearly landings is remarkably regular with a period of 9-10 years and has a large amplitude with peaks yielding an order of magnitude greater annual harvest than the troughs (Botsford and Wickham 1975).

A variety of mechanisms have been proposed to explain the cycle. Correlations were initially investigated to relate abundance with environment (Peterson 1973, Botsford and Wickham 1975, Wild 1980). Botsford and Wickham (1975) found insufficient evidence for environmental forcing due to upwelling. They later proposed age-structure oscillations due to a Ricker stock-recruitment relationship (Botsford and Wickham 1979) where cannibalism was suspected of causing the steep decline in recruitment with high parent stock densities that characterizes a Ricker model. McKelvey et al. (1980) constructed a comprehensive series of 48 discrete-time models to identify, using statistical and qualitative validation criterion, those properties of the population that cause the oscillation. They excluded environmental forcing and human predator-prey by hypothesis, since none of the 48 models they considered incorporate these factors. Within this limited range of hypotheses, they concluded that a Ricker stock-recruitment relation was a likely cause, causing density-dependent mortality of young larvae and eggs. Later, closer examination of the catch and effort data from the commercial fishery revealed a distinct predator-prey response of fishing effort (Methot and Botsford 1982, Botsford et al. 1983). Botsford (1986, see also Johnson et al. 1986) has had better modelling success by assuming that both environmental forcing and age-structure density dependence play a role. Hobbs and Botsford (1989) most recently proposed a combination of a

Ricker cycle with a predator-prey interaction, specifically a nemertean worm preying on the eggs of Dungeness crab.

Historically, the population cycles which have attracted the most detailed and broad-ranging investigation, due in part to their wide extent among species and across habitats, are the cycles in northern mammal populations in North America, Scandinavia and the Soviet Union. Entraining 3 trophic levels, plants, herbivores and carnivores, these cycles occur in two distinct habitats. The populations in the boreal forest cycle with a distinct 10-year periodicity, most conspicuously in the dominant herbivore, snowshoe hare, and its principal predator, the Canadian lynx (Finerty 1980). Lemmings and voles, in the tundra of the subarctic on three continents, cycle with a characteristic 3-4 year period which can be synchronous over thousands of miles. The plants preferred by these fecund herbivores, in the trophic level below, and their primarily avian and canid carnivorous predators in the trophic level above, also cycle with the same period, and in a phase relationship compatible with a predator-prey dynamic (Krebs and Myers 1974). At least 5 significant factors may help to cause, or at least strongly affect the nature of these cycles, summarized in the reviews of Krebs and Myers (1974) and Finerty (1980):

1. The herbivore-plant positive feedback interaction arising from herbivore grazing and excretion speeding up the recycling time of nutrients, especially in the tundra where

the soil micro-detritivores are frozen and thus inactive roughly 9 months out of the year.

2. The herbivore-plant predator-prey interaction resulting from hare and lemming overgrazing.

3. The classical carnivore-herbivore predator-prey interaction typified by lynx-hare.

4. Annual exogenous forcing (e.g. the brief yearly pulse of plant growth, which is likely to be destabilizing and which may, in addition, explain the relatively high r -values which these herbivores have evolved.

5. Migration (whence, undoubtedly, the lemming earned its fame).

Field experimental evidence has identified all 5 processes in these cycling ecosystems and each can cause an animal population to oscillate or significantly affect the properties of these cycles, particularly stability. In general it appears that population interactions of a predator-prey nature underlie these cycles (Hanski 1987, Hansson 1984, Hansson and Henttonen 1985). In addition, no convincing evidence has been found to suggest climatic or other environmental forcing (Krebs and Myers 1974, Finerty 1980).

The wide array of hypotheses which have been proposed to explain cycles of Dungeness crab and northern mammals characterizes the general study of real population oscillations. At present, there is no widely accepted method for validating a dynamical hypothesis. Identifying

the cause of some observed pattern of change in a population, such as a cycle, has remained elusive. This lack of a method of validation may explain why despite 50 years of investigation of northern mammal cycles, that no single cause or specific group of causes acting in concert, has been positively identified, although considerable laboratory, field and theoretical evidence exists to substantiate a number of likely hypotheses.

The problem is that a very wide assortment, in fact practically all dynamical models, have regions in their parameter space which yield a cyclical solution. The statistical closeness of the fit of simulation or model output to real population data is a poor test of model validity, because by selecting the right parameters, modellers can generate output from complex non-linear dynamical models to fit virtually arbitrary time series. However I will argue, in the case of the Georges Bank scallop cycle, that there exist qualitative features of the three distinct models which do not vary and hold true whatever the choice of parameters within their likely range. Thus I attempt to establish testing criteria which are robust, insofar as they can isolate properties which hold true across the range of parameter values and equation modifications which are realistic.

This reflects a similar approach adopted by mathematicians since the inception of dynamical systems analysis by Poincare (1893) and elaborated by the Russian

school of non-linear oscillation theory (Andronov et al. 1973). A simple analytic solution was not usually possible in a large majority of oscillation models, and they instead set out to isolate the qualitative features of these oscillations, which were easier to determine, since they could be inferred from topology, as one can do in 2 dimensions with isoclines. But perhaps more important in application, these qualities yielded information about the dynamical behavior of these systems, which could be generally applied to wide groups of models and parametric ranges, which they identified, delineated and classified.

A classification scheme for population cycle models is presented in Figure 0.1. In this Introduction, I have listed many of the characteristics (i.e. identifying qualities, properties and features) which may serve to distinguish one population cycle mechanism from another in this diagram. The primary goal of this thesis will be to isolate distinguishing properties of the Georges Bank scallop population cycle, and of the models which might serve to explain it; that is, to identify its cause.

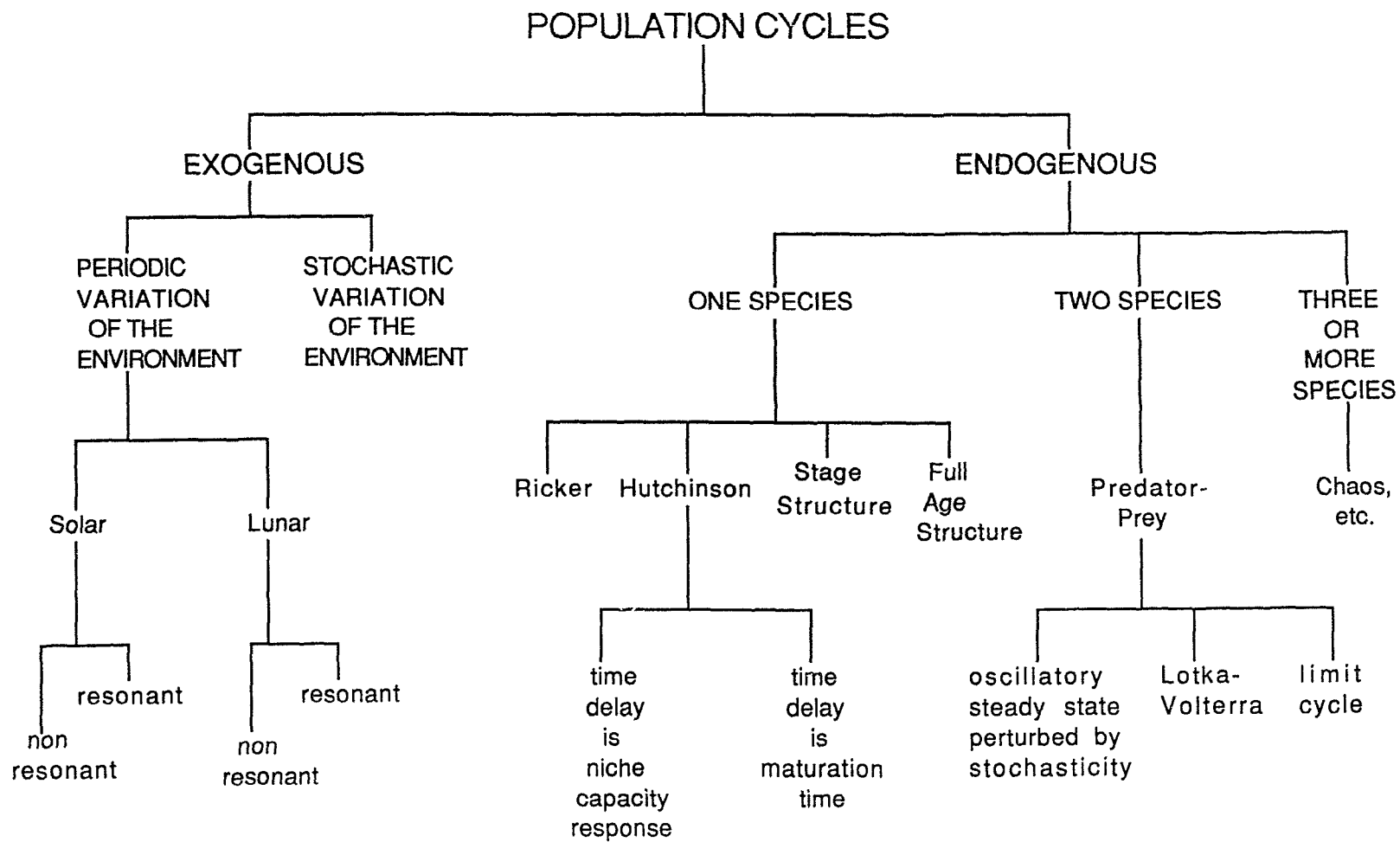


Figure 0.1. A taxonomy of population cycle models.

CHAPTER 1

POPULATIONS, EGG PRODUCTION, AND EARLY LIFE HISTORY SURVIVAL

Introduction

Since 1977, yearly population surveys have been carried out on Georges Bank by the Canadian Department of Fisheries and Oceans in Halifax, and the U.S. National Marine Fisheries Service in Woods Hole. These yearly surveys yield the numbers of scallops captured in each size class, in each subregion. A commercial scallop dredge, fitted with a small-mesh liner, is towed along the bottom at randomly chosen locations in a stratified sampling design (Serchuk and Wigley 1986b, Mohn et al. 1987). Combining U.S. and Canadian survey results, the numbers per tow were stratified (i.e. averaged over all sample trawls considering the area of each sampling stratum) for each subregion.

The size-frequency distributions, of numbers of scallops per tow at sizes 0-5, 5-10, 10-15 mm, etc., provide information about the size and thus any function of size for the population in each subregion.

In this chapter these survey data are used to estimate basic time-averaged demographic statistics of Georges Bank scallop. (1) Population and (2) egg production are obtained both as densities and absolute numbers averaged over the survey years 1977 to 1988; (1) and (2) are then combined, yielding (3) natural mortality for eggs and larvae.

The Georges Bank sea scallop population divides naturally into five subregions (Figure 1.1). Estimates are obtained for each subregion and Georges Bank overall. This time-averaged information is utilized in later chapters analyzing, in particular, the dynamics of population reproduction.

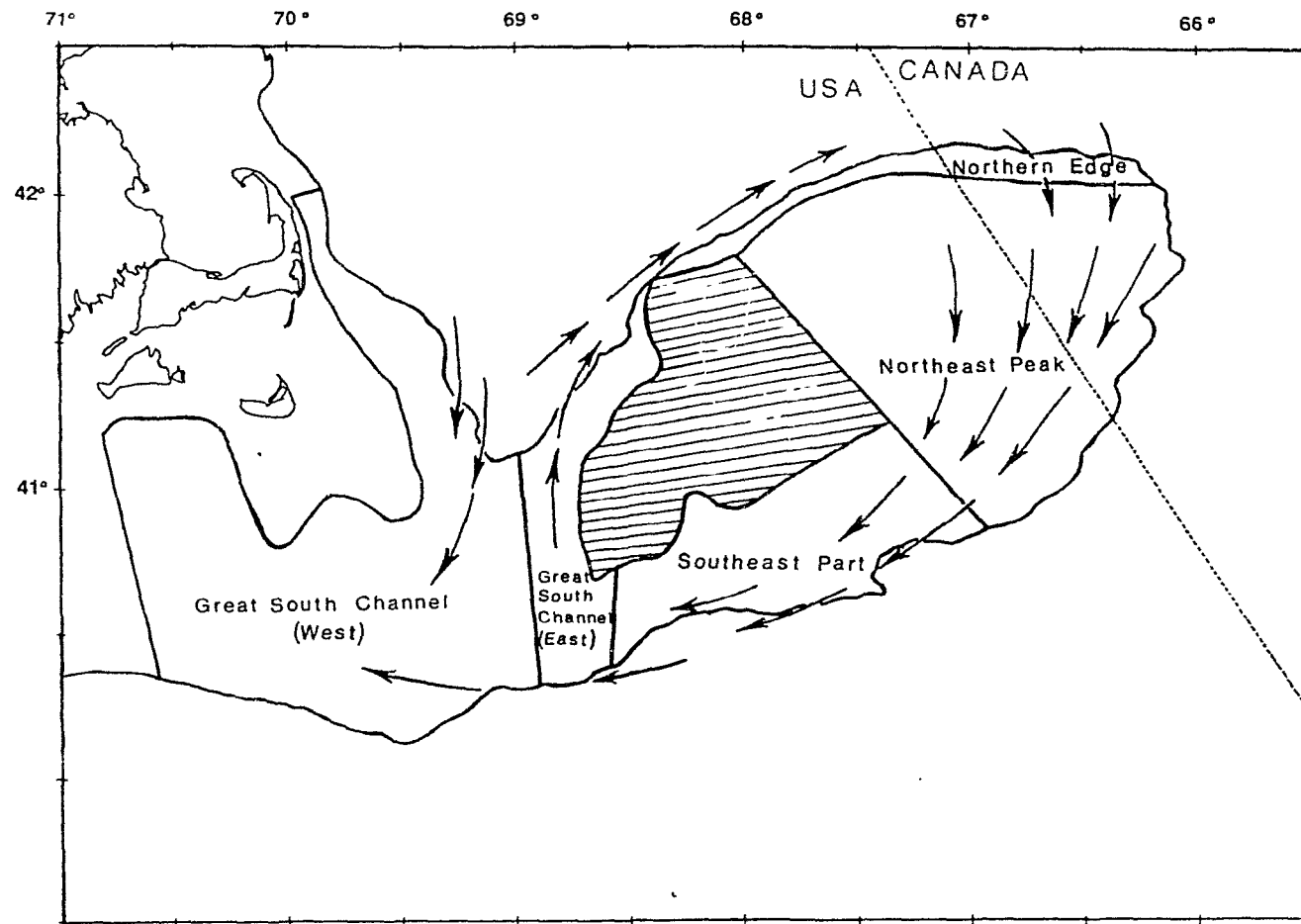


Figure 1.1. Georges Bank and its five subregions.

Methods and Results

Biomass, Population and Recruitment

To estimate absolute population numbers, from the relative density measure of survey numbers per tow, total catch is employed as a scaling factor. This procedure, detailed in Appendix 1.1, is summarized as follows: Averaging the annual catches from 1977 to 1988, yields the total number of scallops harvested in an average year. Employing an independent estimate of average fishing mortality, we deduce the average total number of fishable-size scallops in the Georges Bank population. By comparing this absolute estimate from the fishery with the analogous survey statistic obtained by summing numbers per tow over all commercial sizes (80+ mm) for all of Georges Bank, a scaling coefficient, α , is obtained (Appendix 1.1) which transforms the survey numbers per tow into scallops per m^2 . Employing this scaling coefficient, the data are summed to obtain average population densities, as well as biomasses, annual numbers of recruits, and egg production per unit area for all subregions and for Georges Bank overall.

Specifically, the matrix of survey number-per-tow data, $\{NPT(YR, HT); YR=1977-1988, HT=0-185 \text{ mm}\}$, rescaled by α , yields the average age 2+ biomass,

$$\overline{\text{BIOMASS}} = \frac{1}{12} \sum_{\text{YR}=1977}^{1988} \left[\sum_{\text{HT}=40}^{185 \text{ mm}} \alpha * \text{NPT}(\text{YR}, \text{HT}) * \text{WT}(\text{HT}) \right]$$

the average adult population,

$$\overline{\text{POPULATION}} = \frac{1}{12} \sum_{\text{YR}=1977}^{1988} \left[\sum_{\text{HT}=80}^{185 \text{ mm}} \alpha * \text{NPT}(\text{YR}, \text{HT}) \right]$$

and the average recruitment,

$$\overline{\text{RECRUITS}} = \frac{1}{12} \sum_{\text{YR}=1977}^{1988} \left[\sum_{\text{HT}=30}^{60 \text{ mm}} \alpha * \text{NPT}(\text{YR}, \text{HT}) \right]$$

per m² in each region (Table 1.1).

Population totals (Table 1.2) are obtained directly by multiplying these densities by the area of each region.

The weight-at-height vector, {WT(HT)}, used to calculate biomass, is taken from Serchuk and Wigley (1986a),

$$\text{WT(g)} = \exp(-11.7656) * (\text{HT(mm)})^{3.1693}.$$

Table 1.1. Average population densities (per m^2) for the 5 subregions of Georges Bank. Biomass is measured as harvested adductor muscle meat. Population numbers are commercial sized scallops, 80mm+. Unadjusted age 2 recruits, the numbers between sizes 30 and 60 mm, are underestimates due to lower capture efficiency for smaller sized individuals. More accurate estimates of recruitment, adjusted for gear selectivity, are indicated in brackets. All values are survey averages, scaled by commercial catch, from 1977 to 1988.

Region	Area (km^2)	Biomass density ($g \cdot m^{-2}$)	Population density (m^{-2})	Recruit density (m^{-2})
Northern Edge	1475	4.15	0.172	0.809 [1.804]
Northeast Peak	15582	1.70	0.0739	0.247 [0.580]
Southeast Part	6304	0.31	0.0118	0.011 [0.023]
South Channel (Eastern half)	3838	0.47	0.0170	0.013 [0.028]
South Channel (Western half)	12444	0.43	0.0175	0.065 [0.142]
Northern Edge & Northeast Peak (combined)	17057	1.96	0.0847	0.304 [0.701]
Georges Bank (total)	39643	1.01	0.0431	0.151 [0.347]

Table 1.2. Average population totals, obtained by multiplying the absolute densities from Table 1.1 by the area of each region.

Region	Area (km ²)	Biomass (mt)	Population (millions)	Recruits (millions)
Northern Edge	1475	6120	254	1193 [2660]
Northeast Peak	15582	26440	1152	3856 [9069]
Southeast Part	6304	1970	74	70 [149]
South Channel (Eastern half)	3838	1820	65	50 [108]
South Channel (Western half)	12444	5360	218	808 [1765]
Northern Edge & Northeast Peak (combined)	17057	33390	1440	5180 [11960]
Georges Bank (total)	39643	39950	1710	5986 [13738]

Egg Production

The average number of eggs produced by females in each size class, {EGGS(HT)}, is derived from measurements in Newfoundland by MacDonald and Thompson (1985b) of average gonad weight loss during spawning season. Their results from the 10 m depth sampling location at Sunnyside in 1982 were chosen for calculating size-specific fecundity employed here. This choice is based on a separate study (MacDonald and Thompson 1988) comparing sea scallops from this study site with samples from the open sea off New Jersey and from inshore populations at St. Andrews, New Brunswick and Sunnyside 30 m depth. This comparison showed that energy allocation in the 1982 Sunnyside population at 10 m depth, and in particular, energy of reproduction (gonad weight loss during spawning) as a function of age is about average among the sites studied. The New Jersey scallops, situated where temperatures are considerably warmer, are a bit more fecund and those at Sunnyside 30 m considerably less so.

Spawned biomass as a function of shell height, the relationship originally measured in their field study, was obtained from their published curves of gamete energy production as a function of age. Age was converted back to shell height, and energy converted back to grams of spawned gonad biomass, using the relationships,

$$HT = 176.5 \{ 1 - \exp[-0.19 * (AGE - 0.55)] \},$$

and

$$1 \text{ dry-weight g of eggs} = 26 \text{ kJoules},$$

provided by MacDonald and Thompson (1985a, 1985b).

Finally, total eggs per female (Table 1.3) was estimated from gonad weight change during spawning season using the conversions

$$1 \text{ egg} = 1.6 \times 10^{-7} \text{ g wet weight},$$

and

$$4.0 \text{ g wet weight} = 1.0 \text{ g dry weight}$$

derived by assuming, (Langton et al. 1987), that eggs are spherical, neutrally buoyant and 67 micrometers in diameter.

Further evidence that the fecundity at size from the 10 m depth 1982 Sunnyside population is representative is obtained by comparison to the same measurements of Langton et al. (1987) from the Gulf of Maine graphed in Figure 1.2. They agree particularly closely at sizes below 120 mm, a size range which encompasses the majority of scallops in

Table 1.3. Estimated eggs per female from MacDonald and Thompson (1985b) for an inshore Newfoundland population, measured as the average difference in gonad weight before and after spawning. Numbers of eggs in the third column are rescaled values of the estimated weights of spawned gonad biomass shown in the second column.

Shell height size class (mm)	Estimated gonad weight change per female (g dry-wt)	Estimated eggs per female (millions)
0-45	0.0	0
45-50	0.1	2.50
50-55	0.18	4.50
55-60	0.26	6.50
60-65	0.33	8.25
65-70	0.43	10.75
70-75	0.54	13.50
75-80	0.69	17.25
80-85	0.87	21.75
85-90	1.09	27.25
90-95	1.37	34.25
95-100	1.7	42.50
100-105	2.09	52.25
105-110	2.54	63.50

Table 1.3 (continued):

110-115	3.06	76.44
115-120	3.65	91.24
120-125	4.33	108.40
125-130	5.09	127.24
130-135	5.95	148.72
135-140	6.91	172.72
140-145	7.99	199.76
145-150	9.19	229.76
150-155	10.53	263.24
155-160	12.03	300.76
160-165	13.71	342.76

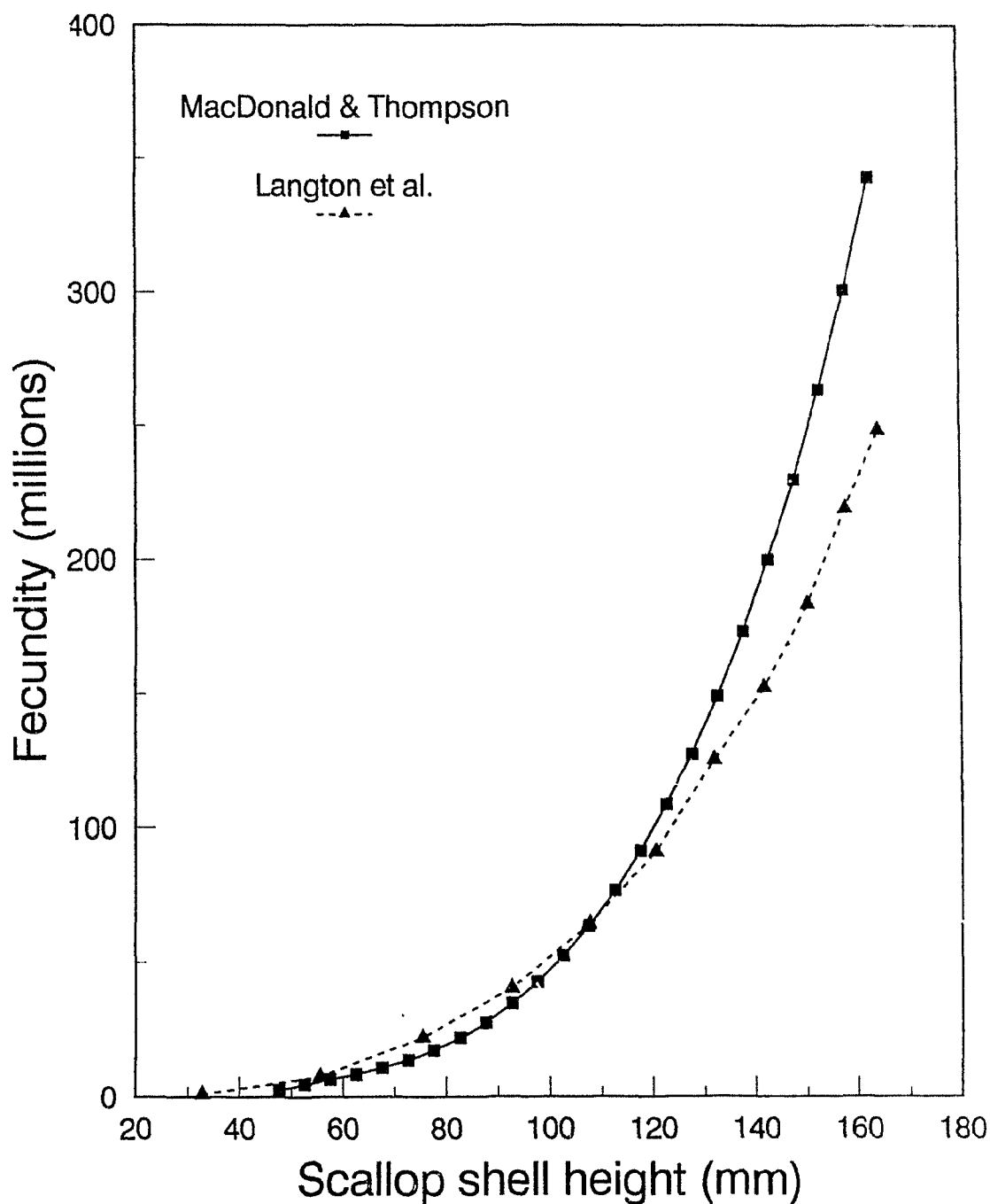


Figure 1.2. Average numbers of eggs per female released in annual spawning as a function of size. The fecundities of MacDonald and Thompson (1985b), used in this study, from the 1982 Sunnyside 10 m depth sampling location, and the same measurements of Langton et al. (1987) for an inshore Maine population.

this heavily fished population, as illustrated in Figure 1.3 below.

Multiplying numbers of eggs produced by an average female of a given size, HT, times the population density at that size, and summing over all possible egg producing size classes, yields an estimate of the average yearly egg production per m² for each region (Table 1.4):

$$\overline{\text{EGGS}} = \frac{1}{12} \sum_{\text{YR}=1977}^{1988} \left[\sum_{\text{HT}=40}^{170 \text{ mm}} \alpha * \text{NPT}(\text{YR}, \text{HT}) / 2 * \text{EGGS}(\text{HT}) \right]$$

The factor of 1/2 inside the sum expresses the observed 1:1 male:female ratio (MacKenzie et al. 1978).

Multiplying $\overline{\text{EGGS}}$ by the area of Georges Bank yields the integrated total under the solid black line of Figure 1.3a, the size-specific total egg production of the Georges Bank population. The peak in this curve at 95-100 mm occurs where scallops, mostly of age 4, are still abundant and egg production is becoming substantial.

Table 1.4. Egg production by female scallops, multiplying the survey data by eggs per female at size and averaging over the years 1977 to 1988.

Region	Egg Production	
	Total	Density
	(10^{15} eggs)	(millions of eggs per m^2)
Northern Edge	8.10	5.49
Northeast Peak	36.60	3.35
Southeast Part	3.19	0.51
South Channel (Eastern half)	2.90	0.76
South Channel (Western half)	7.56	0.61
Northern Edge & Northeast Peak (combined)	45.75	2.68
Georges Bank (total)	55.95	1.41

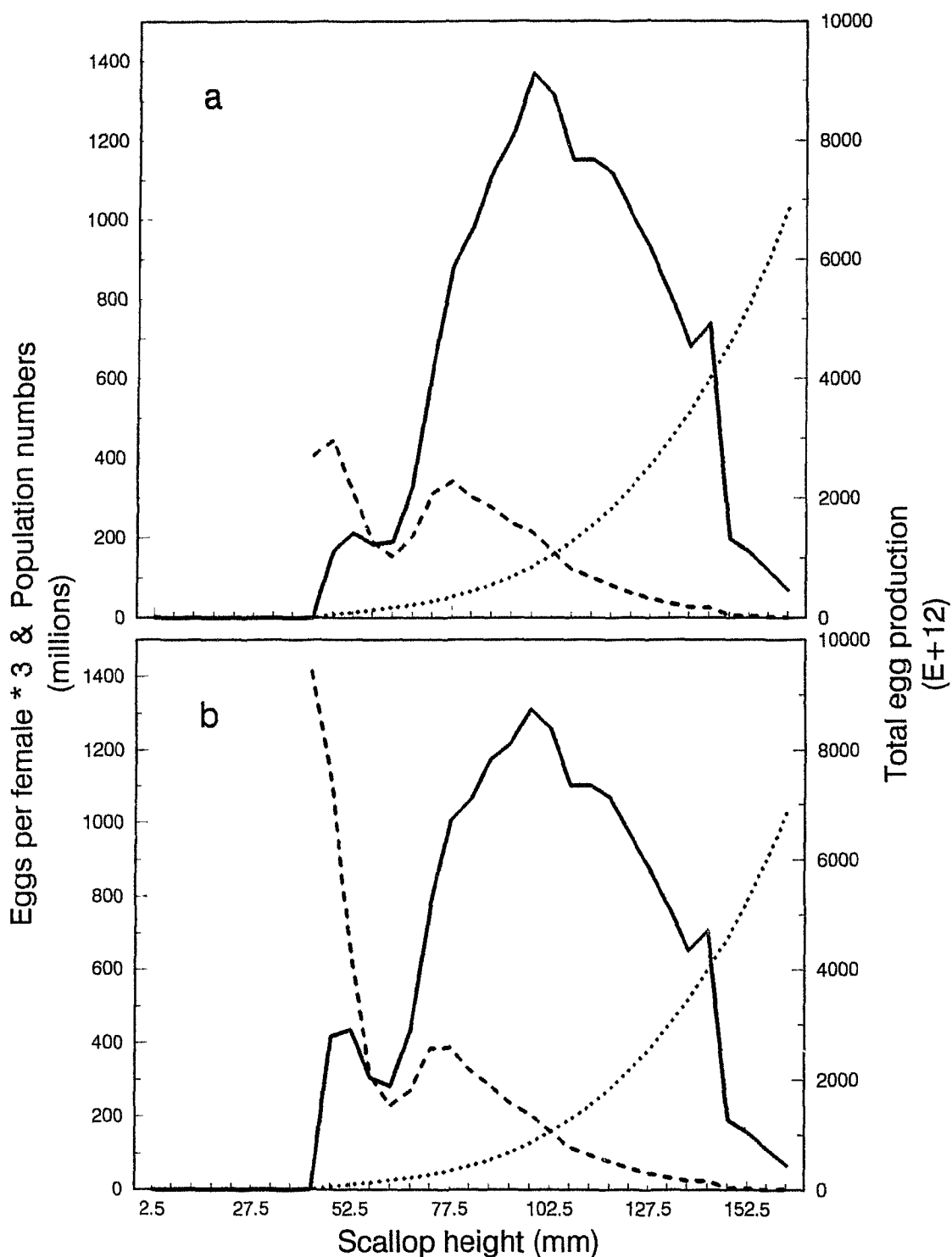


Figure 1.3. Eggs-per-female (dotted), total population numbers (dashed), and their product, the total numbers of eggs produced (solid), by the Georges Bank scallop population in each size class. Figure 1.3b presents the same quantities but with population numbers at smaller sizes adjusted to compensate for lower survey gear selectivity.

Gear Selectivity

The greatest source of uncertainty is the dredge capture efficiency which varies with scallop size, bottom type, scallop energy levels and drag speed (Dickie 1955, Bourne 1965, Caddy 1971, Smolowitz and Serchuk 1988, Robert and Lundy 1989). The problem is particularly acute for recruits. Around 20 mm, below the age 2 year-class peak, scallops are too small to be harvested by the survey drag.

The extent of the bias introduced by survey gear selectivity is evaluated here, based on the work of Dickie (1955). By tagging scallops and distributing them randomly on a Digby fishing ground of fixed area, Dickie estimated selectivity and absolute efficiency for both commercial and survey gear. (Although the commercial ring in the Digby fishery is smaller, at 2 5/8" compared with the standard 3" ring size of the offshore Georges Bank fishery, the survey mesh investigated by Dickie, of interest to us here, is the same at 1 1/2".) We choose a gear selectivity (capture efficiency at size) vector, $\{GS(HT)\}$ which is likely, on the basis of the studies of Dickie, and of Caddy (1971), to overestimate the lower capture rate at smaller sizes (Figure 1.4). Explicitly taking gear selectivity into consideration, survey numbers for all of Georges Bank are rescaled upward at smaller sizes. A new value of α , incorporating the re-estimated D_{npt} was then substituted to

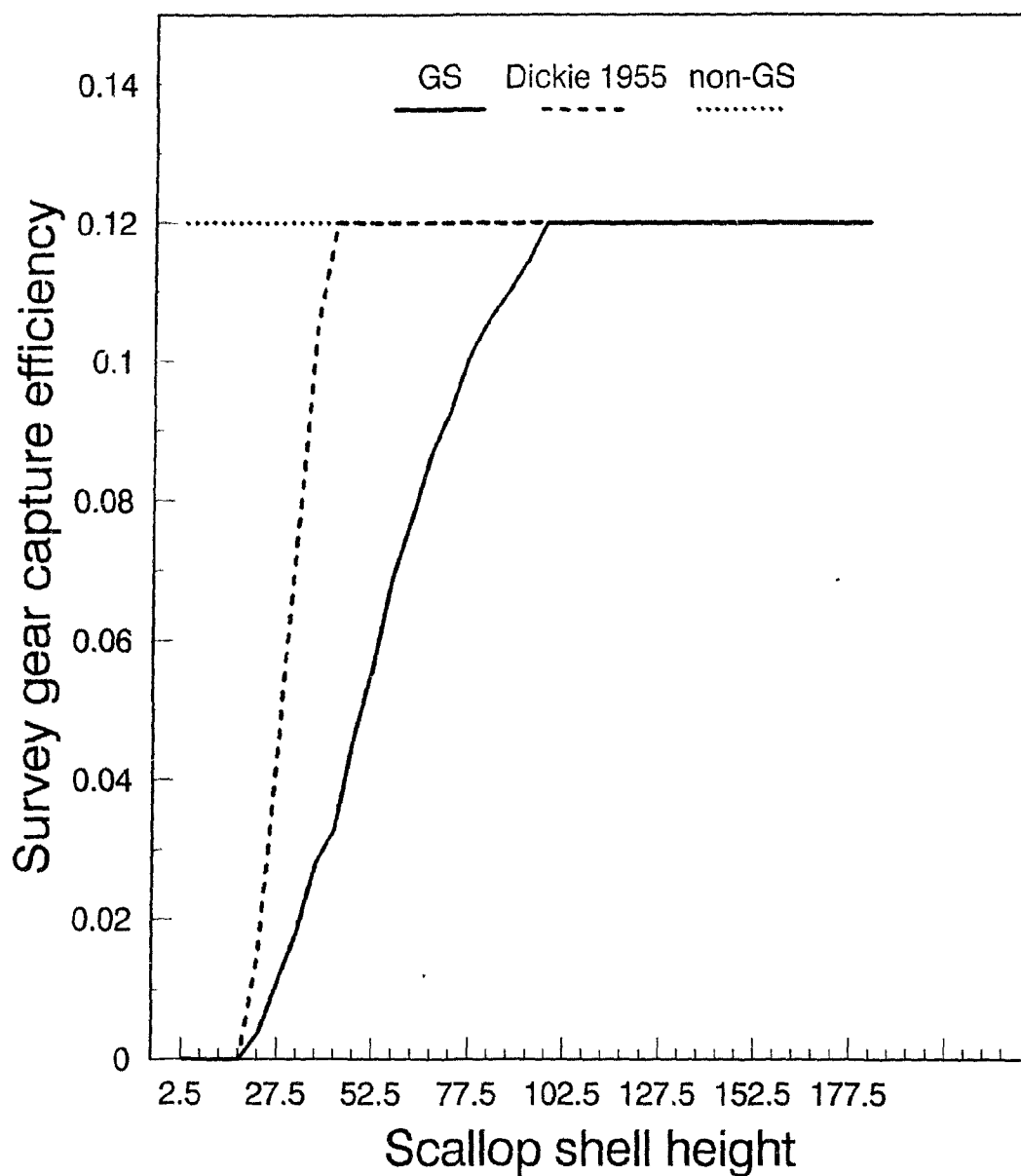


Figure 1.4. Gear selectivity-at-size derived from Dickie (1955) (dashed), intermediate between the uniform capture efficiency implicit when gear selectivity is not considered (dotted), and the gear selectivity curve, $\{GS(HT)\}$, employed here in analysing sensitivity to this source of error (solid).

recalculate $\overline{\text{BIOMASS}}$, $\overline{\text{POPULATION}}$, $\overline{\text{RECRUITS}}$ and $\overline{\text{EGGS}}$.

By comparing the two estimates obtained, with and without {GS(HT)}, we obtain a measure of the sensitivity of each of the 4 population statistics to gear selectivity. Since {GS(HT)} probably overcompensates, the best estimate of these population statistics probably lie between the GS and unadjusted non-GS values are therefore taken as upper and lower limits of uncertainty due to this source of error.

For the 3 adult population variables, namely biomass, 80+ mm population numbers, and egg production, the effect of gear selectivity is small, and may be taken as an additional (not necessarily independent) source of error in the calculation of overall confidence intervals below. For Georges Bank overall, incorporating the effect of gear selectivity yields an estimate of biomass that is 10.0% higher; egg production is 4.5% higher and adult population numbers are unchanged. Because the direction of error in each case is well defined, these uncertainties will be included in the upper confidence intervals for each adult population statistic.

Because recruits are just above the size where lower capture rate becomes important, the estimates of recruit numbers with and without GS differ by a factor of about 3.6, a very substantial difference. By subregion, the factors of increase are as follows: Northern Edge, 3.46; Northeast Peak, 3.7; Southeast Part, 3.27; Eastern South Channel,

3.31; Western South Channel, 3.37; Georges Bank overall, 3.59; Northern Edge and Northeast Peak combined, 3.62). We may take the unadjusted estimates (unbracketed values in Tables 1.1 and 1.2) as lower limits, and the values roughly 3.6 times larger as the upper limits of confidence for recruitment. Taken as halfway between upper and lower limits in each region, roughly 2.3 times the unadjusted lower value, the best estimates for recruitment are listed in brackets in Tables 1.1 and 1.2.

Confidence Intervals

The effect of a constant bias (uniform with respect to scallop size) in the survey data was tested by multiplying the raw mean numbers per tow by factors of 0.9 and 1.1 and then recalculating all 4 population statistics for Georges Bank overall. The results were identical with the unaltered estimates. A size-independent error in the data will, therefore, have no effect on the final outcome. The reason is evident in the full formula for any of these statistics. Taking, for example, EGGS, any such error factor will appear in the numerator, inside $NPT(YR, HT)$, and likewise in the demoninator of alpha, inside D_{npt} , and will therefore cancel. Absolute population and density is

rescaled using total catch and this explains why size-uniform error in the survey data do not affect the final population estimates.

However, two important sources of uncertainty remain, survey gear selectivity and alpha. We cannot presume that these two sources of error are independent since commercial gear selectivity is significant also and may generate bias which has a positive covariance with survey gear selectivity. For the three adult population statistics, we therefore employ the formula for the combined errors of these two sources which make no assumptions of independence.

The errors of +23% and -8% derived for alpha in Apper ix 1.1, apply specifically to the errors in non-survey data factors in alpha, and so may be factored out of the double summations in equations which define the 4 population statistics. To calculate the combined errors due to alpha and due to gear selectivity, since alpha is a simple multiplicative factor, the combined fractional error (i.e. coefficient of variation) in the case of non-independence is simply the sum of the fractional errors (Taylor 1982 p. 178).

The resulting confidence intervals are, for BIOMASS, (+33%,-18%); for POPULATION, (+23%,-8%); and for EGGS, (+27.5%,-12.5%).

Since the commercial and survey gear selectivity act at different scallop size ranges (<~40 mm versus <~80 mm), and

since most of the error in α is not due to gear selectivity, this covariance is probably small, so the resulting confidence intervals for these population statistics are wider than need be, to that extent.

The additional source of uncertainty, in EGGS and BIOMASS, due to uncertainty in the eggs-per-female-at-height and meat-weight-at-height vectors respectively, is small compared to the two principal sources of error described above, especially at the truncated size ranges typical of this heavily exploited population, and can therefore be neglected (Taylor 1982).

Likewise, for recruitment, gear selectivity predominates and uncertainty in α , ten times smaller, may be neglected. The confidence intervals for recruitment are therefore described in the section above. Gear selectivity, at recruitment size classes, remains the greatest source of error in the scallop surveys.

Although size-uniform error will cancel, we will accept these populations estimates more confidently if the data are shown to be reliable. The accuracy and precision of the raw mean number per tow data are evaluated in Appendix 1.2, based on published analyses. 95% confidence intervals are estimated from 3 to 20% for all population variables from the Northern Edge and Northeast Peak in three years when independent coincident surveys were carried out by the US and Canada.

Early Life History Natural Mortality

Tremblay (1991) and Tremblay and Sinclair (1990) measured larval density at locations crossing the Northern Edge and Northeast Peak with pump and bongo sampling at various depths. Timing their cruises with annual spawning, they observed peak densities of 500-2000 scallops per m^3 the first week of October, most concentrated above or at the pycnocline around 30 m depth. These closely match observations (Ventilla 1982) of 1200 per m^3 for maximum larval density of a closely related species, Japanese scallop (Patinopecten yessoensis), but are roughly a full order of magnitude greater than the Placopecten larval densities reported for the Bay of Fundy (Tremblay and Sinclair 1988). Depth-integrating bongo larval densities, and averaging across all sample sites on the Northeast Peak during the week of peak larval density, Tremblay (1991 Table 3.4) reports mean densities of 20,000 in 1986 and 16,800 in 1987, yielding an average of 18,400 per m^2 . We that assume the fraction of total larvae present in the water column at the time of peak sampling represents half of the total spawned \pm 0.25. Wide dispersal of larvae which do survive is unlikely due to currents which retain them above the Bank. The measurements of Tremblay (1991) in regions outside of these peak regions of abundance, are 1 to 4 orders of magnitude lower, confirming this assumption that

most of the larvae spawned are still above the Bank at the time of sampling. A similar synchrony of spawning, in time, is evident in the significant reductions in larval abundance, factors of 3-5, in these regions one week later.

Employing estimates of egg production and recruitment density obtained above, the survival, L , of "potential egg" to larva in the most productive waters above the Northern Edge and Northeast Peak is therefore:

$$\begin{aligned} L(\text{egg to larva}) &= (36,800 \text{ m}^{-2}) / (2.68 \times 10^6 \text{ m}^{-2}) \\ &= 0.014 \pm 0.010. \end{aligned}$$

The survival probability from larva to age 2 recruit is

$$\begin{aligned} L(\text{larva to age 2}) &= (.7 \text{ m}^{-2}) / (36,800 \text{ m}^{-2}) \\ &= 1.9 \times 10^{-5} \pm 1.77 \times 10^{-5}. \end{aligned}$$

This assumes that larvae found in dense concentrations above the Northeast Peak represent eggs that originated in the combined area of the Northeast Peak and the Northern Edge, and which successfully settle largely in that region, which is likely based on stock-recruitment evidence presented in

Chapter 2 and the much lower levels of population abundance in neighboring areas.

Expecting only an order of magnitude level of precision, we may break down mortality into the stage from egg to larva, M_{E-L} , and the subsequent development from larva to age 2 juvenile, M_{L-2} . Assuming that the larvae sampled by Tremblay and Sinclair averaged 17 \pm 5 days old, and that the 2-year-recruits were 700 days old (because the survey cruises were held in August and peak spawning occurs in mid-September on Georges Bank (M.J. Tremblay, Halifax Fisheries Laboratory, Canadian Dept. of Fisheries and Oceans, P.O. Box 550, Halifax, Nova Scotia, pers. comm.)), we obtain daily mortality rates for these two stages of scallop development. Applying the definition of natural mortality, supposing it is fixed during each stage,

$$N_L = N_E \exp(-M_{E-L} * 20),$$

and

$$N_2 = N_L \exp(-M_{L-2} * 683),$$

implies

$$M_{E-L} = 0.25 \pm 0.09 \text{ day}^{-1}$$

and

$$M_{L-2} = 0.016 \pm 0.0014 \text{ day}^{-1}.$$

The confidence intervals are calculated assuming independence in uncertainties of the independent variables, namely larval counts, egg production or recruitment estimates, average age of sampled larvae, and fractions of the total present during the week of peak larval abundance. The relatively narrow confidence intervals result because, due to the exponential, small changes in M correct for large variations in initial and final abundance.

Discussion

Estimated average density for Georges Bank (excluding the shallow central region excluded by the survey at depths less than 50 m where scallops are rare), is 4 scallops per 100 m² (Table 1.2). Densities are four times higher on the Northern Edge and, in the Southeast Part, one fourth the average.

These values may be compared with direct field observations of adult bottom density. Scallops are generally found in beds, discrete aggregations of 0.1 to 1-5 per m² (MacDonald and Thompson 1986b, Naidu 1969, Caddy 1968, Caddy 1970, Dickie 1955). Survey trawls encounter these high densities sporadically. An overall survey density 1 to 2 orders of magnitude less than a typical unfished bed is, therefore, reasonable.

The estimates of total yearly egg production (Table 1.4) range from 5.5 million per m² on the Northern Edge to one-tenth of that in the least populated regions, the Southeast Part and South Channel. Egg production is slightly higher in the eastern half of the South Channel, even though scallops are more numerous in the western half. The eastern half is fished less intensively, so scallops survive to a slightly older age and older scallops produce far more eggs per female.

One fact suggests that the uncertainty in recruitment, due to gear selectivity, is much less dramatic and more limited in extent than suggested by the huge confidence intervals calculated. The comparison presented in Appendix 1.2 of survey numbers per tow by independent US and Canadian surveys (Serchuk and Wigley 1986b, Mohn et al. 1987), shows that, on average, the survey measures of recruitment yield 3 times closer agreement, and are, by that measure, 3 times more accurate than adult population variables. Since gear selectivity primarily affects recruitment sizes only, this suggests that gear selectivity does not cause each yearly relative measure of recruitment to be of lower reliability. This higher accuracy of relative recruitment numbers (due, most likely, to the larger sample sizes), applies to the yearly recruitment time series analyzed in Chapter 2, where implicitly only the relative value of recruitment from year to year is considered.

MacDonald and Thompson (1985b) measured only the average change in gonad weight of scallops during spawning. It is then assumed that all of this gonad weight loss represents spawned eggs. Since many of those eggs may not be viable and many viable ones may not get fertilized, Table 1.4 represents maximum average egg production. Bearing this in mind, for Georges Bank as a whole, the total number of eggs produced (Table 1.4) divided by the best (gear-

selectivity considered) estimate of total recruits yields a survival rate from "potential" egg to age 2,

$$L(\text{egg to age 2}) = 2.5 \times 10^{-7},$$

of two in ten million. For a steady state population, the reciprocal of this quantity is equal to the total lifetime egg production of an average female.

Appendix 1.1. Scaling Survey Numbers to Density

The calculation of the scaling coefficient, α , which transforms the (relative) survey measure of abundance, numbers per tow, into absolute numbers per m^2 , proceeded as follows:

The commercial time series (Mohn et al. 1989, New England Fishery Management Council 1982) of annual catch for all of Georges Bank, was averaged over the years 1977-1988 for which survey data are available, yielding:

$$\overline{CA}_{mt} = 11635 \text{ mt.}$$

From catch in metric tons, the total number of harvested scallops is derived using knowledge of the meat-count restrictions limiting average harvest size in this fishery. Since 1986, a limit of 33 meats (i.e. scallops) per 500 g was instituted (Robert and Black 1990). Analysis of the Canadian commercial catch-at-size data during these years (Mohn et al. 1989) suggests that this limits harvested scallops to be roughly 80 mm or greater. Assuming 33 scallops per 500 g of harvested biomass, the number of scallops captured in an average year was

$$\overline{CA}_{\#}'_S = 768,500,000.$$

Employing the value, $\overline{F} = 0.8$ (Mohn et al. 1989, New England Fishery Management Council 1981), the average size, N , of the Georges Bank scallop population can be estimated. Given

$$\overline{CA}_{\#}'_S = \overline{N} \exp(-\overline{F}),$$

$$\overline{N} = 1.71 \times 10^9 \text{ scallops,}$$

of size 80 mm and greater.

We define a constant, alpha, which rescales the survey density, expressed as number per tow, D_{npt} , into units of scallops per m^2 , D_{m2} :

$$\overline{D}_{m2} = \alpha * \overline{D}_{npt}.$$

Total population equals density times area:

$$\bar{N} = \bar{D}_m^2 * \text{AREA},$$

yielding the formula for alpha in terms of the two population averages,

$$\alpha = \bar{N} / (\bar{D}_{npt} * \text{AREA}).$$

The area of Georges Bank (excluding the shallow central region not included in this study), is

$$\text{AREA} = 39643 \times 10^6 \text{ m}^2.$$

And the average number per tow, \bar{D}_{npt} , for scallops 80 mm and greater, calculated directly from the survey data,

$$\bar{D}_{npt} = \frac{1}{12} \sum_{YR=1977}^{1988} \left[\sum_{HT=80}^{185 \text{ mm}} \text{NPT}(YR, HT) \right]$$

is found to be

$$\bar{D}_{npt} = 64.7,$$

yielding

$$\alpha = 0.0006663.$$

If we make the further, roughly correct assumption that the surveys measure all scallops of sizes 80 mm and above with equal likelihood, multiplying alpha by survey numbers per tow yields the numbers of scallops in each size class, in each year (and in each subregion) in units of individuals per m². In other words, in calculating the egg production, biomass, and population densities, we are supposing that the parameter, alpha, defined by the expression,

$$N = \alpha * \left[\begin{array}{cc} 1988 & 60 \text{ mm} \\ \hline 1 & \sum \\ 12 & \sum \\ \hline YR=1977 & HT=30 \end{array} \right] NPT(YR, HT) * AREA$$

is indeed a constant, so that it may safely be moved inside the summation signs and be employed as:

$$\bar{N} = \frac{1}{12} \sum_{YR=1977}^{1988} \left[\sum_{HT=80}^{185 \text{ mm}} \alpha * NPT(YR, HT) \right] * AREA.$$

Summarizing, the formula for alpha is

$$\alpha = \frac{\bar{CA}_{mt} * \bar{MPT} * \exp(\bar{F})}{\bar{D}_{npt} * AREA}$$

The error in alpha will be due to these 5 input variables.

1. The uncertainty in AREA is negligible.
2. Error in the raw data themselves, in \bar{D}_{npt} , the sum of mean numbers per tow above 80 mm, is predominantly due to gear selectivity and is considered and factored into the overall confidence limits above.

The error in alpha is due to the errors in the three remaining input variables, total average catch in metric tons, \bar{CA}_{mt} , the average number of scallops per ton of meat weight harvested, \bar{MPT} and the average fishing mortality, \bar{F} .

3. Because catch restrictions played no role in the US

fishing at all and in the Canadian fisheries only recently and is still not a significant management constraint, reported catch is likely to be reliable. We may postulate an upper limit of 5% on unreported catch. There is no significant probability that reported catch is an overestimate.

4. 33 meats per half kilo came fully into effect in 1986 (Mohn et al. 1989) and the harvest included more smaller scallops in earlier years. Again, we take our estimate as a lower bound and, based on reported average sizes in earlier years (Serchuk 1984, Robert and Black 1990), choose 40 meats per half kilo as the upper limit for the average over 1977-1988.

5. Average fishing mortality, F , was calculated from the yearly values of F -at-age obtained by Robert and Black (1990) employing cohort analysis. Weighting the F -at-ages by catch-at-age (Robert and Black 1990), and averaging these yearly means over 1977-1988, yields a value of 0.78, with a standard error of 0.05. Rounding, we set $F = 0.8$, and choosing confidence intervals on the safe side, set the uncertainty as ± 0.1 .

Since the information sources for these three input variable estimates are different, the errors are independent. Applying the standard theory of error propagation, I applied the formula for the error of alpha in terms of its formula and the uncertainties of the input

quantities (Taylor 1982 p. 177). The result is an upper limit of 23% of the value of alpha itself. The lower bound of uncertainty is smaller, at 8%.

Appendix 1.2. Survey Data Accuracy and Precision

Two previous assessments of variance of the scallop survey data have been undertaken (Serchuk and Wigley 1986b, Mohn et al. 1987), analyzing and comparing US and Canadian mean number per tow on the Northern Edge and Northeast Peak, which comprises 80% of the Georges Bank population.

Serchuk and Wigley specifically consider the years 1982, 1983 and 1984 when both US and Canadian surveys were undertaken in this subregion. Correcting for small differences in sampling procedure (the US towing a survey dredge for 15 minutes at 3.5 knots, and the Canadians towing identical gear for 10 minutes at 4.0 knots) by standardizing to equivalent distances towed, Serchuk and Wigley found good agreement between the two surveys, both in total and size-specific number per tow (Serchuk and Wigley 1986b, Fig. 6). The Canadian survey in this area (which lies in Canadian territorial waters), set 2 to 3 times as many sample tows overall.

The two surveys primarily differ in stratification scheme. The US survey employs simple random sampling in each stratum (Cochran 1977) while tow locations in the Canadian survey are directed towards areas of higher catch as reported by the Canadian commercial fishery (Robert and Jamieson 1986, Mohn et al. 1987) and on this basis the sampling strata are redrawn yearly. Mohn et al. (1987) find

no significant advantage accruing to either stratification design, comparing their relative variance improvements on a simple unstratified mean number per tow.

The published results of Serchuk and Wigley (1986b) allow direct calculation of standard errors of these surveys by two different methods.

The first method is to apply the standard theory of stratified sampling (Cochran 1977) and calculate the standard error for the whole region, based on the standard deviations of the samples (i.e. tows) within each stratum, weighted by their relative areas (Serchuk and Wigley 1986b). The results for 1982, 1983 and 1984 are presented in the first two columns of Table 1.2.1.

The second method is to consider US and Canadian survey estimates of mean number per tow as independent samples of the same mean, a sample size of two. By this method, the standard error of the means is simply the standard deviation of this small sample of means, i.e. for each year and for each of three size categories,

$$SE = \sqrt{\frac{[\overline{US} - (\overline{US} + \overline{CAN})/2]^2 + [\overline{CAN} - (\overline{US} + \overline{CAN})/2]^2}{2 - 1}}$$

The 95% confidence intervals, expressed as a percentage of the mean, are presented in Table 1.2.2, and the last

Table 1.2.1. 95% confidence intervals (CI) of total mean numbers per tow, calculated from Serchuk and Wigley (1986b) by two methods, expressed as percentages above and below the mean.

Year	Calculated from sample variance		Calculated from standard deviation of US and Canadian means
	US	Canada	
1982	± 36.8	± 22.9	± 9.1
1983	± 45.5	± 17.1	± 40.9
1984	± 62.3	± 28.8	± 6.9
3-year mean	± 40.2	± 17.8	± 9.3
12-year mean	± 20.1	± 8.9	± 4.6

$$CI = 1.96 * SE * 100 / [(\overline{US} + \overline{CAN})/2]$$

column of Table 1.2.1.

The confidence intervals of the 3-year means in both tables are calculated by considering the samples from each year to be independent random variables:

$$SE3 = \frac{1}{3} \sqrt{\sum_{YR=1982}^{1984} [SE(YR)]^2}$$

The estimates of confidence interval for the full 12-year time averages are obtained by assuming the 3-year means and their standard errors are simply repeated 3 additional times:

$$SE12 = \frac{1}{4} \sqrt{4 * SE3^2} = \frac{SE3}{\sqrt{4}} = \frac{SE3}{2} .$$

95% confidence intervals are calculated for 7 population statistics, the 7 columns of Tables 1.2.1 and 1.2.2. In

fact, there are just 5 distinct population variables, since the three columns of Table 1.2.2 are independent estimates for mean number per tow summed over all sizes once from each survey and thirdly from their difference, which serves as an independent measure of standard error and thus confidence interval, allowing a direct comparison of the two methods (Table 1.2.1). The lower standard errors for the Canadian compared with US surveys during these years reflect the greater sample size, which is the number of tows per stratum. Overall, the confidence intervals for 12-year averages lie in the range of 5-20%. The close agreement of US and Canadian means for the four population variables of Table 1.2.2, ranging from 3 to 9%, was better than expected based on the standard deviations of the samples (Table 1.2.1). The opportunity to compare independent simultaneous sample estimates of the same fishstock is rare, and such close mutual verification (for these 3 years) adds considerably to the reliability of these data.

The four statistics in Table 1.2.2, are not defined identically by Serchuk and Wigley (1986b) to the population variables estimated in Methods and Results (listed for convenience in the bottom row). However, the time series of the two forms of each statistic are, in general, very close. As quantified by their correlation over the 12 years 1977 to

Table 1.2.2. 95% confidence intervals (CI) of the mean numbers per tow, derived from Serchuk and Wigley (1986b), calculated from the means of the two independent surveys, expressed as percentages above and below the mean. The associated population variables are indicated below.

Year	Mean number per tow		Mean meat weight per tow	
	< 70 mm	>= 70 mm	>= 70 mm	Total (All sizes)
1982	± 17.4	± 4.3	± 12.4	± 11.0
1983	± 27.1	± 57.2	± 40.5	± 40.4
1984	± 4.75	± 19.2	± 38.0	± 18.3
3-year mean	± 5.8	± 18.0	± 17.5	± 14.3
12-year mean	± 2.9	± 9.0	± 8.7	± 7.2
	RECRUITS	POPULATION	EGGS	BIOMASS

1988, RECRUITS and number per tow < 70 mm ($r=.961$, $P=4 \times 10^{-7}$, $df=10$), BIOMASS and meat weight per tow total ($r=.997$, $P=6 \times 10^{-8}$, $df=10$), and thirdly, EGGS and meat weight per tow ≥ 70 mm, are virtually identical time series, differing by a constant, while yearly adult POPULATION differs slightly from numbers per tow ≥ 70 mm ($r=.846$, $P=3 \times 10^{-4}$, $df=10$). Moreover, it is not the yearly means, but the uncertainty of the average of the 12 means which are being estimated. Because the variances, and therefore surely the standard errors are likely to differ considerably less than the time series of the means, it must be very safe to conclude that the confidence intervals for the population variables defined in the main body of this chapter are well estimated by the confidence intervals of Tables 1.2.1 and 1.2.2.

One possible bias in this analysis is that it considers only the years where a comparison was possible between US and Canadian fisheries research surveys of the Georges Bank scallop stock, namely 1982 to 1984. These were years of relatively low fishstock abundance. The general pattern, however, is towards higher precision when abundance was higher. This is evident spatially in comparing the means and coefficients of variation in different strata (Serchuk and Wigley 1986b, Table 4). It is also expressed temporally in the 3 years analyzed (Serchuk and Wigley 1986b, Table 3) insofar as the closest agreement for < 70 mm (1982), and ≥ 70 mm (1984) number per tow occurred in their respective

years of highest abundance (Table 1.2.2), which may suggest that the 12 year averages reported in Methods and Results are more precise than estimated here.

Overall, recruitment was not particularly low in these 3 years, the age 2 recruitment peak of 1984 being the second largest between 1977 and 1988. This could, in fact, explain the closer agreement (3%) between US and Canadian < 70 mm number per tow counts compared with the other 3 statistics of Table 1.2.2.

Generally I conclude that for all of these estimates a fair measure of their uncertainty is plus or minus 20%, which represents the largest uncertainty among the 3 estimates for overall number per tow in Table 1.2.1, namely from the US survey. If the relatively close agreement between US and Canadian means is not coincidence, and if greater abundance does yield lower uncertainty, then the actual precision is better than the sample variances suggest, at 3-9%.

CHAPTER 2

POPULATION REPRODUCTION

Introduction

In recent years much has been learned about the reproductive biology of the sea scallop. Placopecten spawn yearly, in late summer and early fall (Beninger 1987, Robinson et al. 1981, Naidu 1970) when females produce up to 200 million eggs each. Fecundity increases allometrically with the age of the female (MacDonald and Thompson 1985a, 1985b, Langton et al. 1987) and varies from year to year about twofold due to changing conditions in the water column, particularly phytoplankton food supply, water temperature, or both (MacDonald and Thompson 1986a, 1986b, 1988, MacDonald et al. 1987, Shumway et al. 1987, Barber et al. 1988). Eggs hatch into free-floating zooplanktonic larvae that feed on phytoplankton, which remains the primary food source for Placopecten throughout its adult life. After three to six weeks (Culliney 1974), the larvae settle on the bottom. Scallop populations consistently favor three specific regions of Georges Bank (Figure 1.1), namely the Northern Edge and Peak, the Southeast Part, and the Great South Channel (Sinclair et al. 1985).

The survival rate from egg to age two juvenile is very low, presently about two in 10 million as noted in Chapter 1. Predation, starvation in the water column, and settlement on uninhabitable bottom are all likely contributors to the high rate of egg to adult mortality.

If more eggs do tend to result in larger year classes, this would add additional strength to yield-per-recruit analyses which suggest that annual catches would be higher if scallops were harvested at a later age than at present (Sinclair et al. 1985, Serchuk et al. 1979). In addition, population reproduction is an important aspect of the dynamics of this fishery. Since about 1958, the Georges Bank scallop population has been characterized by a 16 year bust-boom cycle. The results presented here are incorporated in the Chapter 3 analysis of this cycle.

Sinclair et al. (1985) believed that a stock-recruitment relationship should exist. They further reasoned that throughout the Northwest Atlantic, and in particular in each of the three regions on Georges Bank, populations must be self-sustaining, because they are persistent over relatively long times. Tremblay and Sinclair (1988) concluded that larvae in the Bay of Fundy largely originate there, and that scallops are most densely settled where currents would be expected to carry them. On the Northern Edge and Northeast Peak, Tremblay and Sinclair (1990) found larval concentrations an order of magnitude more dense than in the Bay of Fundy, reasonable since adult populations are roughly that much greater.

Enzyme electrophoresis by Zouros and Gartner-Kepkay (1985) revealed no significant differences in genetic make-up among ten populations in coastal waters near Nova Scotia, including three on Georges Bank. Lack of genetic evidence

does not prove that these populations interact reproductively, since the correct genetic markers may not yet have been located which distinguish subpopulations. Of critical importance in this regard is the amount of time necessary for a neutral mutation to become fixed in a majority of individuals in a subpopulation, which is of the order of the mean age of reproduction times the population size. Since the physical oceanography of Georges Bank suggests that larvae are likely to settle in neighboring populations in most years, and since genetic divergence over a number of generations comparable to the size of the population (roughly a billion scallops) seems very unlikely, the result of Zouros and Gartner-Kepkay is not surprising.

Recent studies, summarized by Butman et al. (1987) and Butman and Beardsley (1987) confirm that the prevailing residual current on Georges Bank, driven by the diurnal tidal cycle (Greenberg 1983), is a clockwise gyre. The water above the Northern Edge sweeps onto the Northeast Peak, moves (at about 7 km/day) over the Southeast Part, then, part of this water flows northward through the Eastern South Channel and back over the Northern Edge.

Because of the strong circular pattern of flow on Georges Bank, an alternative hypothesis to reproductively distinct subpopulations (eggs/larvae/spat returning in the variable currents or scallops migrating back to their parents' bed) is that the entire Georges Bank is one largely self-sustaining population. This is investigated here by

analyzing the stock-recruitment relationships within each regional subpopulation and also between neighboring subregions particularly bearing in mind the clockwise direction of the gyre. Stock on the Northern Edge and Peak will be compared with recruits in the Southeast Part, stock from the Southeast Part with recruits in the Great South Channel, and stock in the Great South Channel compared with recruits in the Northern Edge. A stock-recruitment analysis for the aggregate Georges Bank scallop population is also presented. A third level of spatial subdivision treats the survey data from the Northern Edge separately from the Northeast Peak, and likewise for the regions to the east and west of the Great South Channel. Thus, altogether three spatial partitions of Georges Bank are drawn, containing one, three and five subdivisions respectively. Primary focus is directed towards the Northern Edge and Northeast Peak.

Two previous models described the spatial dynamics of recruitment on Georges Bank. Davis (1984) modelled the growth and reproduction of the copepod Pseudocalanus sp. and found strikingly good agreement with the observed development stages of this free-floating zooplankton population as it is carried on an annual migration by the clockwise gyre. The spatial model of Caddy (1975), specifically describing the scallop fishery, investigated the effect of fishing effort being primarily attracted to the dense concentrations of the Northern Edge.

Recruitment Model

The proposed model of recruitment assumes that three factors determine yearly recruitment at age 2:

- (1) total (fertilized) egg production, S ,
- (2) density-independent survival in the water column, L_{WC} , and
- (3) density dependent spatfall and survival to age 2, $L_{dd}(S)$.

The equation for recruitment in any given year of spawning, YR , is therefore

$$R2(YR+2) = S(YR) * L_{WC}(YR) * L_{dd}(S). \quad (1.1)$$

$R2(YR+2)$ = numbers of recruits (as determined by scientific survey) spawned in year YR , that reach age 2 in year $YR+2$.

This chapter investigates the hypothesis that the first factor is actually present in the available time series data, i.e. that recruit numbers are roughly correlated with the numbers of eggs spawned.

Fishery scientists are now quite familiar with the huge year-to-year variability in the second factor, $L_{WC}(YR)$, which often obscures any existing stock-recruitment relationship. This density-independent survival probability

(assuming negligible interaction among scallop larvae in the water column) is largely or entirely determined by the current. If an egg or larva drifts into regions of high predator or low phytoplankton density, either in the water column or at settlement, then it is far less likely to survive. There is strong tidal movement above Georges Bank, and yearly variation in the Labrador Current and Scotia Shelf waters which feed the gyre from the Gulf of Maine; warm core rings flow unpredictably off the Gulf Stream to the south (Halliwell and Mooers 1979). Currents also vary due to the 18.6 periodic variation of the tides (Currie 1981) and due to variation in the prevailing northwesterly winds that sometimes act more strongly than the gyre in determining the residual flow. Thus density-independent sources of mortality, determined by variable currents, explains much of the large yearly recruitment variability observed in many marine species on the Bank, including Placopecten.

Other evidence (Chapter 5) suggests that, in natural scallop populations, strong density-dependent limitations on recruitment can act in the post-settlement stage. During the years for which size-frequency data are available, 1977-1988, fishing has been intense. Because adult scallops are being removed at a rapid rate, density-dependent factors play a smaller role than they would in an unfished population. Assuming that fishing has pushed the densities well below the carrying capacity in most beds on Georges

Bank, we neglect density dependence in this chapter and seek only to discern a rough increasing relationship between $S(YR)$ and $R2(YR+2)$.

Data

As described in Chapter 1, at a several hundred sampling locations, a commercial scallop drag, fitted with a smaller mesh liner, is towed along the bottom for 15 minutes at 4 km/hr. Each yearly survey yields a sample of some 50,000 scallops, which are measured for shell height and counted. The numbers in each size class of 0-5 mm, 5-10 mm, 10-15 mm, etc., at each sampling location are recorded.

The height-frequencies for all of Georges Bank (Figure 2.1) serve as the basis of this stock-recruitment analysis. Height-frequency distributions were also generated for the Northern Edge and Peak, Southeast Part and Great South Channel and the five subregions.

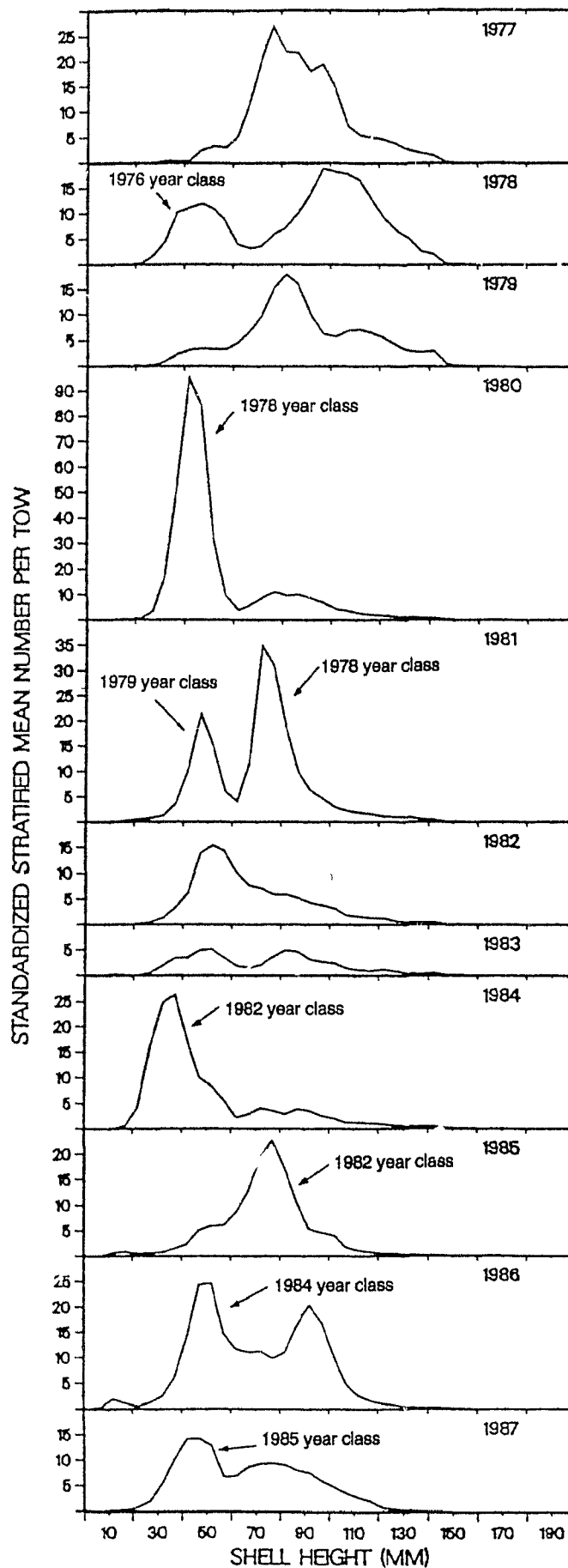


Figure 2.1.
Survey
height-
frequency
distributions
for Georges
Bank
scallops,
1977-1987.

Methods

Time series of parent stock (i.e. total egg production), $\{S(YR)\}$, and recruitment to age 2, $\{R2(YR)\}$, are constructed from the height-frequency data for the years 1977 to 1988. Lagging back two years, the identical recruitment time series,

$$R(YR) = R2(YR+2),$$

$YR = 1975-1986$, identifies recruits by the year they were spawned, rather than the year they reached age 2, $YR+2$.

Once derived, $\{R(YR)\}$ is compared with $\{S(YR)\}$ within or between regions to assess the likelihood they are correlated.

Since the surveys measure scallop density, we obtain a relative (i.e. unscaled or non-absolute) time series of total egg production using the relation

$$S(YR) = \sum_{HT=40 \text{ mm}}^{185 \text{ mm}} NPT(YR, HT) * EGGS(HT).$$

similar year to year bias. The correlations of recruitment between subregions provide a measure, in addition to stock-recruitment, of how closely these subpopulations are dynamically linked, specifically, how much variation in recruitment is driven purely by the environment and how much by egg production.

If there is no correlation between egg production in region X and recruitment in the nearest downstream neighbor, region Y, then we can conclude nothing about egg and larval transport. Even if, from year to year, the vast majority of larvae from region X do settle in region Y, there may be no evident stock-recruitment relationship because environmental variability obscures this correlation in many marine populations. On the other hand, the stronger the correlation between stock and recruitment, the more likely that egg transport from region X is repopulating region Y.

All calculations were programmed in FORTRAN 5 and performed on a VAX 8800 mainframe.

Parent Stock Egg Viability: Variation with Age

A new measure of parent stock was constructed which does not include eggs produced by scallops of size 90 mm or less:

$$S4+(YR) = \sum_{HT=90 \text{ mm}}^{185 \text{ mm}} NPT(YR, HT) * EGGS(HT).$$

The stock-recruitment correlation was calculated using {S4+(YR)} instead of {S(YR)}. Whenever S was correlated with R, using S4+ in its place yielded unexpectedly large increases in the stock-recruitment correlation. In the Northern Edge and Northeast Peak, the r-values rose from 0.721 to 0.841. To further explore this trend (which was revealed fortuitously while investigating the negative density dependence of recruitment on various ages of stock) the egg productions for ages 5+ and 6+ were also derived:

$$S5+(YR) = \sum_{HT=105 \text{ mm}}^{185 \text{ mm}} NPT(YR, HT) * EGGS(HT).$$

$$S6+(YR) = \sum_{HT=115 \text{ mm}}^{185 \text{ mm}} NPT(YR, HT) * EGGS(HT).$$

The size ranges employed in these sums to restrict them to specific ages are derived by visual inspection of the height-frequency year class peaks for ages 2, 3 and 4. At higher ages, where peaks are no longer evident, a more

approximate scale was derived from the published age-height formula of Serchuk et al. (1979):

$$HT = 152.46 \{ 1 - \exp[-0.3374 (AGE - 1.4544)] \}.$$

Including only scallops of ages 5 and older in S5+ yielded another substantial increase in correlation (Tables 2.3 to 2.9). However for a considerable number of cases, correlations with S6+ declined.

Considering the possibility that S5+ may be the more correct measure of viable egg production, it is included in the study of spatial interactions among subpopulations along the gyre. Tables 2.3 to 2.9 will therefore help to address three questions at once: Is there a stock-recruitment relationship? What is its spatial pattern on Georges Bank? How is recruitment affected by the age/size of the parent stock?

Lognormal Recruitment

The normalities of recruitment frequencies for all regions, except the western South Channel, are dramatically improved by log transformations, for example the largest population, the Northern Edge and Northeast Peak as illustrated in Figures 2.2 and 2.3. Visual inspection of Figure 2.3 implies the histogram of ten $\ln(R)$ values is well described by the sampled normal distribution, indicated by a solid line.

The Shapiro and Wilk's test (as coded by the NAG FORTRAN Library, Mark 13) provides a quantitative estimate of the normality of a distribution, as measured by how probable it is that the tested time series of values could be obtained by random sampling from a normally distributed random variable. The $\{\ln(R)\}$ probability density function of Figure 2.3, is normal with an 84% significance, and there is a dramatic increase, 2 to 4 orders of magnitude in the Shapiro and Wilk's statistic for the log-transformed vs. untransformed values from every region except the western South Channel (Table 2.1). This is confirmed, although less dramatically, by the good agreement with the expected normal values of the third and fourth moments. In addition, because the Georges Bank scallop population has been cycling, the distribution of S values is also non-normal, although far less dramatically so than R .

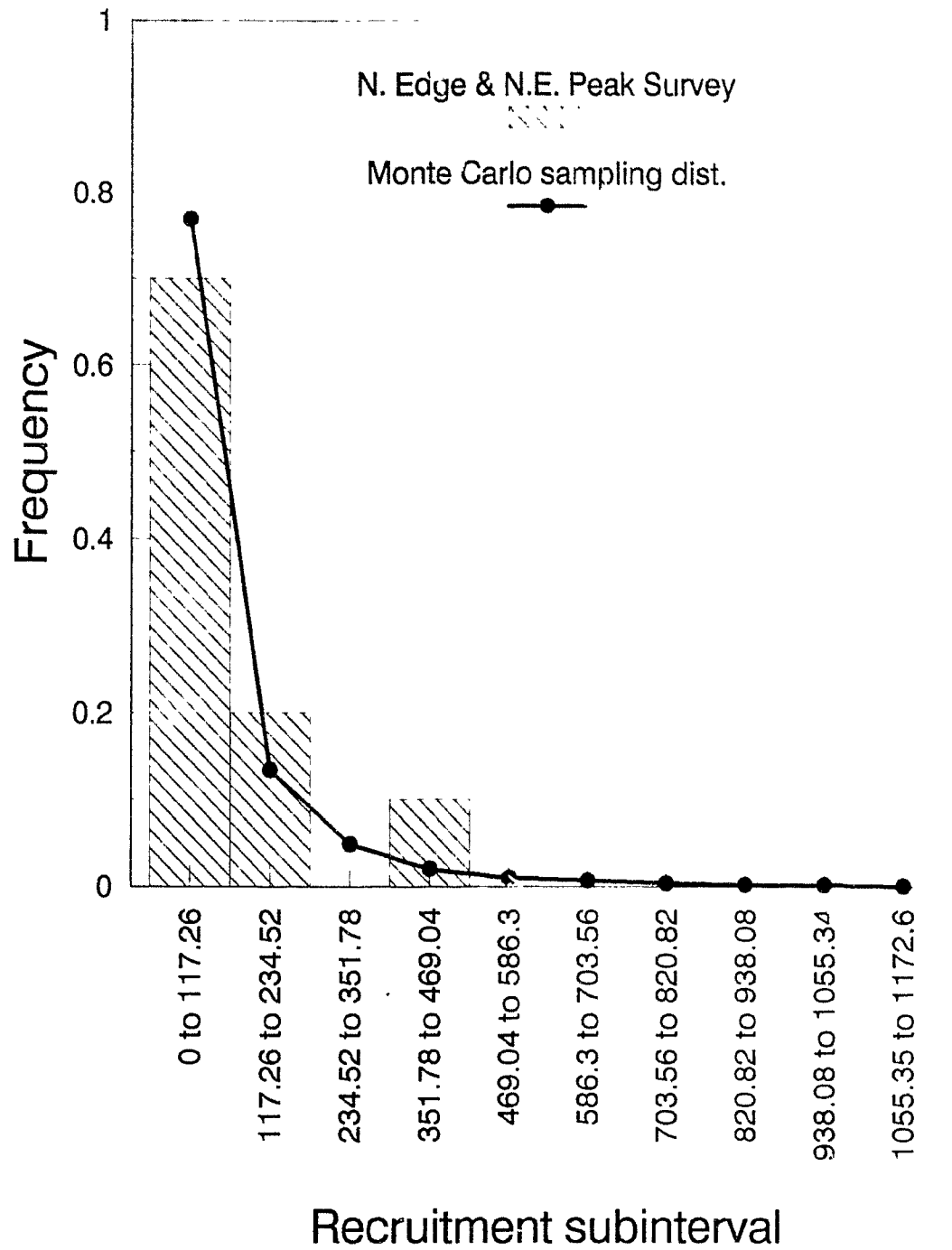


Figure 2.2. Recruitment histogram (bars) from the Northern Edge and Northeast Peak, 1977 to 1986, compared with the predicted Monte Carlo lognormal (line).

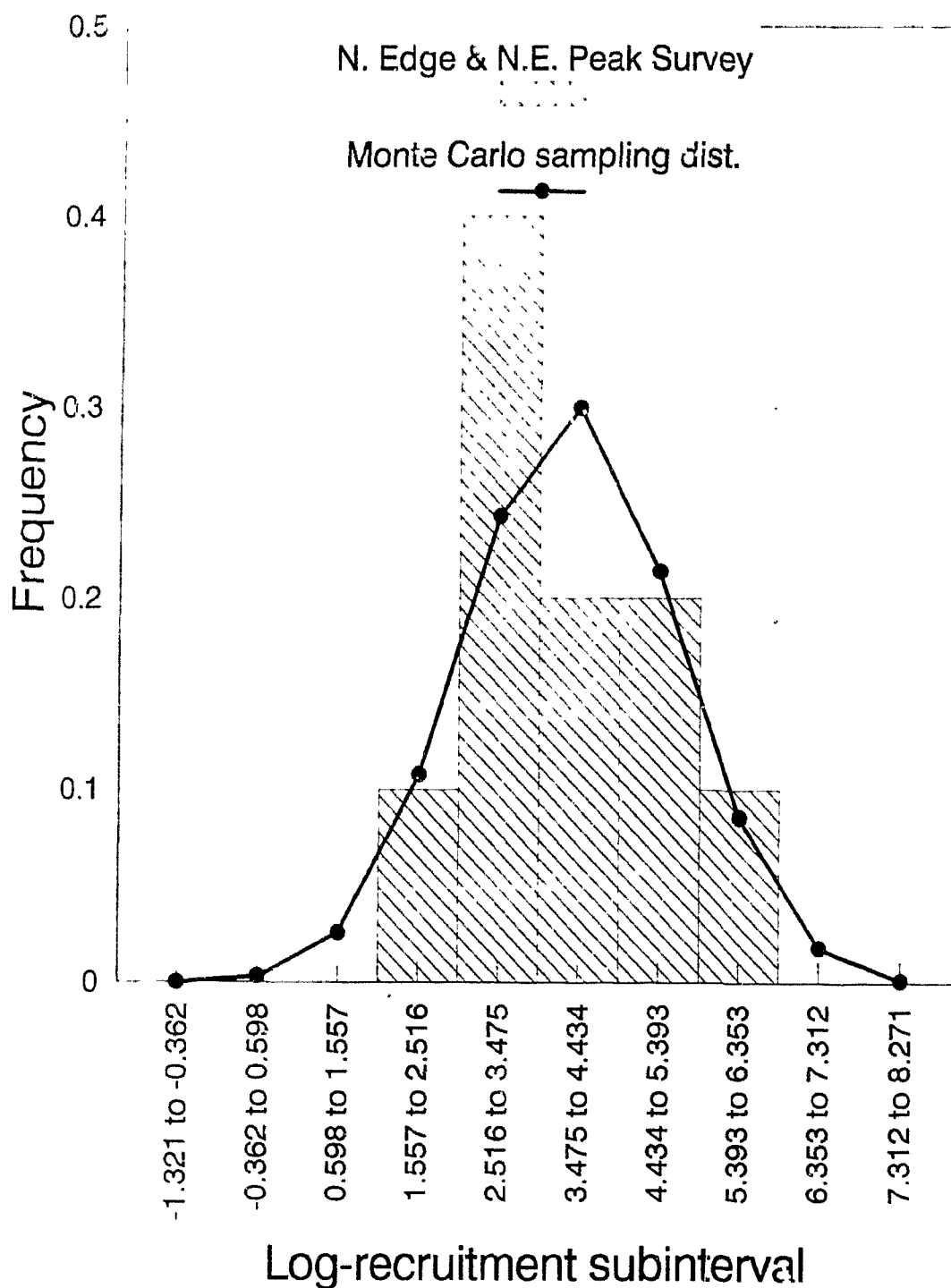


Figure 2.3. Log-transformed recruitment distribution of Figure 2.2 (bars). The Monte Carlo histogram (line), represents 10,000 sampled recruit values, generated using a standard 2 random number normal sampling algorithm (Abramowitz and Stegun 1970).

Table 2.1. Test of normality and lognormality of recruitment frequency distributions from all subregions.

Region	Likelihood of Shapiro and Wilk's W-test for normality	Third moment (= 0 if normal)	Fourth moment (= 3 if normal)
	R ln(R)	R ln(R)	R ln(R)
Georges Bank	0.00005 0.30	2.4 0.76	7.3 3.04
Northern Edge & Northeast Peak	0.0002 0.84	2.2 0.42	6.6 2.3
Northern Edge	0.00001 0.35	2.5 0.91	7.6 3.2
Northeast Peak	0.0008 0.93	2.0 0.02	6.0 2.0
Southeast Part	0.007 0.67	1.7 -0.04	5.0 1.7
South Channel (both halves)	0.016 0.083	0.78 0.31	2.05 1.3
Eastern half of South Channel	0.007 0.98	1.6 -0.2	4.6 2.3
Western half of South Channel	0.013 0.086	0.82 0.35	2.1 1.4

In order to estimate the significance (P-values) of these stock-recruitment correlations, an alternative method must be applied which incorporates the assumption of lognormality for R. A Monte Carlo distribution sampling routine was written and run to carry out these tests (Kleijnen 1974). The y-variable in this routine is assumed to be lognormal with a mean and a standard deviation identical to the observed R-distribution in each subregion tested. The x-variable is simply assigned the S values unchanged directly from observed data. Any effect that an unusual distribution of S might have on estimating significance is thereby included in the most straightforward manner possible. For each tested subregion we can estimate the chance that the observed level of correlation, r , occurred spuriously. Ten random samples of each Monte Carlo y-value, $\{R_{MC}(YR)\}$, yields a non-correlated series to compare with the observed $\{S(YR)\}$ time series. Repeating this process 1000 times, and counting the frequency that the Monte Carlo correlation exceeded the observed stock-recruitment correlation, a P-value is obtained expressing the probability that the observed correlation occurred by chance under the null hypothesis of no stock-recruitment relationship.

Since each subregion contributes a different mean and standard deviation of R and a different set of S-values, a separate Monte Carlo calculation must be run for each. The only assumption is that the log of R be normally

distributed. To that extent, quantified in Table 2.1, this Monte Carlo method is an exact estimation of P.

An alternative would be to sample randomly from a set of discrete y-values, namely the real observed R-values in each case. This obviates the need for any assumption, including lognormality. It has the disadvantage of assuming that no intermediate levels of recruitment can occur, which must certainly be incorrect. Since these R-distributions do appear to be well described by a lognormal, the method of sampling from a continuous distribution is favored.

Because of its demand on computer time, the Monte Carlo method was applied only when the r-values were close to significant. In all tables, these Monte Carlo calculated P-values are designated in brackets, distinguished from the conventional P-values in parentheses. The warnings of statisticians disallowing the conventional P-value estimation technique for non-normal variables are well born out. As the correlation increases, the overestimation of significance by the conventional technique also increases, until for values of r around 0.8, the conventional P-value is an order of magnitude too high and for $r = 0.921$ (Table 2.4), it is more than 1000 times that of the Monte Carlo estimation.

For the Northern Edge and Northeast Peak, the sampled histogram of Monte Carlo r-values is illustrated in Figure 2.4. All Monte Carlo r-histograms had this same basic shape. Among correlations (r's) close to zero, negative

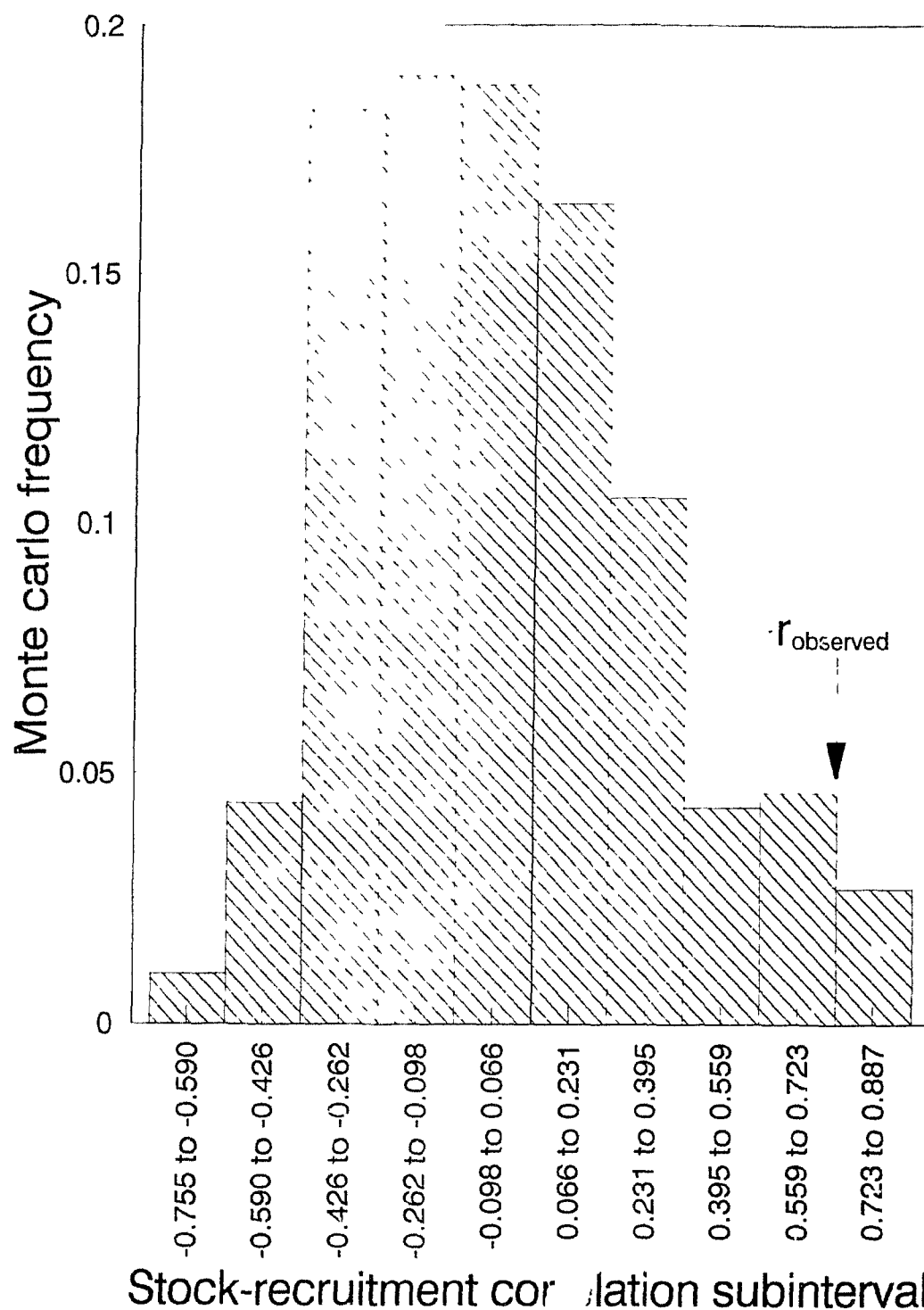


Figure 2.4. Histogram of stock-recruitment correlation (r) values obtained by random sampling from the distribution in Figure 2.3. An arrow indicates the observed correlation of R with S in the Northern Edge and Northeast Peak, $r = 0.721$. The area under the curve to the right of the arrow is the Monte Carlo $P = 0.046$.

values were more likely. However the tail at the positive end was longer and far more probable, expressed as positive skewness quantified in the largely positive third moments of Table 2.1. This long tail reveals how lognormally distributed R-variables can introduce bias, overestimating significance.

Results

Stock-recruitment: Within Subregions

For the Georges Bank scallop population taken as a whole (Table 2.2), the evidence suggests that there is a stock-recruitment relationship. The correlation analysis and the results of the linear least squares regression (Figure 2.5a) both suggest, despite huge variability, that recruitment tends, on average, to be better in years of high egg production ($r = 0.628$). The slope, b , is significantly positive ($t(b) = 2.28$), and the y-intercept, a , is near zero ($t(a) = -0.57$), as predicted for the stock-recruitment regression of a well-fished stock, since well below the carrying capacity extrapolating to zero eggs should tend to yield zero recruits.

Since 82% of the scallops are found on the Northern Edge and Northeast Peak (Table 1.2), the aggregated results for Georges Bank as a whole predominantly reflect the reproductive dynamics of this subregion. The analysis reveals a considerably stronger stock-recruitment relationship (Figure 2.6a). The high correlation (Table 2.2) and the t -value of the slope, $t(b) = 2.94$, imply that

Table 2.2. Stock-recruitment correlation results: Georges Bank overall and the three major subregions. The standard significance level assumes normal variables; the Monte Carlo value assumes a log-normal distribution of yearly recruitment.

Region	r-value	P-value (standard)	P-value [Monte Carlo]
Georges Bank	0.628	(0.03)	[0.047]
Northern Edge & Northeast Peak	0.721	(0.009)	[0.042]
Southeast Part	0.459	(0.09)	[0.123]
South Channel	-0.525	(>0.5)	[0.92]

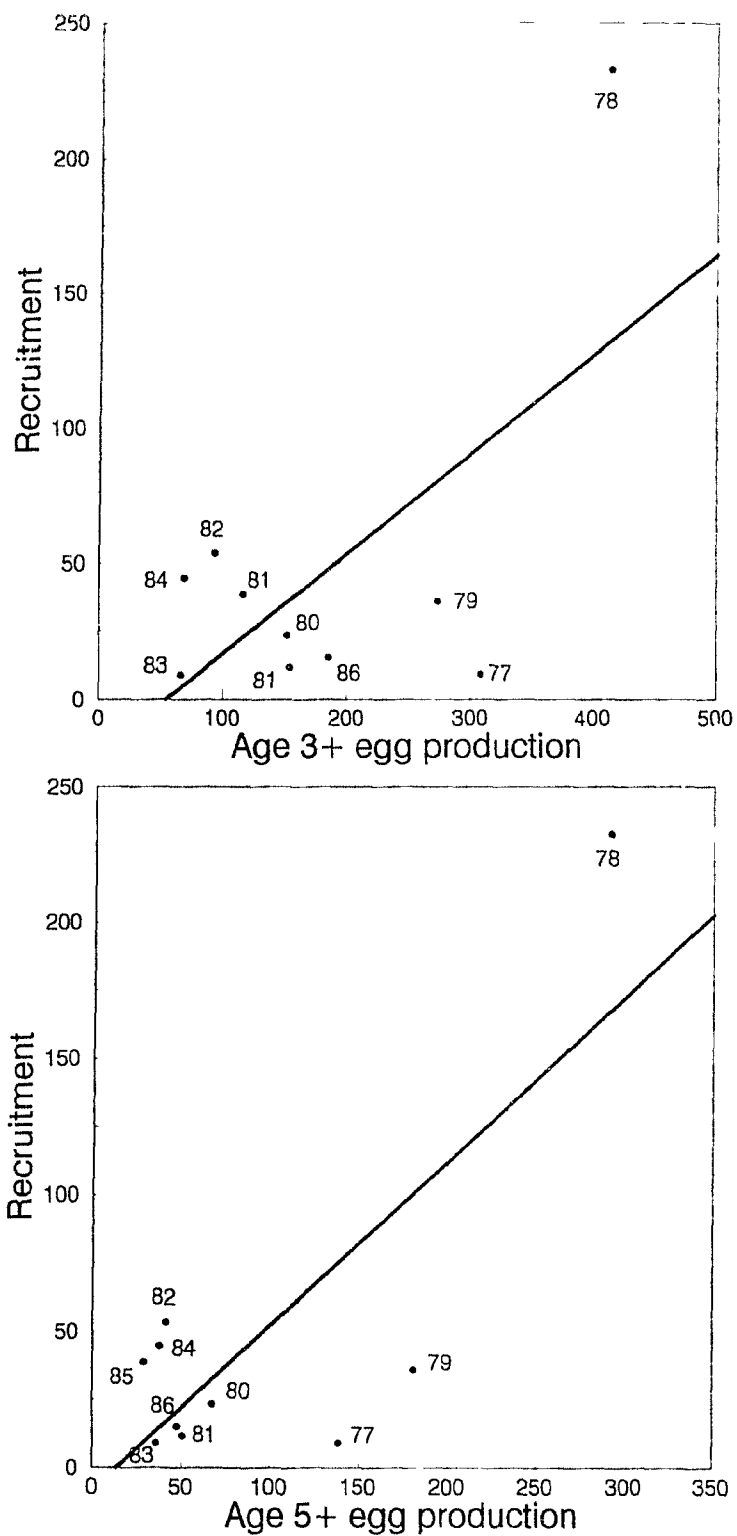


Figure 2.5. Stock-recruitment regression graphs for all of Georges Bank. a) Using S , the estimate of yearly egg production derived directly from the field measurements of MacDonald and Thompson (1985b). b) Using S_{5+} , including only eggs from scallops above 105 mm, roughly age 5.0.

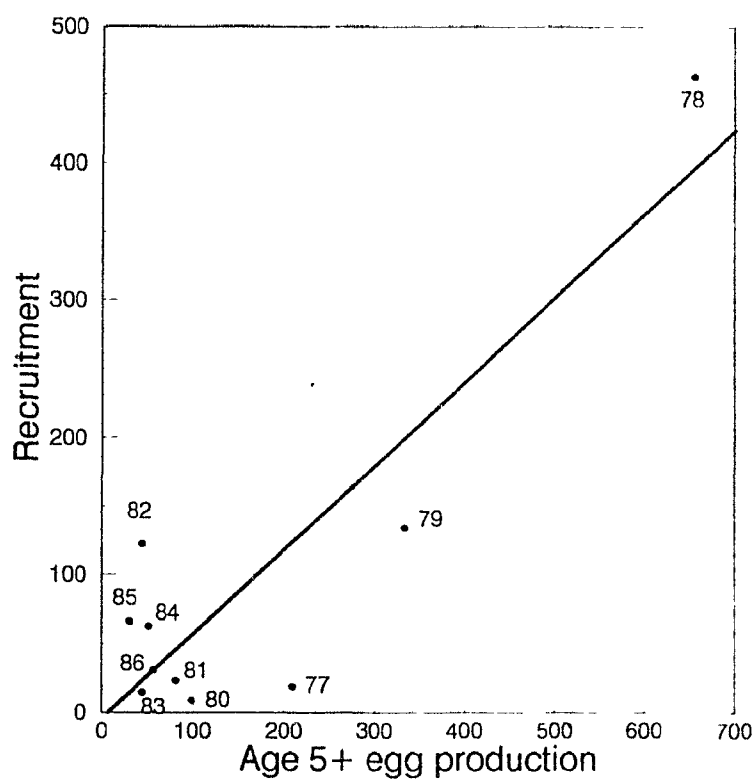
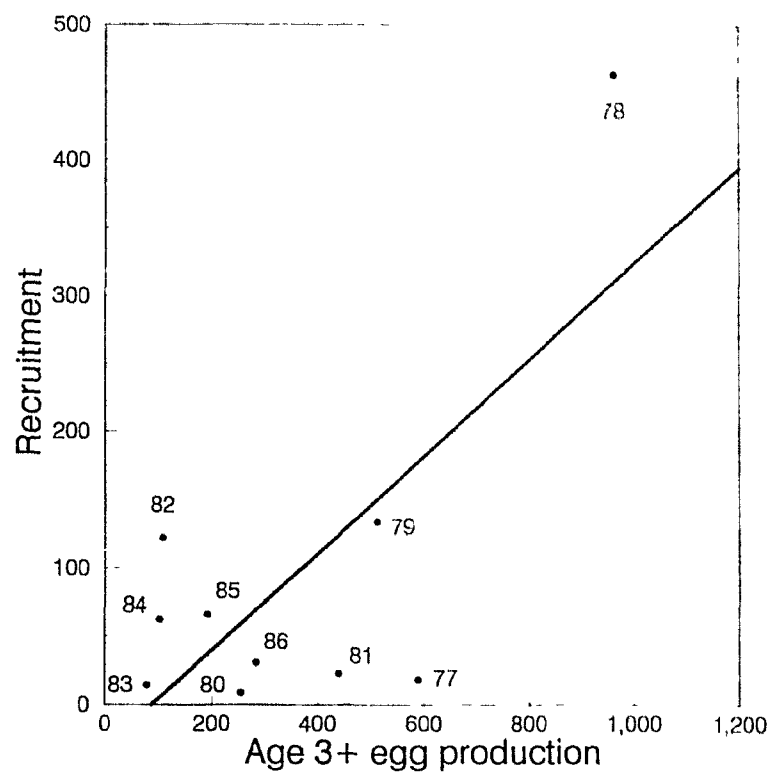


Figure 2.6. Stock-recruitment regression graphs for the combined area of the Northern Edge and Northeast Peak; recruitment versus a) S , and b) $S5+$.

recruitment in the Northern Edge and Peak is higher in years when larger populations of adult scallops there produce more eggs. The $t(a)$ value equal to -0.58 indicates that the intercept is close to zero, again as predicted for an intensively exploited population.

The high anti-correlation between stocksize and recruitment in the Great South Channel where $r = -0.525$, $t(a) = 2.82$ and $t(b) = -1.74$ was not anticipated. It suggests that there is no stock-recruitment relationship within this region and perhaps that eggs which settle in the South Channel originate elsewhere.

On the Southeast Part, there is only weak evidence of a stock-recruitment correlation ($r = 0.459$, $df = 10$, $t(a) = -0.06$, $t(b) = 1.46$).

The variability of recruitment is observed to be enormous in all cases, typical of marine populations. For all subregions and for Georges Bank as a whole, the standard deviation of $\{R(YR)\}$ was greater than the mean, typically by about 20%. And in all cases, the autocorrelation of $\{R(YR)\}$ was negative for lag $K = 1$ (i.e. between successive years).

Stock-recruitment: Between Subregions

The results of correlation analyses between neighboring regions along the clockwise direction of the gyre are presented in Tables 2.3 to 2.9:

Table 2.3. S, S4+, S5+ & S6+: Georges Bank overall and the three major subregions. The standard tabulated P-value for each r is presented in parentheses, and the Monte Carlo estimation of significance in brackets.

Region (from which eggs originate and into which they settle)	R vs. S r (P) [MC-P]	R vs. S4+ r (P) [MC-P]	R vs. S5+ r (P) [MC-P]	R vs. S6+ r (P) [MC-P]
Georges Bank	0.628 (0.03) [0.047]	0.731 (0.008) [0.025]	0.774 (0.004)	0.723 (0.009)
Northern Edge & Northeast Peak	0.721 (0.009) [0.042]	0.841 (0.001)	0.885 (0.0003) [0.008]	0.867 (0.0006)
Southeast Part	0.459 (0.09) [0.123]	0.528 (0.06)	0.535 (0.06) [0.098]	0.527 (0.06)
South Channel	-0.525 (>0.5)	-0.314 (>0.5)	-0.276 (>0.5)	-0.333 (>0.5)

TABLE 2.4. S, S4+, S5+, & S6+: Stock-recruitment correlations for various parent stock ages on the Northern Edge and Northeast Peak.

S-region (from which eggs originate)	R-region (into which eggs settle and survive to age 2)	R vs. S r (P) [MC-P]	R vs. S4+ r (P) [MC-P]	R vs. S5+ r (P) [MC-P]	R vs. S6+ r (P) [MC-P]
Northern Edge	Northern Edge	0.565 (0.040) [0.090]	0.820 (0.002)	0.871 (0.0005) [0.025]	0.834 (0.001)
Northern Edge	Northeast Peak	0.474 (0.080) [0.100]	0.730 (0.008)	0.782 (0.004) [0.023]	0.743 (0.006)
Northeast Peak	Northern Edge	0.814 (0.002) [0.021]	0.893 (0.0003)	0.921 (0.00008) [0.010]	0.902 (0.0002)
Northeast Peak	Northeast Peak	0.699 (0.010) [0.053]	0.789 (0.003)	0.826 (0.0015) [0.0190]	0.805 (0.0025)

TABLE 2.5. S, S4+, S5+, & S6+: Egg production in the Southeast Part and the Northeast Peak correlated with recruitment in the Southeast Part.

S-region (from which eggs originate)	R-region (into which eggs settle and survive to age 2)	R vs. S r (P)	R vs. S4+ r (P)	R vs. S5+ r (P)	R vs. S6+ r (P)
Northern Edge & Northeast Peak	Southeast Part	0.684 (0.015)	0.723 (0.009)	0.726 (0.009)	0.691 (0.010)
Northern Edge & Northeast Peak (1978 omitted)	Southeast Part	0.03 (0.47)	-0.157 (>0.50)	-0.18 (>0.50)	-0.191 (>0.50)
Northeast Peak	Southeast Part	0.690 (0.010)	0.719 (0.010)	0.727 (0.009)	0.697 (0.010)
Northeast Peak (1978 omitted)	Southeast Part	-0.069 (>0.50)	-0.225 (>0.50)	-0.221 (>0.50)	-0.214 (>0.50)
Southeast Part	Southeast Part	0.459 (0.09)	0.528 (0.06)	0.535 (0.055)	0.527 (0.06)
Southeast Part (1978 omitted)	Southeast Part	-0.397 (>0.50)	-0.338 (>0.50)	-0.364 (>0.50)	-0.366 (>0.50)

TABLE 2.6. S, S4+, S5+, & S6+: Egg production in the Southeast Part correlated with recruitment in the Great South Channel.

S-region (from which eggs originate)	R-region (into which eggs settle and survive to age 2)	R vs. S r (P)	R vs. S4+ r (P)	R vs. S5+ r (P)	R vs. S6+ r (P)
Southeast Part	South Channel (both halves)	0.110 (0.38)	-0.011 (>0.50)	-0.030 (>0.50)	-0.025 (>0.50)
Southeast Part	Eastern half of South Channel	-0.216 (>0.50)	-0.288 (>0.50)	-0.297 (>0.50)	-0.299 (>0.50)
Southeast Part	Western half of South Channel	0.117 (0.37)	-0.003 (>0.50)	-0.022 (>0.50)	0.017 (>0.50)

TABLE 2.7. S, S4+, S5+, & S6+: Egg production in the Great South Channel correlated with recruitment on the Northern Edge.

S-region (from which eggs originate)	R-region (into which eggs settle and survive to age 2)	R vs. S r (P)	R vs. S4+ r (P)	R vs. S5+ r (P)	R vs. S6+ r (P)
South Channel (both halves)	Northern Edge	0.211 (0.280)	0.339 (0.170)	0.402 (0.125)	0.208 (0.280)
Eastern half of South Channel	Northern Edge	0.306 (0.190)	0.328 (0.170)	0.415 (0.12)	0.283 (0.21)
Western half of South Channel	Northern Edge	0.112 (0.380)	0.387 (0.130)	0.406 (0.120)	0.171 (0.320)

TABLE 2.8. S, S4+, S5+, & S6+: Stock-recruitment correlations for various parent stock ages on the Northern Edge and Northeast Peak. 1978 is omitted from all all time series yielding 7 degrees of freedom.

S-region (from which eggs originate)	R-region (into which eggs settle and survive to age 2)	R vs. S r (P)	R vs. S4+ r (P)	R vs. S5+ r (P)	R vs. S6+ r (P)
Northern Edge	Northern Edge	0.007 (0.490)	0.337 (0.190)	0.573 (0.050)	0.641 (0.030)
Northern Edge	Northeast Peak	-0.177 (>0.50)	- 0.021 (>0.50)	0.095 (0.40)	0.144 (0.36)
Northeast Peak	Northern Edge	0.186 (0.320)	0.342 (0.180)	0.597 (0.045)	0.645 (0.03)
Northeast Peak	Northeast Peak	-0.205 (>0.50)	-0.113 (>0.50)	0.053 (0.45)	0.080 (0.42)

Table 2.9. S, S4+, S5+ & S6+: Georges Bank overall and the three major subregions, omitting 1978.

Region (from which eggs originate and into which they settle)	R vs. S r (P)	R vs. S4+ r (P)	R vs. S5+ r (P)	R vs. S6+ r (P)
Georges Bank (1978 omitted)	-0.347 (>0.5)	-0.280 (>0.5)	-0.119 (>0.5)	-0.084 (>0.5)
Northern Edge & Northeast Peak (1978 omitted)	-0.036 (>0.5)	0.139 (0.36)	0.359 (0.17)	0.403 (0.14)
Southeast Part (1978 omitted)	-0.397 (>0.5)	-0.338 (>0.5)	-0.364 (>0.5)	-0.366 (>0.5)
South Channel (1978 omitted)	-0.607 (>0.5)	-0.445 (>0.5)	-0.426 (>0.5)	-0.333 (>0.5)

Two trends are evident in Table 2.4. First, recruitment into both the Northern Edge and the Northeast Peak is better correlated with egg production originating in the Northeast Peak. Second, stock from both subregions is better correlated with recruitment into the Northern Edge. These are contrary to expectation since the currents, on average, flow from the Northern Edge onto the Northeast Peak. The explanation of the first trend lies, in the fact that 4.5 times as many eggs are released from the Northeast Peak as from the Northern Edge, primarily because it encompasses 10.5 times as much area. Since most eggs are produced there, a better correlation of stock from the Northeast Peak with recruitment to both regions may be expected. The second trend is explained by the fact that average recruitment per unit area on the Northern Edge is about 3.6 times higher than the Northeast Peak, 5.5 times higher than average. Spat which drift over this area find a considerably more favorable and thus presumably more reliable habitat for survival so it is reasonable to find recruitment on the Northern Edge better correlated with any subpopulation whose eggs regularly settle there. These relative correlations, which imply egg transport upstream from the Northeast Peak to the Northern Edge and throughout this region, corroborate the absolute r-value (Table 2.3) which (for both S and S5+) suggest that this population is self-sustaining. Most of the eggs that settle somewhere on

the Northern Edge and Northeast Peak probably originate there.

When 1978 is included the evidence supports a relationship with egg production to the Southeast Part from the Northeast Peak and from the Southeast Part itself (Table 2.5). When 1978 is omitted, the opposite conclusion is drawn. Since overall scallop density is more than an order of magnitude less than the Northern Edge, it is not surprising that recruitment there should be more erratic yielding lower correlations with likely sources of egg production. Warm core rings, flowing up from the Gulf Stream to the south, are also more of a factor in this part of Georges Bank where they impinge radically on the marine environment perhaps three to ten times per year (Halliwell and Mooers 1979).

No relationship is observed between Southeast Part egg production and South Channel recruitment (Table 2.6).

For recruitment in the Northern Edge from eggs originating in the Great South Channel, the analysis (Table 2.7) again reveals that leaving out three and four year old scallops improves the stock-recruitment correlation. Given previous evidence that eggs from the Northern Edge and Northeast Peak settle in large numbers on the Northern Edge, we should not expect the correlation with egg production from any other area to be large. An r -value of 0.4 is not negligible in this circumstance and may well imply a moderate transport of eggs from the South Channel to the

Northern Edge. This result depends on the supposition that S_{5+} is a better measure of total viable egg production than S .

Lastly we consider the correlation of recruitment time series between neighboring subregions (Table 2.10). The correlation of recruitment on the Northern Edge with age 5+ egg production from the Northeast Peak ($r = 0.921$) is slightly higher than with recruitment in the Northeast Peak ($r = 0.909$). If these two subregions share equally the same environmental conditions and the same egg stock, this rough similarity in correlation suggests that yearly recruitment in this population is about equally influenced by egg production as by variation in the environment.

Table 2.10. Summary of recruitment correlations between all neighboring major and minor subregions.

Two regions whose recruitment time series are being compared		r
Northern Edge	Northeast Peak	0.909
Northeast Peak	Southeast Part	0.799
Southeast Part	South Channel (both halves)	0.383
Southeast Part	Eastern half of South Channel	0.271
Southeast Part	Western half of South Channel	0.378
South Channel (both halves)	Northern Edge	0.302
Eastern half of South Channel	Northern Edge	0.021
Western half of South Channel	Northern Edge	0.305
Eastern half of South Channel	Western half of South Channel	0.545

The stock-recruitment relationships become stronger as spatial consideration is restricted to the populations near or including recruitment to the Northern Edge from egg production in the Northeast Peak. For the regions of (i) Georges Bank taken as a whole, (ii) the Northeast Peak, (iii) the Northern Edge, (iv) the Northeast Peak and Northern Edge combined, and (v) recruitment to the Northern Edge with egg production from the Northeast Peak, the correlations of recruitment with $S/S5+$ increase as (i) 0.628/0.774 (ii) 0.699/0.826 (iii) 0.565/0.871 (iv) 0.721/0.885 and (v) 0.814/0.921.

Thus the clearest association between stock and recruitment appears in the regions of greatest, densest and most consistent population.

Stock-recruitment: Age of Parent Stock

The large increases in stock-recruitment correlations between and within the Northern Edge and Northeast Peak, supposing that scallops aged three and four do not contribute viable eggs (Figures 2.6 and 2.7), were exhibited to a smaller extent by the other sub-regions and Georges Bank as a whole (Figure 2.5). This improvement was observed in every case when a stock-recruitment relationship was already in evidence.

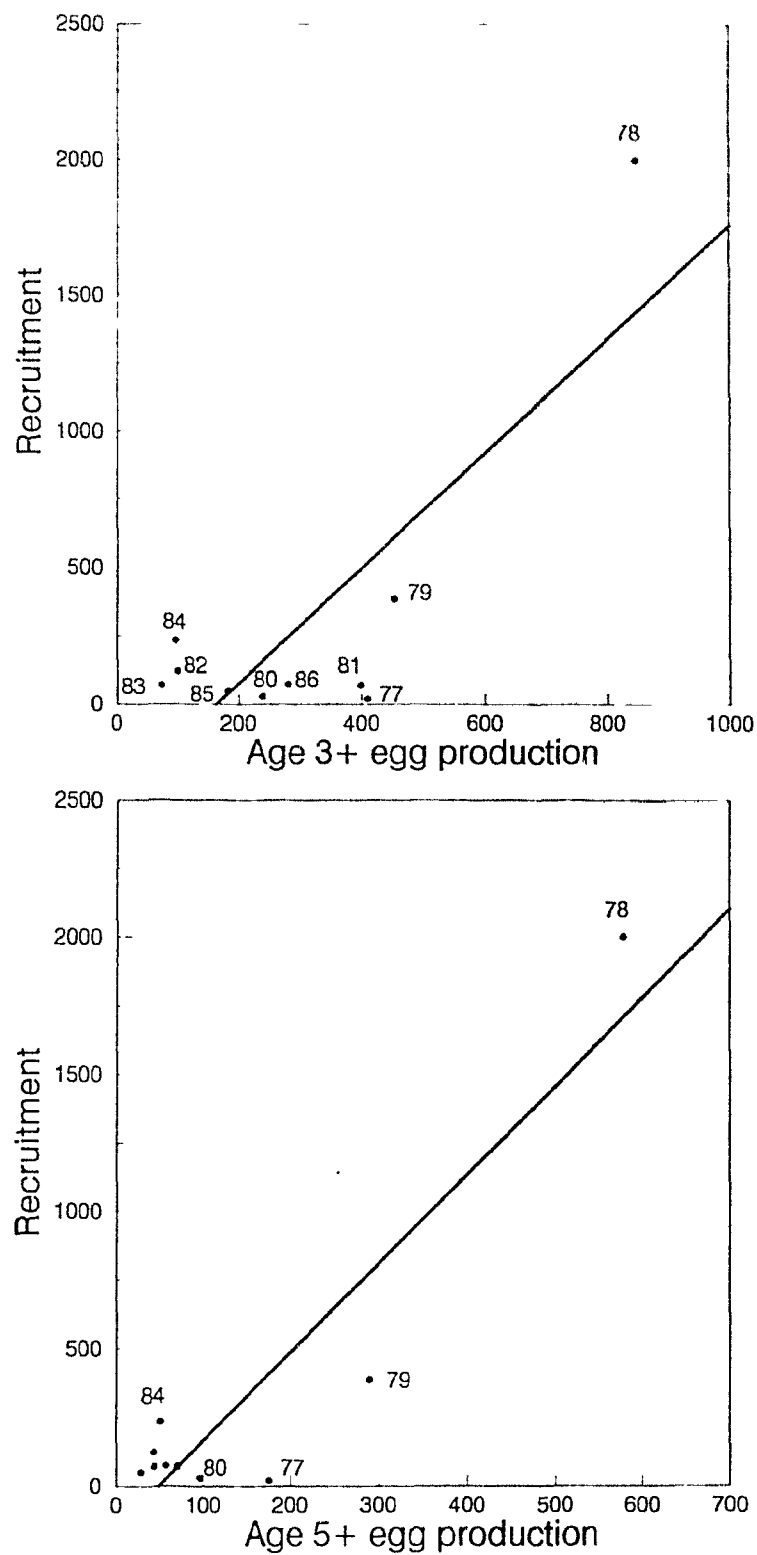


Figure 2.7. Interregional stock-recruitment regression graphs; recruitment to the Northern Edge versus a) S from the Northeast Peak, and b) S5+ from the Northeast Peak.

It is worth noting that an improved correlation is observed in the Northeast Peak and Northern Edge even when 1978 is omitted (Table 2.8). This particular year when both egg production and recruitment were particularly high dominates the regression, and without it, the results would be quite different using the regular S. For Georges Bank overall we observe the same trend. The stock-recruitment correlations increase when age three and age four scallops are excluded from total egg production for every case, with or without 1978 (Table 2.9).

Discussion

The year 1978 dominates the regressions. Except where the populations are most dense, namely S5+ egg production from the Northeast Peak compared with recruitment to the Northern Edge, 1978 is primarily responsible for the significant correlations. Characteristic of stochastic processes, the tail of the distribution is critical. For fish populations, large year classes often represent much of overall catch averaged over a number of years (Hennemuth et al. 1980, Sissenwine 1984, Rothschild 1986). Therefore we ask, Is it coincidence that the most profitable year class in recent history occurred during a peak in scallop egg production?

Though 1978 was distinguished by high recruitment and high egg production, nothing else about that year makes that data point doubtful. It falls in the reliable part the time series (based on self-consistency between age 2 and age 3 year class peaks).

Environmentally, 1978 was not the best year for egg to age 2 survival, expressed in the time series of $\{R(YR)/S(YR)\}$. By this measure (i.e. recruits per egg), the years 1982 and 1984 were more hospitable for young scallops. In the combined area of the Northern Edge and Northeast Peak, $R(1982)/S(1982) = 3.6 \times 10^{-7}$ and $R(1984)/S(1984) = 1.9 \times 10^{-7}$, compared with $R(1978)/S(1978) = 1.5 \times 10^{-7}$.

The two principal factors that may cause a large recruitment year class are egg production, S , and favorability of the environment reflected in R/S , the survival rate per egg. Comparing them with their mean values allows us to assess roughly how important each was in causing the large 1978 year class. In 1978, the R/S value was 1.49 times higher, while total egg production was 2.73 times higher than average. So it appears that most of that year's recruitment success was due to a much larger than average egg production.

Overall, in no year when egg production was particularly large (especially if we accept the non-viability or non-production of eggs by younger scallops) was recruitment poor, and vice versa. This rough relationship is the best one might expect in a population whose

recruitment time series is so variable that the standard deviation is 20% larger than the mean and whose autocorrelations at lag 1 are negative.

The appearance of a very large year class is characteristic of lognormal recruitment. When this lognormality is statistically accounted for, as shown in Figure 2.3, 1978 is no longer distinguished. The Monte Carlo method is particularly valuable in this way, the log transformation effectively removing the bias introduced by a single large year class.

Furthermore, the lognormality of recruitment is compatible with the model (Equation 1), since mathematically a lognormal distribution is expected from a product of independent normally distributed survival probabilities. We can expect to find lognormal recruitment for a species subject to wide annual variability at several stages of its development. Hennemuth et al. (1980) have indeed observed this trend, finding annual recruitment was better described by a lognormal distribution in 15 of 18 fishstocks. The spawning of an egg is only one of several independent processes, all of which determine the chance of an egg entering the adult population.

We may summarize the evidence for a stock-recruitment relationship in Georges Bank scallops, and in particular, on the Northern Edge and Northeast Peak:

- 1) The stock-recruitment correlations themselves are statistically significant, despite lognormality.

- 2) The y-intercepts pass close to the origin.

The pattern of spatial reproductive interactions was highly consistent with what we should expect:

- 3) Regions of higher absolute recruitment (e.g. the Northern Edge) yielded stronger correlations with a wide number of neighboring egg production source regions.

- 4) Regions where absolute egg production are higher (e.g. the Northeast Peak) were better correlated with recruitment to neighboring regions.

- 5) Overall, the stock-recruitment correlations were higher where scallops were more abundant and recruitment more consistent, with the notable exception of the South Channel.

- 6) The increases in correlation when eggs from younger scallops were excluded from the count for essentially every case where some correlation was evident also implicates a relationship between eggs and recruits. If it should turn out, by independent experiment, that 3 and 4 year olds are not fully mature, the hypothesis of a stock-recruitment relationship would be very greatly strengthened, verifying a prediction derived from this pattern of increases in correlation which is based on that hypothesis.

- 7) These increases also follow the geographic pattern predicted by a stock-recruitment relationship: the regions with the largest increases in correlation from (R,S) to $(R,S5+)$ were precisely those regions where the original (R,S) correlations were highest.

Egg Transport

At observed average daily flow velocities, the residual current, would displace free-floating larvae 100-200 km downstream before settlement. The persistence of the adult populations, and the evidence presented that the Northern Edge and Northeast Peak are reproductively self-sustaining, suggest that some larvae diverge from this average displacement. A number of dynamical mechanisms may explain how eggs or larvae can settle upstream against the gyre.

The gyre is only the residual displacement. Most water movement above Georges Bank is a semi-diurnal tidal flow which twice each day, would displace a typical larva 45 kilometers to the north, in the direction of the Gulf of Maine, against the direction of the gyre on the Northeast Peak and Northern Edge, and then to the south again (Butman et al. 1987), a total of 180 km, compared to the daily mean residual drift of about 7 km.

The second feature of these current patterns above Georges Bank is their nearly turbulent character. In the shallow central region, of 50 m depth or less, the entire water column is mixed, very rare in the open sea. Loder et al. (1982) estimate that 10% of the particles in this well-mixed region would remain there 60-80 days. Tremblay and Sinclair (1990) found significant concentrations of scallop larvae in this central region in the weeks after spawning, although their numbers were lower than in the stratified

water where the eggs are spawned. This well-mixed water could perhaps serve as a continuous depository and supply of larvae for subsequent settlement on the Northern Edge or Northeast Peak, particularly since phytoplankton concentrations are highest in the mixed zone (O'Reilly et al. 1967) and the water is warmer and thus more favorable for larval growth and survival. In the outlying deeper areas of the Bank, about which the gyre circulates and where nearly all scallops are found, the currents are complex and variable.

In 1988 and 1989, drifters were released in clusters from various locations above the Northern Edge and Northeast Peak, and in the adjacent central mixed zone, in a comprehensive study of the currents near the tidal front which separates the mixed and stratified waters (K. Drinkwater, Bedford Institute of Oceanography, Dartmouth, Nova Scotia, pers. comm.). Most drifters followed elliptical trajectories, carried by the semi-diurnal tides back and forth across the Bank.

The overall trend of residual movement confirms the clockwise trend of the gyre, but divergences from this movement were frequently observed. In particular, four clusters, groups of 4 to 9 drifters floating at the surface or at 10 m depth, moved along trajectories that would result in retention of larvae above or upstream of the parent spawners:

(1) In 1989, 9 drifters, released by Drinkwater near the tidal front in the stratified (outer) region above the Northeast Peak, circulated elliptically for the length of the experiment, 5 days, without significant residual movement.

(2) 4 drifters, released at locations crossing but close to the tidal front, revealed a perceptible trend of convergent movement towards the frontal surface from both directions. The retention near the front observed in cluster (1) may be associated with this frontal current convergence.

These first two examples occurred in light wind. Heavier winds can also act to reverse the prevailing direction of currents on Georges Bank, particularly at the surface.

(3) With winds blowing strongly towards the west, drogues released above the Northern Edge drifted north, perpendicular to the wind direction and the prevailing residual gyre flow, and up into the Northeast Channel where they were then carried eastward relatively rapidly and, for several drifters, back onto the Northern Edge itself farther east.

(4) These easterly winds also acted on drogues released farther south on both sides of the front, pushing them in the direction of the wind, deep into the central mixed zone. Once these winds died down, this movement was

reversed, and these drifters returned towards the front and the general area of their release.

Overall, the trajectories deviated significantly from the synoptic gyre flow in roughly half of the clusters of drogues released in Drinkwater's study.

In addition, lab experiments in a 10 m column of seawater have demonstrated that scallop larvae migrate vertically on at least a daily basis (Silva and O'Dor 1988, Balch 1990). Depending on whether they were deep or shallow at various phases of the tidal cycle, they would be carried considerably greater distances against, perpendicular to, or with the residual flow. If vertical migration were uncoordinated with the tidal cycle, there would be more rapid dispersal of larvae in all directions and thus a greater degree of (essentially random) movement "upstream".

It has been determined by seasonal hydrographic studies (Flagg et al. 1982 cited in Butman et al. 1987) that the gyre is most tightly closed, with the lowest escapement of water off the Bank during late summer and early fall, when scallop spawning occurs. The estimated time for a complete circulation is about 60 days, on the high side (30-45 days) of estimated time for egg to larval settlement, but vertical migration and natural variability could allow the additional hypothesis that significant numbers are dispersed almost the entire distance from, for example, the southern stretches of the Northeast Peak to the Northern Edge. This may include larvae which pass through the central mixed zone.

Robert and Black (1990) provide maps of high resolution detailing the distribution of scallop concentrations in the Canadian waters of Georges Bank. Horne et al. (1989) note the proximity of these concentrations to the tidal front between mixed and stratified waters. Higher rates of vertical diffusivity along the tidal front are shown to be important in supplying new nitrate to Georges Bank waters. Horne et al. note the proximity of these concentrations to the tidal front between mixed and stratified waters. However the dense concentrations identified by Robert and Black tend to occur along an arc that extends from the Northern Edge, near the front itself, to the far western end of the Bank quite distant from the tidal front. Other factors, in addition to productivity, are probably important--the highest productivity occurs above the mixed zone where virtually no adult scallops are found.

The high-resolution numerical models of Greenberg (1983), predicting the residual current pattern in the entire Gulf of Maine from tidal processes, yield close agreement with observation, particularly over Georges Bank. Above the Northern Edge and Northeast Peak, Greenberg predicts relatively slow residual flow compared to the rest of Georges Bank, and a weak subgyre when the prevailing winds combine with tidal forces, in rough agreement with the observations of Drinkwater mentioned above which suggest that the residual gyre is weaker in these waters of high scallop concentration.

The pattern of scallop distribution identified by Robert and Black (1990) corresponds most closely with the feature of strong gyre-like isotropic flow around the outer edge of the Bank. In particular, most scallops appear to lie just inside this stronger flow around the outer edge both on the Northern Edge and the Northeast Peak. This might suggest that this strong current carries dense concentrations of healthy larvae. Speculating further, if the success of larval survival in the mixed central zone is much greater than in stratified waters, this jet of current around the edge of the Bank, which is partially fed by the mixed zone, may be a source of larvae for the Northern Edge and Northeast Peak.

In the Gulf of Maine overall, there is a distinct correspondence between the regions identified in the numerical models of Greenberg, which exhibit gyres in the currents, and greater abundances of Placopecten. Two clear biological reasons for this association are evident. First, these regions, namely the Northern Edge and Northeast Peak and the western South Channel of Georges Bank, Brown's Bank, and the Bay of Fundy, are areas of relatively high productivity. Second, the effect of larval retention, proposed in connection with herring by Iles and Sinclair (1982), is likely to be an even stronger effect with mollusc species (Sinclair et al. 1985).

The unpredictability of these currents would explain why scallops have been selected to produce vast numbers of

eggs compared with virtually all other animal species. They inhabit a chaotic medium that is fundamentally variable and unpredictable. They cannot swim great distances to favorable locations for settlement, in particular back to their parents' bed. So they must rely on the variability of those currents to carry a small fraction of their spawn upstream against the residual flow which is, in any event, a modest distance compared to daily tidal flow.

It was estimated in Chapter 1, for all of Georges Bank, that 2% (more accurately, 1.4%) of the eggs survive to an advanced larval stage and that 2 (2.45) in ten million eggs survives to age 2. If just 1 in 100 advanced larvae survive to settlement, and by chance, in the variable currents, 1 in 10 of those end up settling upstream of the parent spawner, this would still leave 1000 settled spat the chance to grow to age 2 and replace the two parents needed to assure long-term stability of the upstream population.

Egg Viability

Perhaps the most striking and important result for fisheries management and aquaculture is the indirect implication that the eggs of 3 and to a lesser degree 4 year old scallops in these stocks have a much lower chance of survival. In the Canadian fishery, scallops become large enough to harvest at the age of around 3.25 years, at a size

of about 80-90 mm (Tables 3 and 5 Mohn et al. 1989). By 5.0 years of age the cohorts are typically reduced to less than 10% and by age 6 less than 1% of the age 3.0 level (Tables 6 and 7 Mohn et al. 1989). If scallops are not producing many viable eggs before age 5, the total egg production of the Georges Bank population is a small fraction of what it would be if they lived out a natural lifespan of 20 years, or, more relevant for management purposes, if intensive harvesting were delayed until scallops reached age 5 or 6. The one factor that could diminish the strength of this conclusion is the inhibiting effect of density dependence. These results, and a more detailed analysis of density dependence in Chapter 5, suggest that this limiting effect is real but secondary, and discernible only by comparison to a natural unfished population.

At least two different yield-per-recruit investigations (Sinclair et al. 1985, Serchuk et al. 1979) have concluded that raising age at first capture would almost certainly increase yields, perhaps quite dramatically. This study suggests that, in addition, recruitment would also be significantly enhanced by raising age at first capture.

CHAPTER 3

THE CYCLE

Introduction

Sea scallop (Placopecten magellanicus) is the third most lucrative species in Atlantic Canada after cod and lobster, worth \$120 million in 1988. The Georges Bank population, by far the largest, supports a single-species fishery, employing 70- to 100-foot vessels designed specifically for the bottom-dredging and on-board shucking of sea scallops (Bourne 1964, Caddy 1989).

The time series of annual harvest for the Georges Bank scallop fishery is illustrated in Figure 3.1a. Around 1958 the series appears to change from the steady state (in CPUE) of 1944-1958 into a cycle, which continues to the present. In this chapter, the properties of this population oscillation are investigated to identify the specific mechanism giving rise to this dynamical behavior.

Cycles have been studied previously in a number of fishstocks, including Soviet Pacific saffron cod (Vasil'kov et al. 1981), Dungeness crab (Botsford and Wickham 1979, Methot and Botsford 1982, McKelvey et al. 1980, Botsford 1985), Brown's Bank haddock (Allen and McGlade 1986), Bay of Fundy scallops (Dickie 1955, Caddy 1979) and Lesser Slave Lake Whitefish (Bell et al 1977).

Three hypotheses dominate the literature of model, laboratory and natural cycling populations:

- I. Environmental forcing;

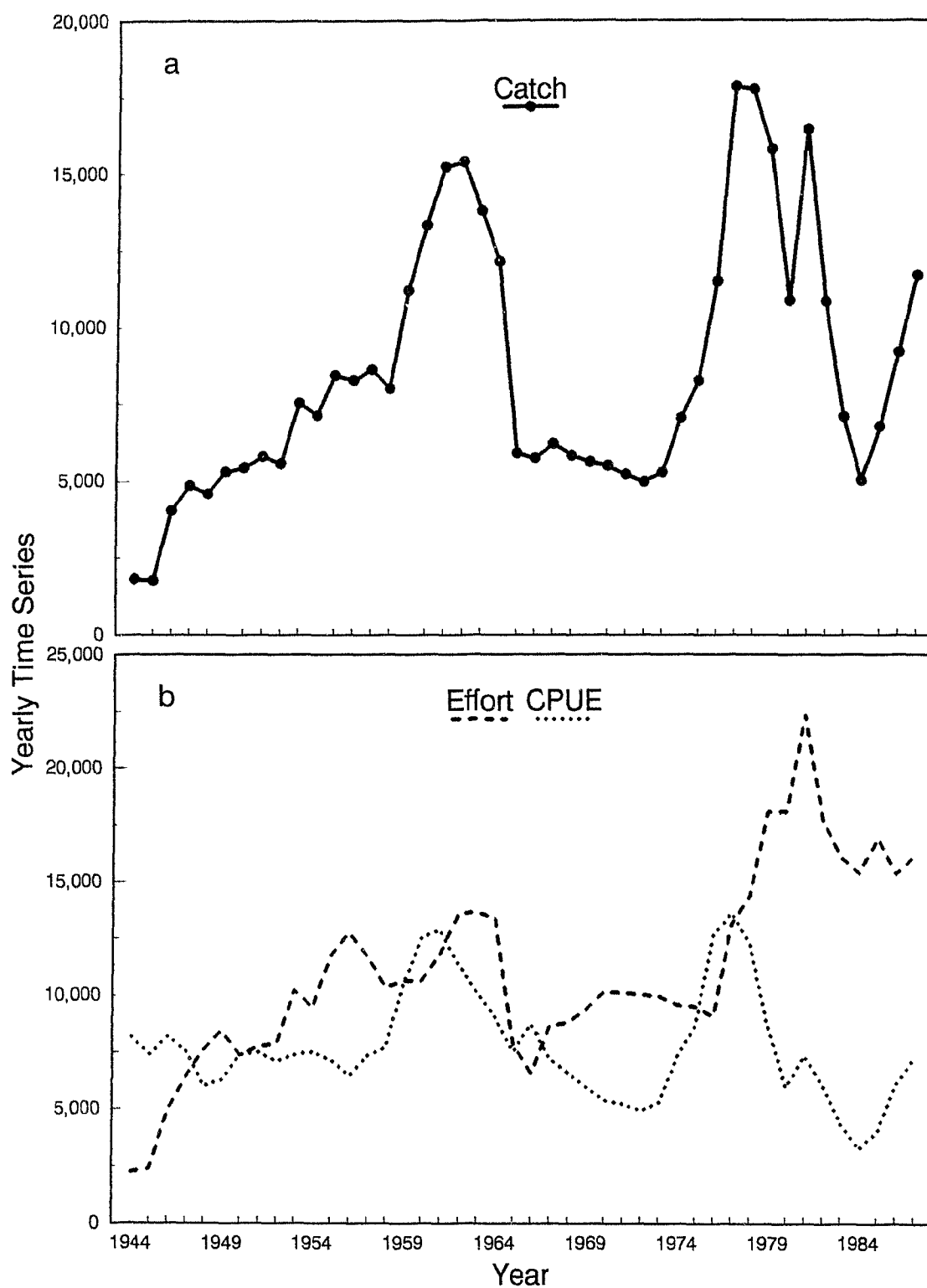


Figure 3.1. Georges Bank scallops, 1944-1987. a) Total annual harvest in metric tons. b) Effort in equivalent days of conventional scallop dredge dragging time and catch per unit effort, rescaled by a factor of 10,000.

II. The Schaefer model with fishermen as predator and scallop stock as prey; and

III. Overcompensatory (i.e. Ricker) density dependence.

These reflect three active schools of thought about the cause of change in fishstocks. The first hypothesis suggests that the population is exogenously entrained by a similar periodic variation in the marine environment; the second, that population size is largely determined by fishing, as described by the Schaefer model of classical fisheries economics. Fishing boats are thought of as a predator species which preys on the fishstock, the level of effort changing in a manner which is, in all respects, analogous to a Lotka-Volterra cycle. Ricker cycles theoretically occur when strong density dependence within a population causes a perturbed steady state to become unstable. If recruitment becomes even more inversely dependent on stock density, then chaos ensues (May et al. 1974). Evidence obtained from time series data and from the literature will allow us assess the three hypotheses.

Data

The time series data were obtained from two sources-- commercial fisheries landings records and scientific

sampling. The commercial data are composed of yearly total catch (in meat weight) and total fishing effort (hours of scallop dredge time spent on the bottom) dating back to 1944.

Because of its gyre, Georges Bank is often treated as one large ecosystem. This closed current pattern which is tightest during scallop spawning in late summer and early fall (Flagg et al. 1982, cited in Butman et al. 1987), appears to create a single, large source population of sea scallops which is reproductively self-sustaining. In particular (Chapter 2), the Northern Edge and Northeast Peak exhibit a stock-recruitment relationship, probably supplying the Southeast Part with spawn and perhaps receiving immigrants from the South Channel. US and Canadian data have therefore been combined yielding total catch and effort for all of Georges Bank.

The survey data were also aggregated from US and Canadian sources. Spanning a shorter time (1977-1988) than the commercial series (1944-1987), they are richer in information, providing the height-frequency distributions used to construct the stock-recruitment results of the two previous chapters. This first stage of data analysis thereby yields time series of recruitment, R , and total egg production, S , spanning the years 1977-1986, calculated in Chapter 2.

Because they provide entirely independent information about the Georges Bank population, the accuracy of

commercial and survey data can be assessed by comparing how closely they measure a common population variable, total biomass. The survey height-frequencies are summed to obtain a survey equivalent of commercial size biomass, multiplying the numbers sampled per tow by the meat weights in each size class and summing over the range of harvestable sizes. The commercial measure is taken directly as catch per unit effort.

The match is surprisingly good ($r=0.905$, $P=0.00007$, $df=9$), as visual comparison confirms in Figure 3.2.

The accuracy expressed by these two independent sources of data, together with the relative simplicity of cyclical dynamics, makes the Georges Bank scallop population amenable to the methods of dynamical systems modeling and time series analysis which follow.

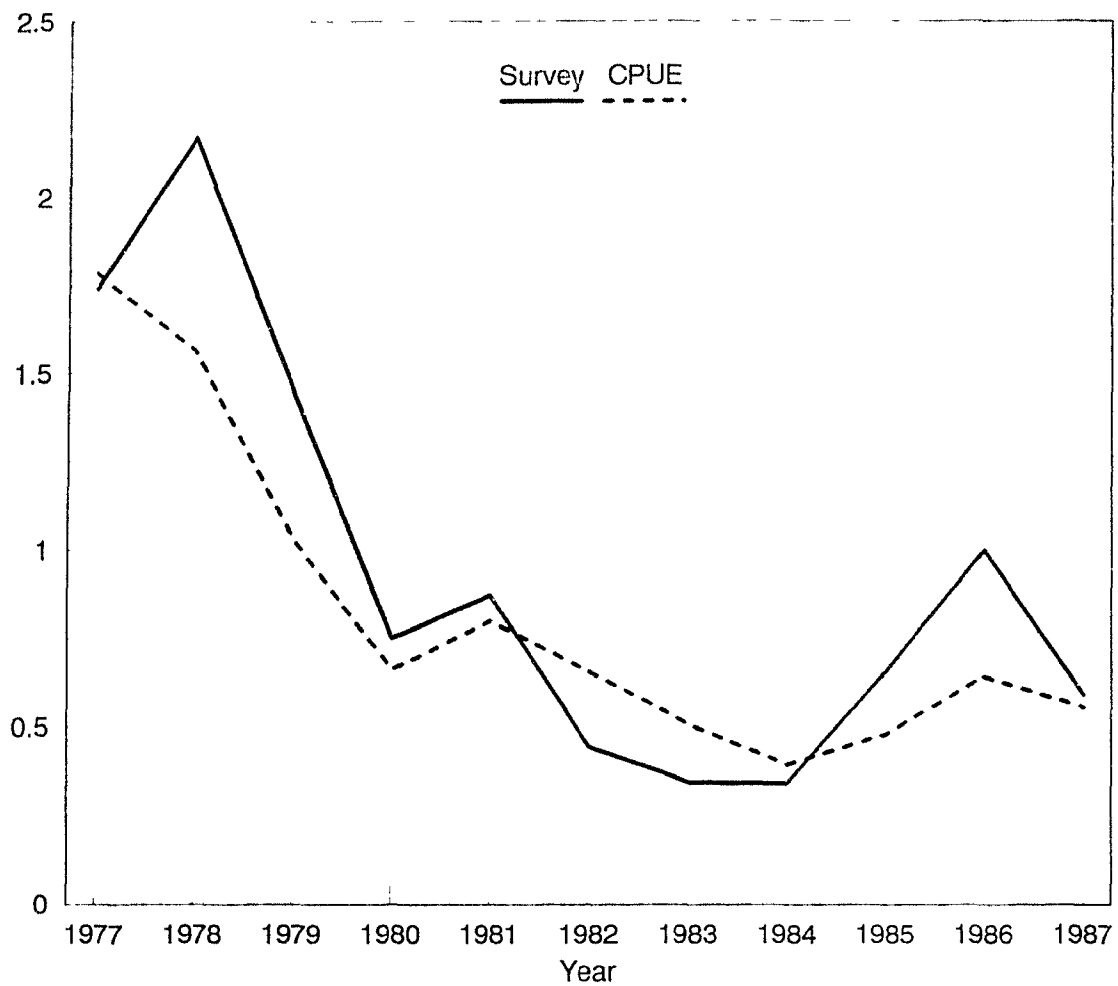


Figure 3.2. Survey adductor muscle (i.e. meat-weight) biomass of scallops >70 mm, compared with the commercial measure of biomass, catch per unit effort. Time series are rescaled to equate their means.

Methods

In deciding which dynamical mechanism actually causes a real population to cycle, researchers have long been hampered by the ambiguity of their hypotheses: Many different models, each embodying a different potential cause, can all yield time series as output which fit the data. This is particularly true since in all real systems there is noise which reduces the value of a statistical goodness of fit test. The best fits may merely reflect circumstances and luck rather than confirm the correct cycle-causing mechanism. To resolve this ambiguity for the Georges Bank scallop cycle, I will place primary emphasis on those dynamical qualities of the time series that follow from the biological or environmental causes of the cycle, and which may therefore distinguish one mechanism from another.

To test each hypothesis, certain qualitative features of the population cycle are isolated from the time series. Hypotheses which do not express these features observed in the real system can be eliminated while those which do can be retained. This is a taxonomic approach, and the trick, as in systematics, is to choose characteristics which distinguish one model from another. In practice, no real population is entirely affected by just one process. However in choosing populations for study, the simplest

dynamical behavior, such as a cycle, are more likely to be governed predominantly by a single cause.

Of particular value in the study of population cycles are the auto- and cross-correlation functions. Cole (1951, 1954) and (Palmgren 1949) showed that random time series can appear to "cycle", if that term is taken loosely (Moran 1954, Finerty 1980), with a period of roughly 3 time steps. The autocorrelation function was proposed (Moran 1949) and applied in a large number of population cycle studies (e.g. Caddy 1979, Moran 1952, 1953, Doi 1955, Finerty 1980) as the means of assessing the reality of apparent cycles.

The autocorrelation function of a discrete sine wave with a period of 15.5 time units is presented in Figure 3.3. The period is plainly revealed by the maximum at lag $K = 15$ or 16. Note that the autocorrelation function of a cyclical series is itself cyclical, behaving much like a Fourier transform. The autocorrelation and cross-correlation functions used in this study are detailed in Appendix 3.1. The sign and relative strength of correlation at different time lags, K , made possible by auto- and cross-correlation, provides intuitively meaningful information about the responses between interacting populations and within the cohorts of a single population, through their time series.

The autocorrelation functions of the catch and catch-per-unit-effort time series (Figure 3.1b) are presented in Figure 3.4. The form of these autocorrelations

strongly implies the existence of a cycle. The period for catch is about 17.3 years, while for CPUE it is 15.8 years.

The analysis of effort reveals a moving average (Box and Jenkins 1976). In the direct autocorrelation function of the effort series from 1958, no cycle is evident. If, however, we hypothesize a steady increase in the mean level of effort from 1958 to 1987, about which the effort series oscillates, which is obtained by simple linear regression of effort versus time, a different pattern is revealed. Substituting the yearly values of this linearly increasing mean level of effort into the definition of the autocorrelation function (Appendix 3.1) yields the revised autocorrelations graphed in Figure 3.5b. The characteristic pattern of a cycle is evident, with a period of 19.2 years.

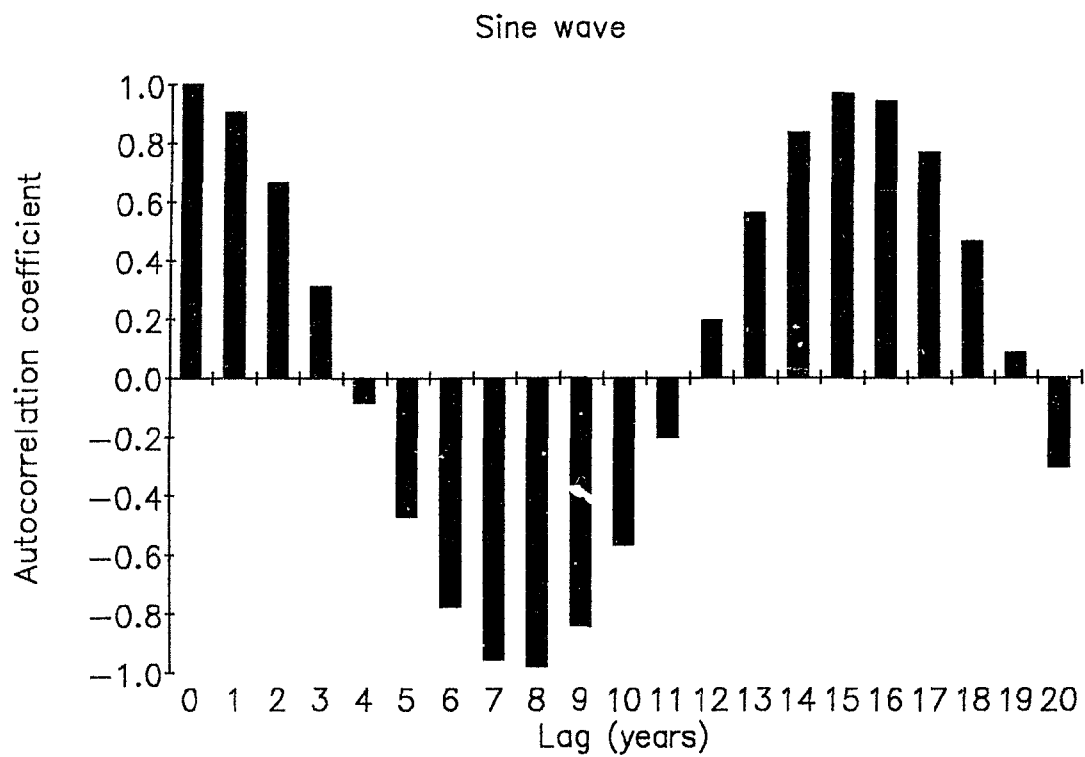


Figure 3.3 Autocorrelations of a 30 point sine wave time series whose period is chosen to be 15.5 years.

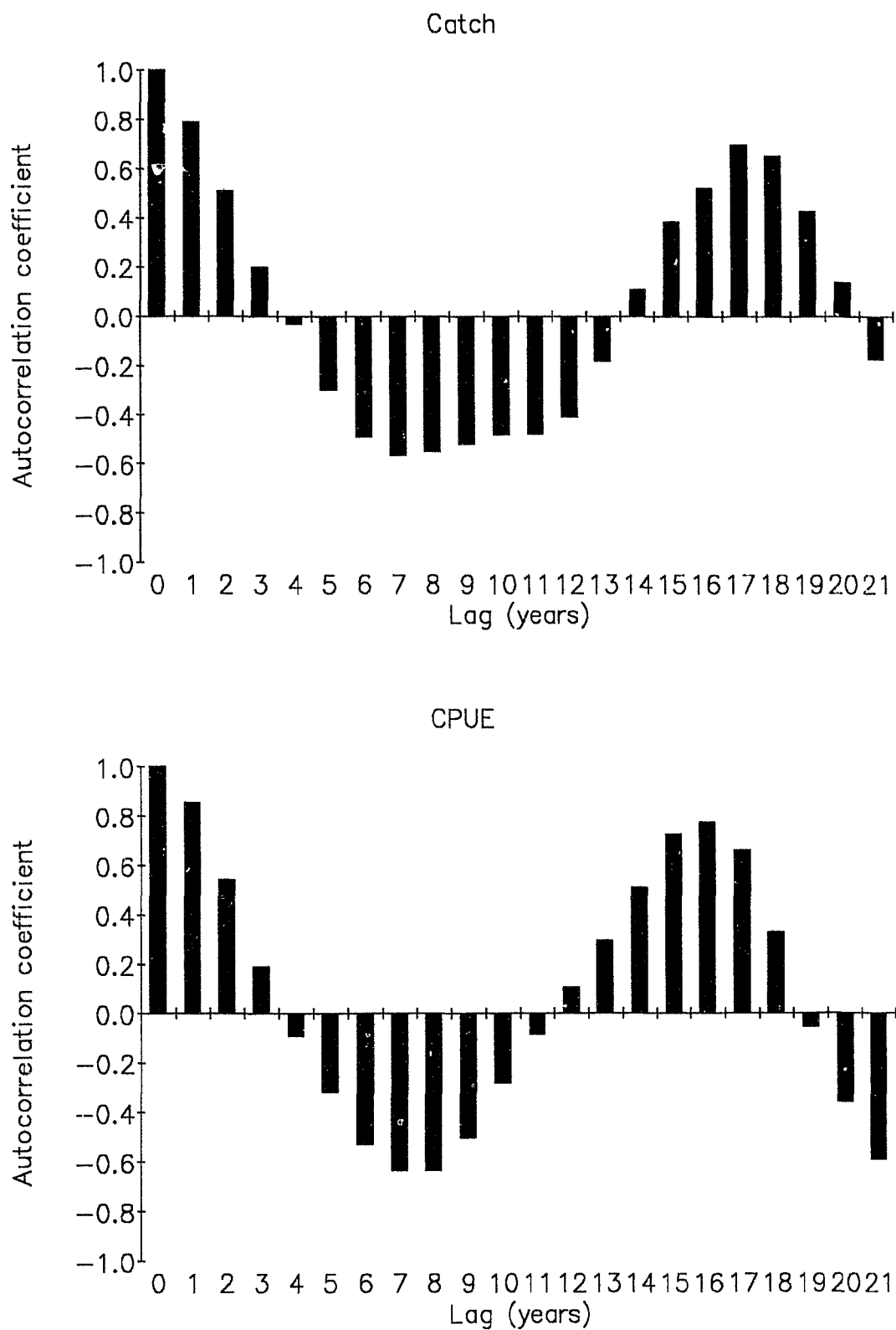


Figure 3.4. Autocorrelations of catch and catch per unit effort, 1958-1987.

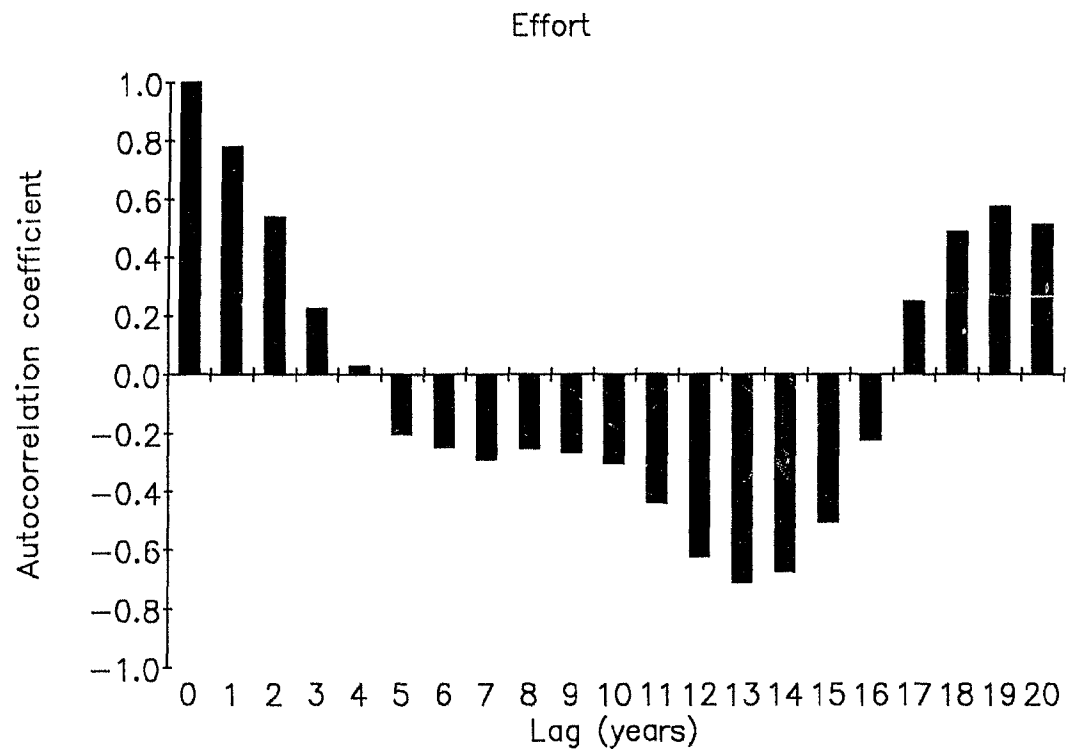


Figure 3.5. Autocorrelations of effort, 1958-1984, about a linearly increasing mean.0

The trend of steady increase in average effort over time is statistically significant (for slope b , $t(b) = 4.3$, $P(b) < 0.0001$) and implies a near doubling of average effort, measured as hours of dragging time, from 1958 to 1987.

Although statistically evident, the assumption of a process independent of the cycle, causing effort to steadily rise, would be more persuasive if that cause could be identified and documented. The steadily rising demand for seafood in the North American market is a likely explanation, due to a broadening of tastes, increased emphasis on healthier diet, and greater population size. This greater demand is expressed in the change in the real (1977-equivalent) price of scallops from 1958 to 1987, rising from 3 to about 8 Canadian dollars per kilo. The near tripling in price to the fisherman places pressure on the Georges Bank scallop fishery to increase production, and explains the steady increase in effort despite the lack of any parallel increase in CPUE.

Environmental Forcing Hypothesis

Most periodic environmental mechanisms that purport to explain cyclical variation in a population originate with the angular motions of the earth, the sun or the moon (Caddy

and Gulland 1983, Gilliland 1982). The diurnal cycle of the earth's rotation and the annual cycle of the earth's orbit plainly affect every aspect of the biosphere in temperate habitats. For the Georges Bank scallop cycle, the environmental forcing hypothesis, requiring an environmental variation with a 15 to 20 year period, is made plausible by the identification of the 18.6 year lunar nodal cycle. This 18.6 year rotation in the plane of the moon's elliptical orbit about the earth (Godin 1972) is known to strongly affect the tides and the surface layer of the oceans (Currie 1981, Loder and Garrett 1978, Cabilio et al. 1987). The current patterns on Georges Bank are largely driven by the tides (Greenberg 1983), and since currents must influence yearly recruitment success through the production of phytoplankton food, the match of larvae and food, the coincidence of larvae and predators, and the final settling place of spat, one reasonable explanation for the Georges Bank scallop cycle is that the 18.6 lunar cycle, mediated by yearly recruitment success, controls population size. The following evidence suggests, however, that this is not the cause:

(1) If recruitment were entrained by periodic environmental forcing, there should be evidence of a cycle in the autocorrelation function of the time series of recruitment, $\{R(YR)\}$. The pattern which would identify a cycle is illustrated by the autocorrelation analysis of stock size, $\{S(YR)\}$, (Figure 3.6a), where $\{S(YR)\}$ was

constructed from the same shell height-frequency data over the same time period (Chapter 2). The results of this analysis for $\{R(YR)\}$, presented in Figure 3.6b, exhibit no sign of an oscillation. The autocorrelation at lag 1 is, in fact, negative and no pattern typical of a cycle is evident.

(2) If there is both a stock-recruitment relationship, so that R was in part determined by the number of eggs spawned each year, together with an environmental cycle affecting the survival rate of each egg, then this exogenous forcing would be more evident in the $\{b(YR)\} = \{R(YR)/S(YR)\}$ time series, because it represents the survival rate per average egg in year YR . By dividing out the influence of egg production, and thus stocksize, b is a measure of recruitment success due to any other factors besides egg production which are important, and these are largely environmental. Yet again, the autocorrelation of b , illustrated in Figure 3.7, exhibits no indication of a cycle. The autocorrelation at lag 1 is also negative.

Any hypothetical environmental forcing must, therefore, affect the population by some process other than recruitment. The only other likely possibility is natural

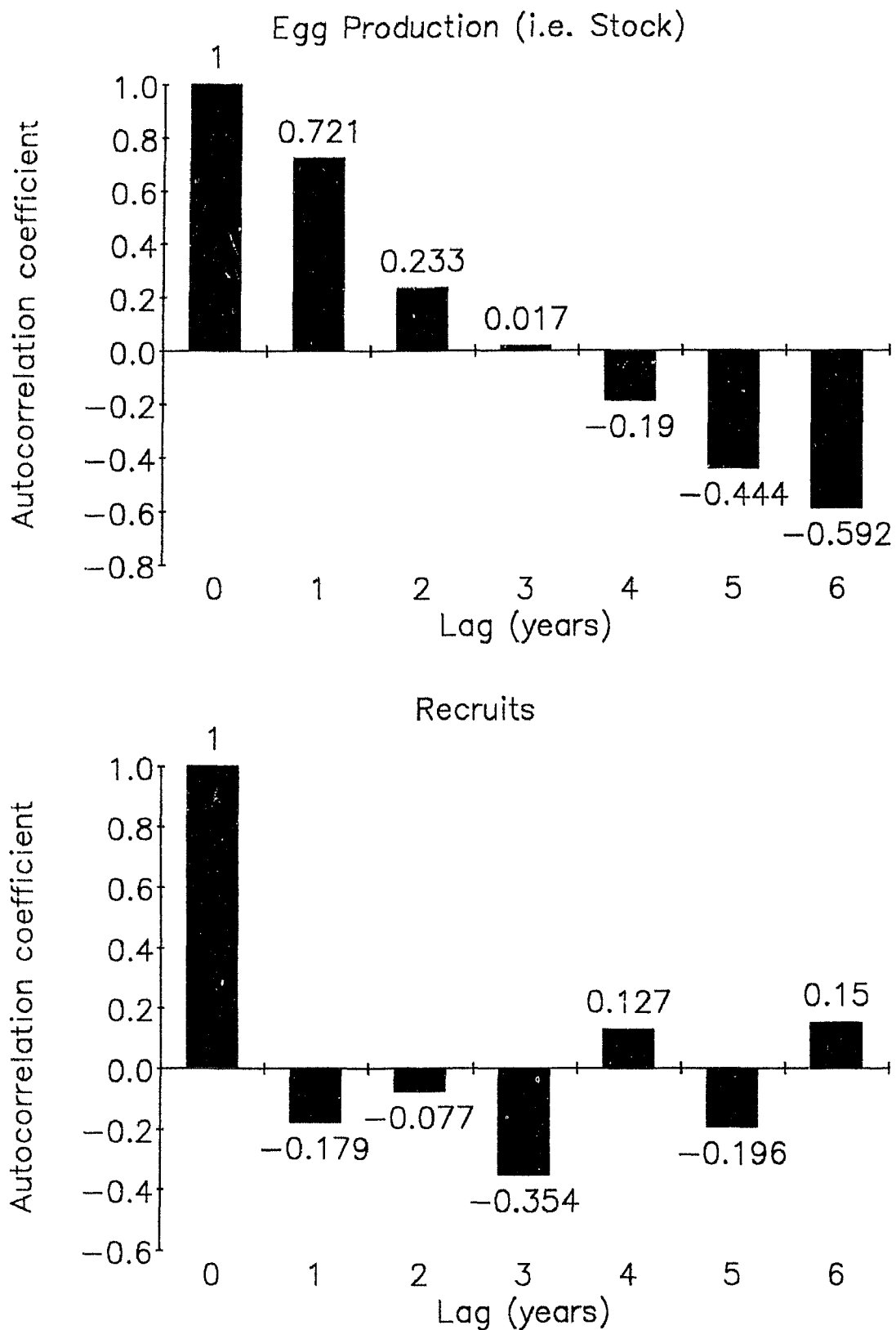


Figure 3.6. Autocorrelations of the time series for recruitment and egg production, 1977-1988.

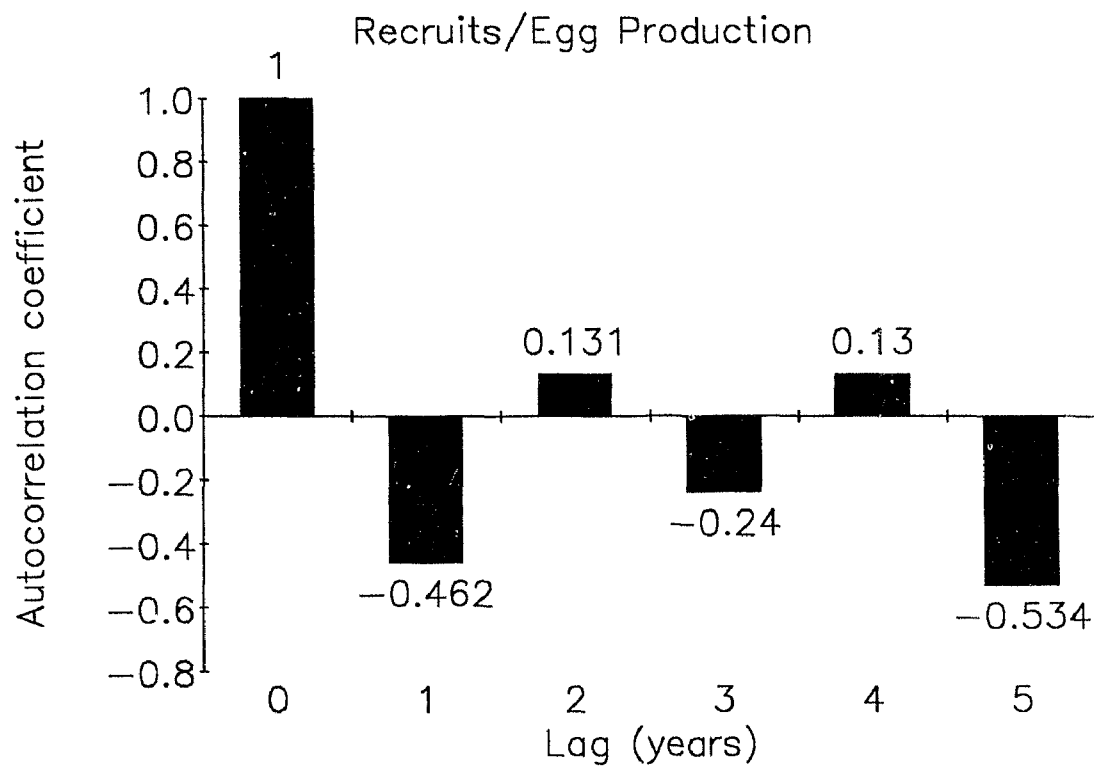


Figure 3.7. Autocorrelations of "b", recruitment divided by egg production, 1977-1986.

mortality in adults estimated by wide agreement at 0.1 (Merrill and Posgay 1964, MacDonald and Thompson 1986b). Fishing mortality is an order of magnitude higher at around 0.8 (Mohn et al. 1989, New England Fishery Management Council 1982), varying with the cycle between about 0.5 and 1.2. If adult mortality is the process which mediates the cycle, then since fishing rather than the marine environment is the far more dominant influence on adults, changes in fishing effort, rather than changes in the marine environment, are a more likely cause.

(3) One additional piece of evidence argues against environmental forcing. All proposed environmentally induced cycles are driven by the rotational motion of the earth, sun or moon, which have been nearly constant sine waves for geological time scales, certainly long before there was a fishery. Yet the time series of Figure 3.1b indicates that stock size as CPUE was stationary from 1944-58, exhibiting no cycle. Then around 1958, coincident with the commencement of intense fishing, the cycle began.

Just as they argue against forcing, these two observations represent important positive evidence in support of a second potential cause: (1) The sudden development of cycling simultaneous with the commencement of intense fishing implicates the fishery. (2) Fishing effort is identified as the dominant influence on adult stock size.

Schaefer Cycle Hypothesis

The second hypothesis is that the cycle represents a Schaefer predator-prey oscillation, in which fishermen, driven by economics, are the predators and scallops are the prey. Examples of this kind of cycle were noted in the Introduction.

It is straightforward to show that the Schaefer model (Schaefer 1954, 1957) is mathematically identical to the classical damped Lotka-Volterra model, and thus predicts the same kind of cycle (Schaefer 1954, Clark 1976a).

The Schaefer model has three fundamental assumptions: It supposes 1) a stock-recruitment relationship, 2) a catch rate linearly proportional to both stock size and effort, and 3) a rate of change of effort which varies in rough proportion to profit. By "Schaefer model" we shall mean the very broad class of Schaefer models which have for solution a predator-prey cycle. As we shall see, this includes the large majority which have deterministically stable spirals (foci) for solutions.

In the Lotka-Volterra model, recruitment increases linearly with stock size. This might apply for a population driven below its carrying capacity by continuous harvesting. In fact, a strict linear relationship is not necessary and cycles are predicted for a wide range of compensatory and depensatory reproduction curves (May 1973). Yearly recruitment in the Georges Bank scallop population is

correlated (at $P < 0.05$) with total yearly egg production (Chapter 2). Therefore the Georges Bank scallop system satisfies the first mathematical criterion required of a Schaefer cycle model. It will be shown that the very rough nature of that stock-recruitment relationship, resulting from very large yearly variations in recruitment success, is also a key feature of this fishery, required in the model to perturb and destabilize an otherwise globally stable steady state.

The second feature of a fishery which obeys the assumptions of a Schaefer model is that the catch rate should be jointly proportional to the levels of stock abundance and effort. This assumption is incorporated into nearly all theories of fisheries science, although evidence for it is often difficult to obtain. For Georges Bank scallops, CPUE and survey-estimated commercial biomass, as two measures of stock size, are proportional (Figure 3.2):

$$S_{\text{survey}} \sim \text{CPUE}.$$

$$\text{Since} \quad \text{CPUE} = \text{CATCH}/E,$$

to within their observed level of mutual agreement ($r=0.905$, $P=0.00007$) we may suppose S_{survey} and CPUE are both proportional to stock abundance, S , and therefore

$$\text{CATCH} \sim S * E,$$

showing that the Georges Bank scallop fishery satisfies the second criterion for a Schaefer model.

The third assumption describing the economic behavior of fishing effort is the most crucial. It states that the rate of change in effort should be proportional to the level of profit fishermen enjoy, which in turn depends on stock abundance. If profit is positive, boat numbers increase; if negative, i.e. if fishermen are losing money, boats leave the fishery. Intuitively compelling, this reasoning explains why the Schaefer model serves as the underlying basis of much of classical fisheries economics (Anderson 1977, Clark 1985).

The predator-prey behavior in the scallop fishery is understood as follows: When fish or scallops are abundant, their exploitation is financially attractive and boat numbers rise. After a time, this relatively large population of fishing boats reduces the stock below the level at which profit is zero, and so fishermen, again after a time, leave. Lower predation then allows stock reproduction to raise fish population size well above its zero-profit level and the cycle begins again.

The predator behavior of the Georges Bank scallop fleet may be seen in the time series for effort and stock (Figure 3.1b). During the time period of the cycle, 1958 onward, there were two clear peaks in fishstock, centered at 1960-61 and 1977-78. After both peaks, two to four years later,

there follows a similar peak in fishing effort. Furthermore, during both peaks in effort, stock levels declined rapidly. This suggests a classical predator population response; growth when prey are abundant, and decline when prey are hunted to low population levels where the relatively high predator numbers can no longer be sustained.

Formal demonstration of this interaction, essential to generate a Schaefer cycle, is presented in the cross-correlation analysis of stock and effort (Figure 3.8). The large correlation peak at lag $K = +3$ confirms the time series observation that effort levels follow scallop abundance with a response lag of about three years. The predator behavior is evident: a rise in stock size causes a rise in effort after a time. The slightly weaker negative correlation at lag $= -3$, also needed in any predator-prey dynamic, implies that when effort is high, three years later stock size will tend to be low.

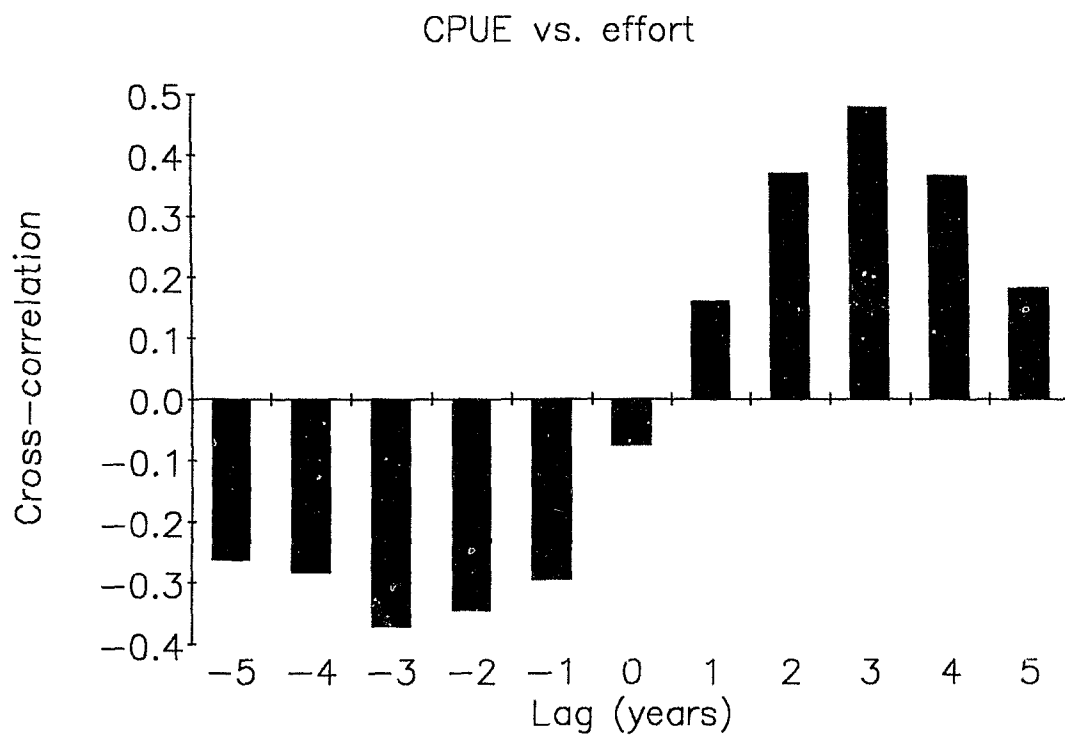


Figure 3.8. Cross-correlations of catch per unit effort in year YR, with effort in year YR+K, for each lag K, 1958-1984.

Two assumptions are implicit in the Schaefer model: the fishery is single-species, and effort must be unregulated by management, free to vary with stock size. The Georges Bank scallop fishery satisfies both of these assumptions. First, the vessels are designed specifically to drag for this mollusc, and by-catches of other species are generally quite small. Similarly, other kinds of bottom trawlers harvest a negligible percentage of the resident sea scallop population. Second, management restrictions in both the United States and Canada have, until recently, been designed to raise age-at-first-capture, rather than to limit effort (Sinclair et al. 1985, Serchuk 1984).

The cross-correlation function of stock, S , as egg production, versus recruitment, R , is presented in Figure 3.9. The relatively high cross-correlation between $R(YR)$ and $S(YR+K)$ at lag 0 is important independent evidence for a Schaefer cycle. If recruitment were driving stock size, as assumed in an environmental forcing hypothesis, then the peak would lie at $K = +3$ or $+4$, because big pulses in recruitment would give rise three years later to big pulses in numbers of adults. The peak at lag $K = 0$ implies the opposite is true; that on average, despite environmental noise, it is stock which drives recruitment as the Schaefer model assumes, and not the other way around.

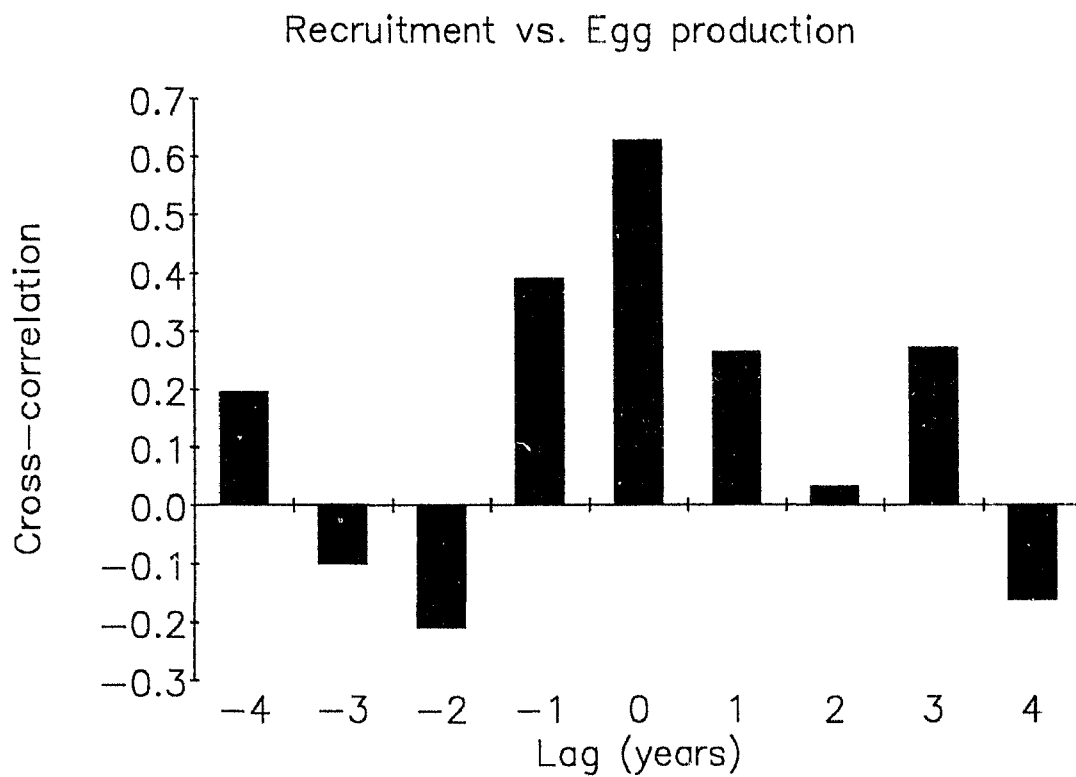


Figure 3.9. Cross-correlations of $R(YR)$ with $S(YR+K)$, 1977-1986, for each lag K , from survey data.

These cross-correlations for stock versus effort and recruitment versus egg production can be taken as identifying features of the predator-prey interaction and represent strong quantitative evidence substantiating the Schaefer predator-prey hypothesis.

To be certain that this is what is predicted by a predator-prey model, once full age-structure, density dependence and stochastic recruitment are considered explicitly, a discrete age-structured model was constructed and will be described below and in detail in Chapter 4.

Stochasticity of Recruitment

Usually Schaefer cycles are damped by the finite carrying capacity of the fishstock, i.e. by density dependence, and are expected to steadily diminish in amplitude, effort and stock eventually stabilizing at the classically predicted equilibrium. However, theoretical model investigations by Nisbet and Gurney (1982) showed that environmentally induced recruitment variability will counter this stabilizing tendency, and result in irregular, long-term predator-prey cycles of large amplitude. To illustrate, four numerical simulations of the Schaefer model are presented in Figure 3.10. The topmost is the classical deterministic model (Clark 1976a) where all the parameters

are held fixed. In the succeeding three simulations, increasing levels of recruitment variability are modeled by increasing the stochastic variation of "b", a parameter closely related to the "r" population growth coefficient of classical population ecology. As noted earlier, $b(YR) = R(YR)/S(YR)$ represents the survival rate of an average egg each year which is largely controlled by the marine environment. The stochastic variation of b is simulated by allowing it to vary from year to year, specifically by sampling from a known probability distribution (Hightower and Grossman 1985, Allen and McGlade 1986).

In the graph, the descending figures represent successively greater standard deviations of the normal distribution from which b is sampled. When the standard deviation is 0.75 of the mean, the steady state has become destabilized, undergoing a "stochastic bifurcation" (Horsthemke and Lefever 1984) to long-term irregular predator-prey cycles. This effect was first applied in a fisheries context by Allen and McGlade (1986).

In the case of Georges Bank scallops, the standard deviation of the time series for b is greater than 0.75, at 0.89 of the mean. This degree of recruitment variation is more than sufficient to sustain the kind of cycles predicted by the Schaefer model. And, indeed, the irregular

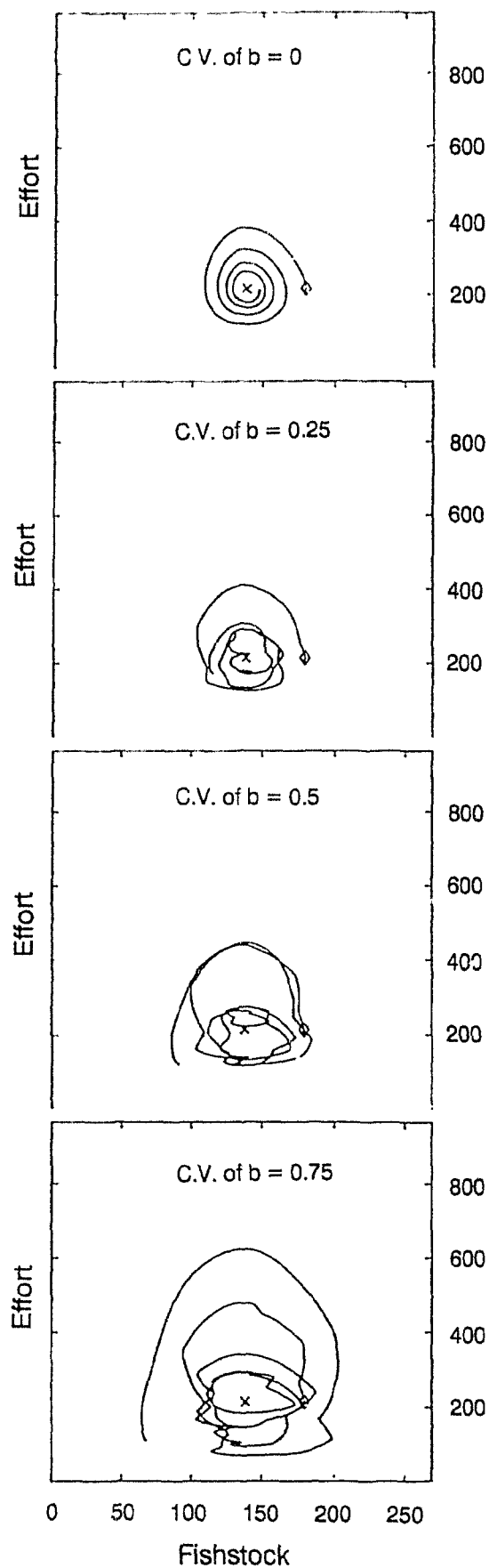


Figure 3.10.
Effect of
recruitment
stochasticity
on the 2-
variable
Schaefer model.

form of the cycles in the time series data, reflecting, in part, yearly variation in year class strength, is very similar in form to the model prediction. The negative autocorrelation of $\{R(YR)\}$ and $\{b(YR)\}$ at lag 1, and the general appearance of these autocorrelations, basically indistinguishable from white noise in a finite time series, bear witness to the random nature of the environmental signal. In this way, variability in the marine environment does appear to play a crucial role in causing the population to cycle, but it is a random rather than a cyclical variation.

Ricker Cycle Hypothesis

Two factors remain to be considered. First, age structure, interacting with various non-linear processes in a population, can generate oscillations (May et al. 1974, Nisbet and Gurney 1983, Cushing and Saleem 1984). Second, Ricker (1954) showed that, with or without age structure, a highly non-linear stock-recruitment relationship can cause a single-species population to cycle (see also Allen and Basasibwaki 1974, Levin and Goodyear 1980). The characteristic period is slightly more than double the mean age of fecundity. A Ricker cycle is anticipated when density dependence is strong, i.e. when recruitment

decreases rapidly with increasing stocksize. Since some evidence suggests that scallop recruitment is density-dependent in natural populations (Chapter 5), the Ricker mechanism represents a third possible hypothesis to explain the Georges Bank scallop cycle. However, two considerations make this unlikely as the primary cause.

First, as we have seen in Chapter 2, the stock-recruitment relationship for Georges Bank scallops is significantly increasing. Presumably this is because population density, under intense fishing, is kept well below the natural carrying capacity where crowding or intraspecific competition would limit recruitment and, therefore, more eggs tends to yield more recruits. In the cross-correlation analysis of Figure 3.9, the density dependence necessary for a Ricker cycle would be identified by a negative correlation at lag 0, since the slope of the stock recruitment curve should be steeply negative (with slope $b < -1$). The significant positive value obtained for Georges Bank scallops is direct evidence against a Ricker hypothesis.

Second, Ricker (1954) showed that the cycles he analyzed become strongly damped when harvesting drives population levels below the highly density-dependent range (Introduction). Yet with Georges Bank scallops, as pointed out in evidence against the forcing hypothesis, precisely the opposite effect was observed. As effort rose, the previously stable population was transformed into a cycle.

The Ricker mechanism is thereby ruled out as the primary cause.

A Discrete Model

To investigate the influence of age structure and density dependence and verify that they do not significantly alter the predictions of the Schaefer model, a discrete simulation model was constructed. The model includes age structure, a Schaefer effort response and a non-linear, highly variable stock-recruitment relationship. In addition, it assumes a constant price, p , for scallops and a constant cost per year per unit of fishing effort, c .

The time step is one year. Natural mortality for ages 2+ is assumed to be 0.1, a widely agreed upon value (Merrill and Posgay 1964, MacDonald and Thompson 1986b). The average level of fishing mortality (which determines the catchability) is 0.8.

The elements of the Georges Bank scallop population dynamics explicitly represented in the model are detailed in Chapter 4 and summarized as follows:

The variables are yearly scallop population numbers by age, and total scalloping effort in hours of dragging time. Implicit are two assumptions of any Schaefer dynamic; the fishery is single-species and effort is free to vary,

unregulated by management. A Shepherd, three-parameter stock-recruitment relationship was chosen for its generality (Shepherd 1982, Garrod 1983). The carrying capacity, is taken as double the recently observed level of stock biomass, although a variety of values of relative carrying capacity were simulated. The gear selectivity and weight-at-age were taken from the literature (Dickie 1955, Serchuk et al. 1979). The yearly catch of each age class is the natural extension of $CA = qES$, q being the usual Schaefer catchability. Effort changes proportionally to profit. The b -parameter, the linear proportionality coefficient between eggs and recruits representing yearly recruitment variation due to factors other than total egg production, is sampled yearly from a log-normal distribution, which has been shown to faithfully describe the real b -distribution (Chapter 2). Thus all the components of an age-structured, stochastic recruitment, density-dependent Schaefer fishery are incorporated in the model.

The key test, chosen here for identifying a predator-prey interaction, is the cross-correlation of stock and effort. The cross-correlations of the model output are presented in Figure 3.11, each series spanning 30- K time points (increasing lag K reduces the range of overlapping time series points), for comparison with the commercial series, 1958-1987. The close resemblance between model (Figure 3.11) and data (Figure 3.8) is strong evidence for the Schaefer hypothesis.

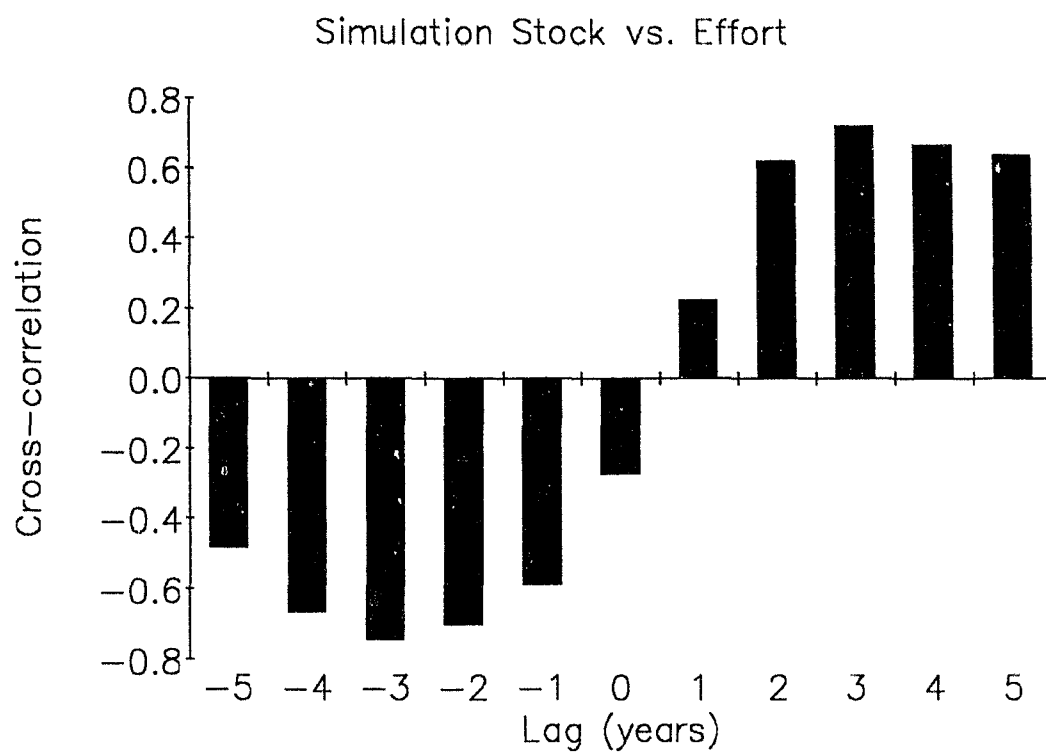


Figure 3.11. Cross-correlations from the discrete simulation comparing the output variables of stock from year YR and effort in year YR+K.

Discussion

The evidence for and against each hypothesis is summarized in Table 3.1.

The predicted periods of all three hypotheses fall within the range of 15-20 years observed in the data. Period, which would otherwise be an important validation criterion, cannot, therefore, be applied in this case.

One point of contention may be the reliability of the recruitment data which, if moderately accurate, would alone be sufficient to rule out environmental forcing. This potential unreliability would be due to a less consistent survey sampling at smaller shell sizes. Yet the comparison of independent measures of total numbers at sizes 70 mm and less by US and Canadian surveys (Appendix 1.2), finds the recruitment time series to be more accurate than the three measures of adult population abundance, probably due to the larger sample sizes (see also Serchuk and Wigley 1986b, Fig. 6). It is therefore unlikely that the measure of recruitment is significantly less reliable than adult stocksize, which autocorrelation analysis reveals to be plainly cyclic, in contrast to recruitment.

We may note two features of time evolution of stock abundance in the Georges Bank fishery that deviate from the predictions of the pure logistic Schaefer model. First, CPUE is, on average, about equal to and even a bit higher under the developed fishery, 1958-1987, than before, 1944-

Table 3.1. Evidence for three hypotheses of cycling in the Georges Bank scallop population.

Independent line of evidence	Implication for each hypothesis		
	Forcing	Schaefer	Ricker
Autocorrelation of R: No cycle in recruitment	argues strongly against		
Cycle commences suddenly coincident with a rapid rise in fishing effort	argues against	strongly supports	strongly opposes
Fishing is, by an order of magnitude, the primary cause of mortality among adults and possibly juveniles	argues against or neutral	supports	
Single-species fishery		necessary for a simple cycle	
Effort unregulated		necessary	
Significant stock-recruitment relationship		important evidence for	directly opposes; effectively refutes this hypothesis
Catch proportional to stock and effort		basic assumption of model	

Cross-correlation
of CPUE and Effort
(commercial data):
(i) Effort follows
stocksize by lag +3

argues
neither
for nor
against

prediction
strongly
substantiates
model

Cross-correlation
of CPUE and Effort
(commercial data):
(ii) Peaks in
Effort coincide
with declines
in CPUE at lag -3

prediction
strongly
substantiates
model

Cross-correlation of
Recruitment and Egg
Production (survey
data): Large positive
peak at lag 0
(not independent of
stock-recruitment
evidence)

argues
against

important
supporting
evidence

rules
out
this
hypothesis
by same
reasoning
as above

1958, when effort was rising (Figure 3.1). In a logistic Schaefer model, while catch at first rises, stock density can only decline with increasing levels of effort. Second, the outset of the cycle was marked by a substantial increase in CPUE, specifically during 1958-1961, rising from the previous steady state. These two closely related features are not, however, excluded within the general class of Schaefer models and, in particular, can occur for forms of density dependence stronger than a logistic. These considerations will motivate investigation of density dependence in Chapter 5.

The evidence thus suggests that the Georges Bank scallop fishery is governed by a Schaefer predator-prey cycle. The next question may be, How likely is it to observe this interaction as a significant dynamical mechanism in other exploited populations? There are two approaches possible without comprehensive investigation of other fisheries.

First, the models themselves afford a way to assess the structural robustness of the predator-prey cycle, considering a wide diversity of realistic modifications of the basic model and checking wide regions of the parameter space, to see if the cycle persists under these modifications. If so, this theoretical ubiquity suggests that the mechanism could conceivably be widespread. This question is considered in the Introduction and in the Conclusion and it is observed that the predator-prey cycle, based particularly on the

Kolmogorov theorem (1936), as noted by May (1973) and others, is very robust and is therefore anticipated in nearly all modifications of the basic Schaefer model and, often, globally in both the state and parameter spaces.

Second, we can analyze this particular case of Georges Bank scallops, to consider the circumstances which made the identification of the Schaefer mechanism in this situation unambiguous to determine whether those circumstances would be likely to inhere in other fisheries as well. If not, then the interaction may, in truth, be important, but difficult or impossible to substantiate. In particular, we would be like to know the chance of identifying Schaefer dynamics in real populations which are strongly but not solely affected by that mechanism.

The simple form of dynamical behavior, a cycle, is itself not exceedingly common. A number of clear hypotheses presented themselves, and the data unambiguously singled out one and excluded the other two. In other fisheries, there is no reason to expect the dynamics to be so simple. The features of a single-species fishery and unregulated effort are rare. The non-autocorrelated random nature of the environmental influence on this population may also be unusual. Equally fortunate was the ready availability of two independent sources of time series data, one stretching back to 1944 and the other based on a yearly scientific sample of 50,000 individuals, which agreed closely and corroborated the Schaefer hypothesis independently and

jointly. These circumstances which allowed a validation of one model to explain the cycle are not likely to be encountered often.

On the basis of these theoretical considerations, the Schaefer interaction between stock and fishing effort may be acting commonly but, combined with other important factors, be difficult to distinguish.

A second question is whether the primary factors driving changes in fishstock abundance are environmental or endogenous, the latter including fishing and fishstock population dynamics, in light of the example of the Georges Bank scallop fishery. The very magnitude of the yearly recruitment variation makes it essentially certain that recruitment processes involving environmental factors are also important in this population as in most others. This example suggests that not merely environment and not merely human predation, but both are major factors affecting the dynamics of intensively exploited fish populations.

Appendix 3.1. Auto- and cross-correlation formulas

The autocorrelation and cross-correlation functions used in this study are defined as follows:

For a time series, $\{x_i; i=1, n\}$, the autocorrelation at lag K is

$$\text{Autocor}(\{x\}, K) = \frac{\frac{1}{n-K} \sum_{i=1}^{n-K} [x_i - \bar{x}] [x_{i+K} - \bar{x}]}{\frac{1}{n} \sum_{i=1}^n [x_i - \bar{x}]^2}$$

(e.g. Box and Jenkins 1976). For the moving average of effort, employed in the autocorrelation function of Figure 3.5, the linear increasing trend in the effort time series, obtained by simple regression, is substituted for \bar{x} .

The cross-correlation function of $\{y_i; i=1, n-K\}$ with $\{z_{i+K}; i=1, n-K\}$ for positive lags, $K \geq 0$, is

$$\text{Xcor}+(\{y\}, \{z+K\}) = \frac{\frac{1}{n-K} \sum_{i=1}^{n-K} [y_i - \langle y \rangle_K^+] [z_{i+K} - \langle z \rangle_K^+]}{\sqrt{\frac{1}{n-K} \sum_{i=1}^{n-K} [y_i - \langle y \rangle_K^+]^2 \cdot \frac{1}{n-K} \sum_{i=1}^{n-K} [z_{i+K} - \langle z \rangle_K^+]^2}}$$

where

$$\langle y \rangle_K^+ = \frac{1}{n-K} \sum_{i=1}^{n-K} y_i$$

and

$$\langle z \rangle_K^+ = \frac{1}{n-K} \sum_{i=1}^{n-K} z_{i+K}$$

and for negative lags, $K < 0$, is

$$\text{Xcor}-(\{y\}, \{z+K\}) = \frac{\frac{1}{n-K} \sum_{i=1-K}^n [y_i - \langle y \rangle_K^-] [z_{i+K} - \langle z \rangle_K^-]}{\sqrt{\frac{1}{n-K} \sum_{i=1-K}^n [y_i - \langle y \rangle_K^-]^2 \quad \frac{1}{n-K} \sum_{i=1-K}^n [z_{i+K} - \langle z \rangle_K^-]^2}}$$

where

$$\langle Y \rangle_K = \frac{1}{n-K} \sum_{i=1-K}^n y_i$$

and

$$\langle Z \rangle_K = \frac{1}{n-K} \sum_{i=1-K}^n z_{i+K}$$

This definition, taken from the fully general formula of Kendall (1973, p. 40), was chosen to obviate bias among different lags, K . By normalizing each sum with the absolute value of $1/(n-K)$, rather than simply $1/n$, a common practice in estimation (e.g. Chatfield 1984), the cross-correlation of smaller lags are not favored.

CHAPTER 4

STOCHASTIC AGE-STRUCTURED SCHAEFER MODEL

Introduction

A discrete simulation model for an exploited population with age-structure, lognormal exogenous yearly recruitment variability, density-dependence, and a Schaefer mechanism of effort entry and exit is detailed in this chapter. This model was employed in Chapter 3 to ascertain that the qualities isolated to identify the Schaefer cycle-inducing mechanism are indeed predictions of the predator-prey hypothesis. In particular, the cross-correlations of simulation S (egg production) and E (effort), were shown to closely resemble the cross-correlations of these same variables in Georges Bank scallop time series data. It was claimed that this pattern of cross-correlations could be applied as a distinguishing quality of a Schaefer dynamical mechanism.

A number of discrete age-structured models, similar to the one constructed here, have been developed in recent years (Hightower and Grossman 1985, see also Getz and Haight 1989 for a comprehensive review). The principal contribution of this chapter is its method of parametrization. Because the kind and quantity of data available varies from fishery to fishery, and because of the increasing complexity of these models, parametrization is sometimes an ad hoc process. In this chapter, a method which is systematic and therefore repeatable is applied to

the Georges Bank scallop fishery to evaluate parameters for a discrete-time Schaefer model.

The basis of this method is an observation by Volterra (1927) that, in a pure Lotka-Volterra model, the average values of predator and prey abundance, over one full cycle, are exactly equal to the steady state values of the model rate equations. Using the discrete simulation model itself in a Monte Carlo analysis, it is shown that this feature extends, with a high degree of accuracy, to models which include the extensions and modifications of the pure Lotka-Volterra model that are incorporated to represent the Georges Bank scallop fishery.

The chapter consists of four parts: 1) the full set of model rate equations, 2) the method of parametrization, and 3) the fundamental parametrization assumption, followed by 4) a concluding discussion.

Model Equations

Four fundamental population processes are modelled: (1) Yearly cohort survival, in this discrete-time formulation, is modelled in the usual fashion, much like a Leslie matrix or VPA which incorporates a variable harvest mortality. (2) Population reproduction is modelled with a Shepherd (1982) density-dependent relationship between egg

production and subsequent age 2 recruitment. (3)

Recruitment is also subject to yearly environmental stochastic perturbation, simulated by sampling values of the population growth coefficient in Shepherd's model from a lognormal distribution, which was shown, in Chapter 2, to characterize Georges Bank scallop recruitment variability.

(4) Effort follows profit, as in a Schaefer model.

The input data, a complete list of variables, both dependent and independent, and all parameters are summarized in Tables 4.1, 4.2 and 4.3. (The "s" subscript stands for "simulation", to be distinguished from variables directly representing real data. The "m" subscript signifies that a variable is a time-averaged mean.)

Table 4.1. Summary of input data.

Data variable symbol	Data variable name	Description
{CA(YR);1958-1987}	Yearly catch time series	Figure 3.1a
{E(YR);1958-1987}	Yearly effort time series	Figure 3.1b
F	Fishing mortality- mean	0.8
M	Natural mortality- mean	0.1
{EGGS(AGE)}	Average eggs-per- female-at-age	Figure 1.2 & Table 1.3
{W(AGE)}	Meat-weight-at-age	
{GSC(AGE)}	Gear selectivity- commercial	see text
<u>Aggregates:</u>		
CA _m	Mean of {CA(YR);1958-1987}	
E _m	Mean of {E(YR);1958-1987}	

Table 4.2. Summary of simulation variables.

Variable symbol	Variable name	Description
<u>Independent:</u>		
AGE	Age	discrete; changes yearly at time of spawning
YR	Year	indicates discrete yearly spawning event and continuous processes, of survival, harvest and effort entry and exit from YR to YR+1
<u>Dependent:</u>		
$\{S_S(YR, AGE)\}$	Stock-simulation	Population numbers of each age and simulation year
$\{E_S(YR)\}$	Effort-simulation	represents total hours of dragging in each simulation year
$\{EPT_S(YR)\}$	Egg production total-simulation	Eq. 4.3; yearly eggs spawned by simulation parent stock
$\{SBIOM_S(YR)\}$	Stock biomass-simulation	Eq. 4.4; total population meat-weight biomass
$\{CA_S(YR)\}$	Catch-simulation	Eq. 4.7; annual harvest

Table 4.3. Summary of parameters.

Parameter symbol	Parameter name	Description
<u>Constants:</u>		
Q	Catchability	derived from reported fishing mortality, F
MDIS	Natural mortality in discrete time	derived from the accepted value of continuous time natural mortality, $M=0.1$
K		in Shepherd 3-parameter stock-recruitment relationship; both K and BETA chosen by modeller
BETA		
r_E	r-Effort	determines the response rate of Effort to profit; chosen by modeller to yield correct cycle period
p/c	(Landed price) / (Cost per unit effort)	derived from steady state-as-average assumption in Effort rate equation
<u>Functions of Age:</u>		
{GSC(AGE)}	Gear selectivity-commercial	applies to 3" ring size offshore dredge
{EGGS(AGE)}	Eggs per female	Fecundity and Weight vectors are the same as in Chapter 1, but expressed as functions of age
{W(AGE)}	Adductor muscle meat weights	

Table 4.3 (continued): Summary of parameters

Stochastic in time:

{BSHEP(YR)}	b-Shepherd	third parameter in Shepherd stock-recruitment; sampled each simulation year from lognormal distribution with mean $BSHEP_m$ and C.V. chosen by modeller
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Intermediates, employed in calculations from data:

{ $SR_m(AGE)$ }	Stock-relative-mean	derived from steady state-as-average assumption in cohort survival rate equation
{ $S_m(AGE)$ }	Stock-mean	absolute mean population numbers; $\alpha_S * SR_m(AGE)$
EPT_m	Egg production total-mean	
α_S	Alpha-simulation	
KFACTOR	K-Factor	determines the ratio of carrying capacity to mean population biomass; chosen as 1.7
$SBIOM_m$	Stock biomass-mean	

Initial values of the dynamical variables:

{ $S_{S0}(AGE)$ }	Stock-simulation-initial	recruitment age class set proportional to 1980 peak; all others are set to steady state values
E_{S0}	Effort-simulation-initial	set to steady state value

Independent Variables

With discrete time, the interpretation of the model equations depends on the choice of time-origin. For this model, the discrete time step is thought to change during the year when scallops spawn, roughly September 15. The eggs released are age 0, until the following September when they reach age 1. Continuous processes such as catch, natural mortality and change in boat number, occur from September 15 of simulation YR to September 15 of YR + 1.

In this way, independent variables of time and age coincide: the natural origin for age becomes the origin for both. The variable $\{S_S(YR, AGE)\}$ is numbers of scallops of each age on September 15 of that year and $E_S(YR)$ is total hours of time a scallop drag was towed on the bottom during the year YR (to YR + 1). Stock is a vector broken down by age, while effort is thought to be uniform.

Cohort Survival

The basic stock equation is as follows: For all age classes, survivors to the subsequent year are calculated as

$$\begin{aligned}
 S_S(YR+1, AGE+1) = & S_S(YR, AGE) \\
 & - Q * E_S(YR) * GSC(AGE) * S_S(YR, AGE) \\
 & - MDIS * S_S(YR, AGE).
 \end{aligned}
 \tag{4.1}$$

$Q * E_S(YR) * GSC(AGE) * S_S(YR,AGE)$ represents the number of scallops harvested in each year and age. Q is the catchability coefficient. The commercial gear selectivity, $\{GSC(AGE)\}$, taken (like the similar vector for survey gear employed in Chapter 1) from Dickie (1955) and Caddy (1972), expresses the age-specific capture efficiency of the commercial fishery, increasing to a flat asymptote at age 5. The presence of effort, E_S , and stock, S_S , as straightforward linear factors in the catch term is characteristic of Schaefer (and Lotka-Volterra) models. For Georges Bank scallops, this bilinearity was substantiated in Chapter 3 by the close agreement of commercial and survey measures of fishable biomass.

The (discrete-time step) natural mortality, $MDIS$, is assumed constant for scallops of age 2 and up, which was surprisingly well verified in field measurements by MacDonald and Thompson (1986b).

Density-Dependent Stochastic Recruitment

The total egg production each year, which is the measure of parent stock

$$EPT_S(YR) = \sum_{AGE=2}^{15} S_S(YR, AGE) * EGGS(AGE), \quad (4.2)$$

and the total biomass of the population

$$SBIOM_S(YR) = \sum_{AGE=2}^{15} S_S(YR, AGE) * W(AGE), \quad (4.3)$$

are employed in the Shepherd 3-parameter stock-recruitment relationship (Shepherd 1982, Garrod 1983) from which recruits are determined, stochastically, each simulation year,

$$S_S(YR+2, 2) = \frac{BSHEP(YR) * EPT_S(YR)}{[1 + (SBIOM_S(YR)/K)^{BETA}]}. \quad (4.4)$$

BSHEP(YR) is sampled from a log-normal distribution with a fixed mean, $BSHEP_m$, and a coefficient of variation chosen by the modeller.

Schaefer Response of Fishing Effort

In addition, to stock population dynamics, the Schaefer response of effort to changing stock abundance and, thus, of profit is also incorporated. The effort variable, $E_S(YR)$, changes at each time step according to the equation 4.6:

$$E_S(YR+1) = E_S(YR) + r_E * \left[\frac{p * CA_S(YR) - c * E_S(YR)}{c * E_S(YR)} \right] * E_S(YR). \quad (4.5)$$

Since total yearly model catch is

$$CA_S(YR) = \left[\sum_{AGE=2}^{15} GSC(AGE) * W(AGE) * S_S(YR, AGE) \right] * Q * E_S(YR). \quad (4.6)$$

$$p * CA_S(YR) = \text{Gross yearly revenues.}$$

Likewise,

c = constant cost per unit effort per year,

and

$c * E_S(YR)$ = total yearly costs incurred in the fishery

so

$$\left[\frac{p * CA_S(YR) - c * E_S(YR)}{c * E_S(YR)} \right] = \left[\frac{p}{c} * \frac{CA_S(YR)}{E_S(YR)} - 1 \right]$$

represents the ratio of profit to cost, which expresses profit as a percentage. If we set r_E equal to 1, Eq. 4.5 therefore says that a 10% profit causes effort to increase by 10% per year. This seems intuitively reasonable, so by expressing the effort rate equation in this form, we obtain two advantages: First, an estimate of r_E , somewhere in the neighborhood of 1, can be supposed. Second, p/c may now be estimated as a single parameter. As we shall see, the value of p/c may be obtained by the equilibrium-as-average assumption, so that the vital economic parameters can be determined without recourse to detailed research into the cost of fishing and price of fish.

so

$$MDIS = 1 - e^{-M}. \quad (4.7)$$

Step 2: Catchability is calculated from fishing mortality. From the Georges Bank scallop fishery literature (Robert and Black 1990, New England Fishery Management Council 1981), we obtain an independent estimate of

$$F = 0.8.$$

Defining

$$Q * E_m = 1 - e^{-F},$$

we obtain Q:

$$Q = 1 - e^{-F/E_m}. \quad (4.8)$$

F refers to average fishing mortality on adults. For younger age classes, F, and thus Q, will be smaller, which is expressed in {GSC(AGE)}.

Step 3: Cohort survival generates relative populations-at-age. The steady state numbers at age are derived using the basic survival relationship between age classes in a single cohort, the stationary age distribution, first derived by Lotka (1907). The cohort survival rate equation, 4.1, at the steady state, yields Eq. 4.9.

$$SR_m(AGE) = SR_m(AGE-1) - Q * E_m * GSC(AGE-1) * SR_m(AGE-1) - MDIS * SR_m(AGE-1). \quad (4.9)$$

$SR_m(AGE)$ represents the relative mean population of each simulation age class. The steady state-as-average assumption is applied here for the first time in this parametrization procedure, substituting the mean level of effort from the data time series, E_m , in place of the steady state value.

Step 4: Relative populations are scaled to obtain absolute numbers at age. Analogous to the method used for (real) population estimates in Chapter 1, total catch is the absolute quantity by which absolute population numbers are calculated from relative ones. The mean catch, by weight is, according to the Schaefer model, a linear function of mean effort E_m and of mean stocksize, S_m :

$$CA_m = Q * E_m * \sum_{AGE} GSC(AGE) * S_m(AGE) * W(AGE). \quad (4.10)$$

We define a scaling factor, α_S , relating the relative measure of stocksize to the absolute measure:

$$S_m(AGE) = \alpha_S * SR_m(AGE). \quad (4.11)$$

$SR_m(2)$ may be set arbitrarily to a constant. We choose 1, and iterate Eq. 4.9.

$$SR_m(AGE) = SR_m(AGE-1) [1 - Q * E_m * GSC(AGE-1) - MDIS], \quad (4.9)$$

to obtain $\{SR_m(AGE)\}$ for older ages, $AGE = 3, 4, 5$ etc.

Inserting Eq. 4.11 into Eq. 4.10, we have

$$CA_m = Q * E_m * \sum_{AGE} GSC(AGE) * \alpha_S * SR_m(AGE) * W(AGE), \quad (4.12)$$

which yields an estimate of the simulation conversion coefficient:

$$\alpha_S = CA_m / \left[Q * E_m * \sum_{AGE} GSC(AGE) * SR_m(AGE) * W(AGE) \right]. \quad (4.13)$$

Then

$$S_m(AGE) = \alpha_S * SR_m(AGE), \quad (4.14)$$

for all ages.

Step 5: Population reproduction. The parameters needed to calculate the Shepherd population growth coefficient (analogous to "b"), are then calculated directly: The stock biomass mean is

$$SBIOM_m = \sum_{AGE} S_m(AGE) * W(AGE) \quad (4.15)$$

and the mean egg production total is calculated as

$$EPT_m = \sum_{AGE} S_m(AGE) * EGGS(AGE). \quad (4.16)$$

The parameters BETA and KFACTOR, in Eq. 4.4, may then be chosen according to the form of density dependence. BETA affects the steepness of the decline in recruitment success at high densities. The carrying capacity, $K = KFACTOR * SBIOM_m$, is expressed as a factor of the mean stock biomass. Here they are chosen as $BETA = 2$ and $KFACTOR = 1.7$.

Employing the steady state-as-mean approximation a second time, substituting mean variable values for steady state values in the steady state condition of the Shepherd stock-recruitment relationship, Eq. 4.4, yields

$$S_m(2) = \frac{BSHEP_m * EPT_m}{[1 + (SBIOM_m / K)^{BETA}]}, \quad (4.17)$$

implying

$$BSHEP_m = \frac{S_m(2) * [1 + (SBIOM_m / K)^{BETA}]}{EPT_m} . \quad (4.18)$$

Step 6: Effort parameters. The average-as-steady state assumption is applied a third and last time to the effort rate of change Eq. 4.6. In a steady state, $E_S(YR+1) = E_S(YR)$. Assuming

$$E_S(\text{steady state}) = E_m$$

and

$$CA_S(\text{steady state}) = CA_m,$$

Eq. 4 6 at steady state yields

$$0 = r_E * [p * CA_m - c * E_m],$$

or

$$p/c = E_m/CA_m. \quad (4.19)$$

Testing the Assumption of Steady States as Means

The principal assumption of this method of parametrization is that the steady state values of the model are equal to mean values of the variables effort and catch, E_m and CA_m , obtained directly from the real time series by averaging over the years 1958 to 1987, nearly two cycle periods. This connection between model and data was applied three times, in parametrization steps 3, 4 and 6, respectively, substituting E_m , CA_m , and E_m and CA_m together, for their steady state equivalents. This equality is likely to be roughly true since any oscillation will tend to drive the variables, for roughly equal times (1/2 period each) and (more roughly) equal distances above and below their steady state values in the phase plane.

The first proof is due to Volterra. In the same early work that proposed the Lotka-Volterra model (Volterra 1927, Scudo 1971), Volterra proved that the means over one cycle were mathematically identical to the steady states of the two variables of predator and prey. This assumption is now analyzed formally using a Monte Carlo adaptation of the simulation model itself to determine how broadly it may be extended.

Ideally we seek to establish whether the steady state of the model is well-approximated by the averages of the real time series summed over 30 years of cycling. Although there are unknown factors that must affect this

approximation, we can determine, for a specific subset of predator-prey models, whether this assumption is robust. In particular, the discrete simulation model embodies dynamical modifications of the pure Lotka-Volterra model which are almost certainly of considerable influence, including age-structure, density dependence in recruitment, and a large degree of exogenous recruitment variability.

Monte Carlo Algorithm

The method is a form of sensitivity analysis. Modifying Volterra's model, we test the robustness of this property of predator-prey systems under a number of important alterations simultaneously.

Running the discrete Schaefer simulation 1000 times, each with a new lognormal random sample of the $BSHEP_m$ parameter, the 30-year time averages of effort and catch were calculated from each run.

Monte Carlo Results

The resulting frequency distributions are presented in Figures 4.1 and 4.2. Three levels of recruitment stochasticity were tested, allowing $BSHEP_m$ to vary annually in the simulation by sampling from a distribution with

coefficients of variation of 0.20, 0.35 and 0.45. These were chosen to span the range of recruitment stochasticity which produced a cycle amplitude (measured by overall standard deviation) similar to that observed in the real system.

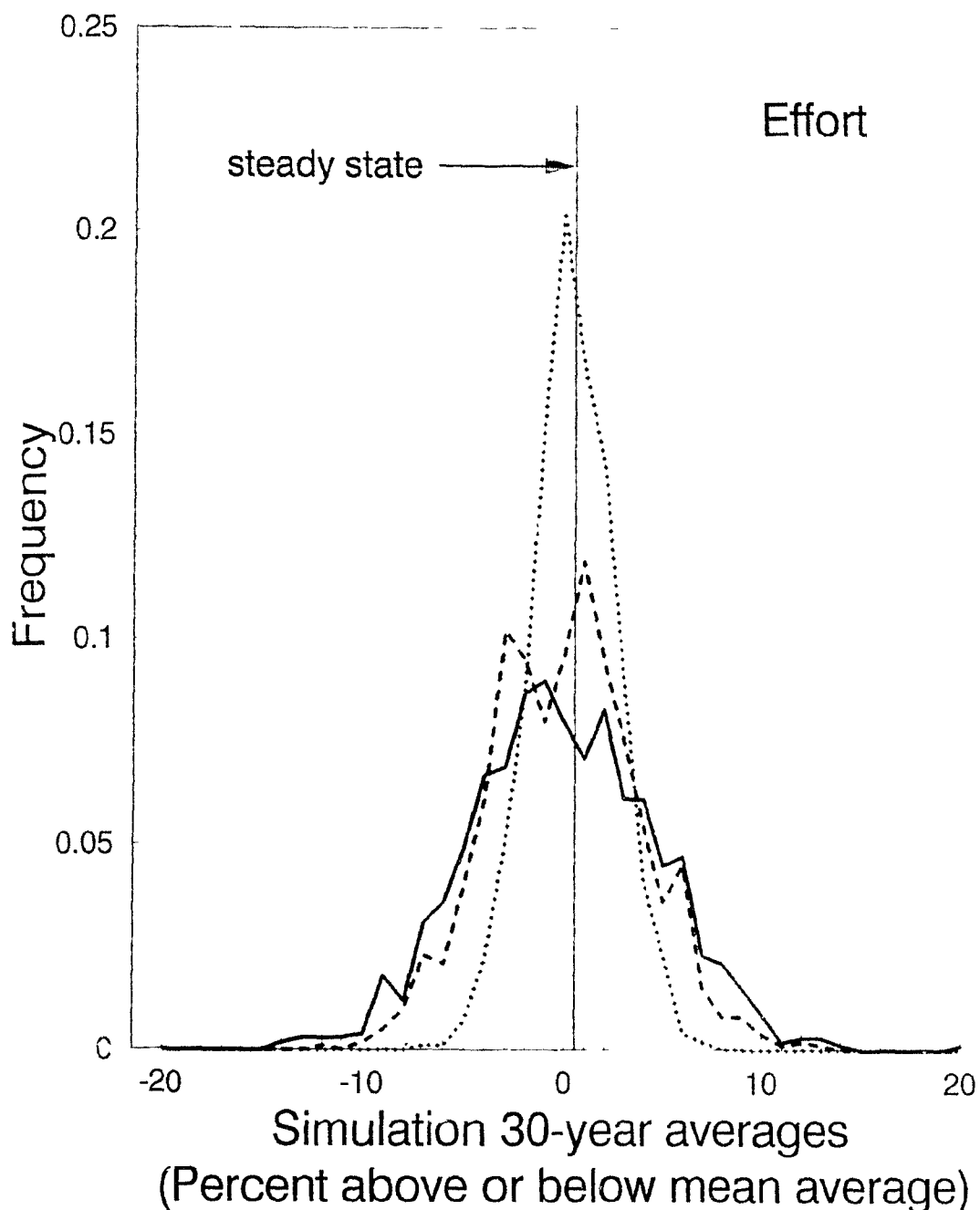


Figure 4.1. Frequency distribution of simulation time averages for effort in 1000 runs of the discrete Schaefer model with age structure, density dependence and lognormal recruitment stochasticity. The zero value along the x-axis is mean effort. The steady state is the level to which the simulation settles when recruitment is not stochastic. The range of lognormal recruitment variabilities is indicated by the 3 histograms representing BSHEP_m sampling coefficients of variation of 0.20 (dotted curve), 0.35 (dashed) and 0.45 (solid).

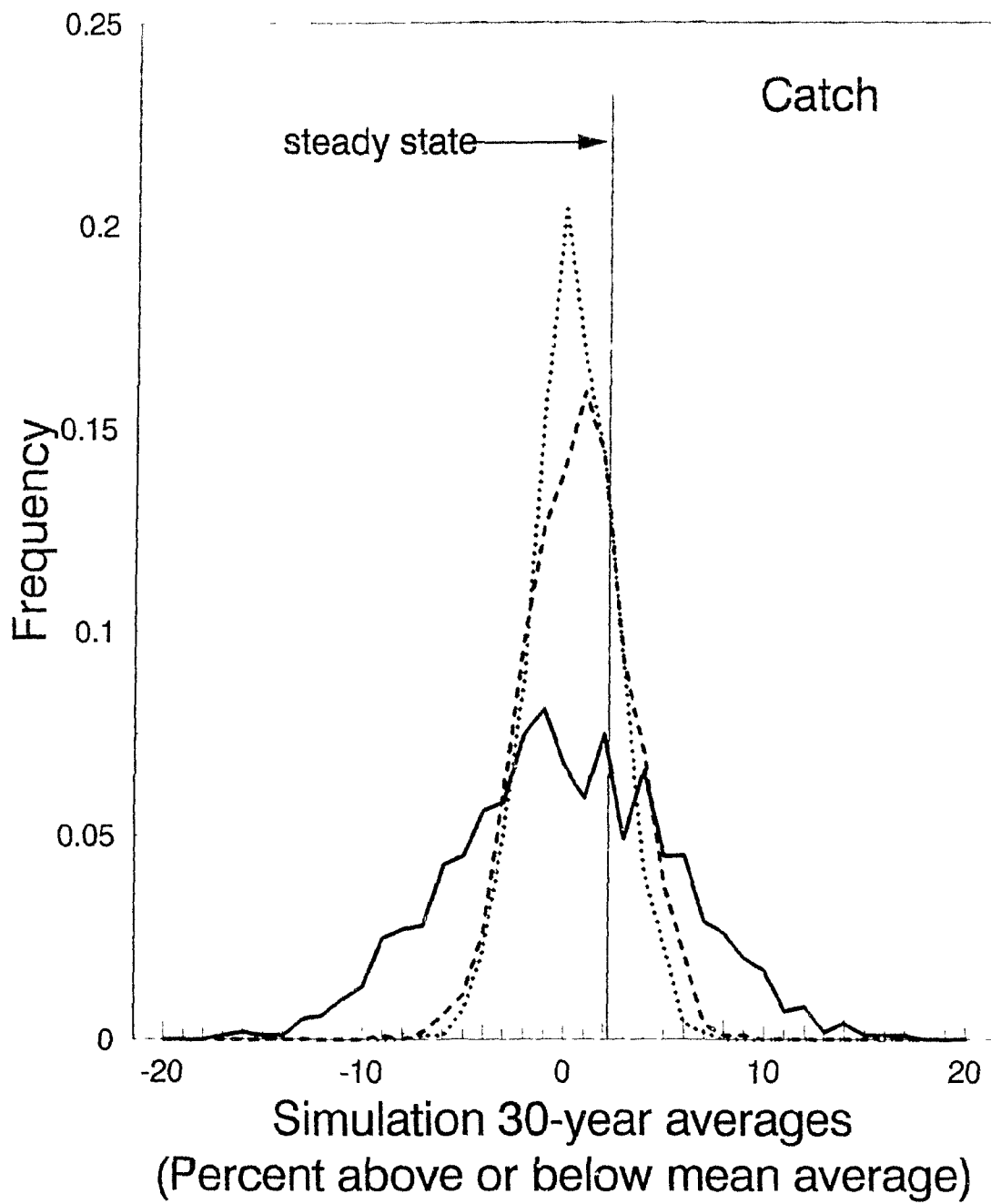


Figure 4.2. Histogram of catch simulation averages compared with the steady state, as in Figure 4.1.

Overall, the difference between the steady states and the means of 1000 30-year averages, for the case of (maximum) 0.45 recruitment variability (Figures 4.1 and 4.2), were 0.5% and 2.2% for effort and catch respectively. The simulation averages were distributed over standard deviations of 4.5 and 5.2%. Thus, even considering this relatively small dispersion of averages, the steady states fell well within one standard deviation. Considering also the 3-20% standard error in the data (estimated for 12 year survey time series averages in Appendix 1.2), the 0.5-2% deviation of means from steady states implies that setting steady states to their (dynamical) time averages is a relatively safe approximation. Such close agreement was observed even though 30 years in the simulation did not quite span a full 2 cycles, while the autocorrelation functions of simulation effort and catch, with peaks at lags of 17 to 18 years, imply 34 to 36 years for a 2 cycle period. The 30-year simulation time series length and 17-18 year simulation cycle period were chosen to correspond to the real system time series length of 1958 to 1987 and to the observed cycle period expressed in the peak autocorrelation lags (Figures 3.4 and 3.5).

Discussion

Volterra proved the equality of means and steady states for the purely bilinear deterministic model. This Monte Carlo analysis suggests that the Volterra assumption continues to hold when the pure model is elaborated by adding (i) stochastic (ii) non-linear prey recruitment, (iii) a full age structure, and by less significant modifications, including explicit consideration of (iv) gear capture efficiency which decreases with scallop size, and (v) a fecundity with age which increases allometrically, implying a stock measure, egg production, which is non-linearly (but still monotonically) related to the original prey stock measure of population numbers implicit in Volterra's formulation. In addition, the time averages were taken over time series of less than two full periods. Furthermore, this model is formulated in discrete time rather than the continuous time of the Lotka-Volterra model.

The outcome of the Monte Carlo analysis appears to show that the approximation is robust under a wide number of important improvements on the original model, which are likely to characterize many real predator-prey systems, and in particular, the Georges Bank scallop fishery.

Having passed such a rigorous test, with such close agreement, the assumption of steady states as means could conceivably be applied to a variety of predator-prey systems and be employed as a satisfactory basis for a self-

consistent parametrization method. In each model where parameters were to be evaluated by setting the steady states of the model equal to the means of the time series data, this assumption could be subjected to a similar test to assess its reliability.

We may ask whether it is reasonable to set the steady states equal to time averages if we are not sure that the Georges Bank scallop cycle is, in fact, driven by a Schaefer-cycle mechanism. After all, this model is used to answer precisely that question. But because the model is used to obtain qualitative features, the aim, in parametrization, is to determine the neighborhood of parameter values where the Georges scallop fishery must lie if it is driven by a Schaefer model. If we propose the Schaefer model as a hypothesis, it is with those parameters that it should be examined.

A practical advantage is obtained by this method of parameter estimation. The value of p/c is now obtained as a consequence of the model steady state, applying the time average approximation to the effort rate equation, without need of detailed financial data. True price and cost are sometimes difficult to ascertain, even when financial data are available, because, in particular, the opportunity cost of fishing is an often very uncertain quantity.

CHAPTER 5

DENSITY DEPENDENCE

Introduction

A fundamental question of scallop life history strategy is how the populations persist over long times, when yearly egg, larval and settlement phases are subject to such high rates of mortality (Chapter 1) and are so variable (Chapter 2). This question is closely related to the stock-recruitment and fishery dynamics of Chapters 2 and 3, and here I will extend and develop those lines of investigation. Three important elements of scallop reproduction act to mitigate environmental variability, namely high fecundity, long lifespan and density-dependent recruitment. Evidence is presented in this chapter to demonstrate the importance of these three elements of scallop reproduction which, taken together, represent a strategy typical of marine bivalves.

I will argue that density dependence in a fished population, like Georges Bank scallops, can be demonstrated by comparing the age structures of the population before and after intense harvesting. From changes in the average lifespan, the change in average lifetime egg production may be inferred. In a steady state, lifetime egg production equals eggs per recruit, which is, in turn, equal to the reciprocal of the survival probability of an egg to maturity. In heavily fished populations, average reproductive lifetime is cut short. When the relatively much higher fecundity of older fish or molluscs is also

considered, average lifetime egg production in the harvested fishstock becomes smaller still. If a fished population persists, even though females have the chance to release only a small fraction of their natural lifetime reproductive output in the short time from maturity to capture, it must be that the rate at which those eggs survive to maturity is greater. If recruit per egg did not rise accordingly, the greatly reduced supply of eggs would mean lower average yearly recruitment, both in absolute numbers and as a fraction of a declining parent stock, which, in a matter of a few generations, would lead the population to extinction.

One way to consider scallop reproductive characters is by comparison with the most abundant demersal fish in the Northwest Atlantic Shelf waters, namely cod (Gadus morhua). The reproductive strategies of molluscs and groundfish are distinguished, in particular, by total fecundity. Marine bivalves are among the most fecund animals on earth, particularly over a full lifetime, so that this two-species comparison may have general implications for other important bivalve species.

One may first ask why a pelagic larval stage was selected to carry spawn through the most critical phase in scallop reproduction. One answer, convincingly promoted by Vance (1973a, b) is that production of abundant small eggs and larvae which float freely and feed in the water column, is one of three evolutionarily stable strategies for marine benthic invertebrates, intermediate strategies yielding

lower fitness. Extending and corroborating the earlier work of Thorson (1946, 1950), pelagic larval development was shown by Vance to be theoretically superior when pelagic food was relatively abundant, temperatures relatively warm, water relatively shallow and pelagic predation relatively lower than benthic predation. Georges Bank does indeed largely satisfy these environmental criteria, and in particular Vances's arguments may strengthen the hypothesis that the warmer, phytoplankton-rich central mixed waters serve as a kind of larval incubator, a possibility mentioned in Chapter 2.

Lifespan

Scallops have a lower natural mortality than cod. The widely accepted values are $M = 0.1$ (MacDonald and Thompson 1986b, Merrill and Posgay 1964, Dickie 1955) for scallops and $M = 0.2$ for cod (Baird and Bishop 1989) and other groundfish, yielding the survival probabilities to a given age illustrated in Figure 5.1. Scallop natural lifespan is estimated at 20 years (MacDonald 1986). Thus, conservatively assuming that age 3 and 4 scallops are not mature, this allows a female living a full lifespan 15 successive spawning seasons to procreate the single daughter that will replace her. Among a population, some of which

will not live a full 20 years, assuming a continuous mortality of $M = 0.1$, an average age 5+ female spawns 8 successive seasons (see Appendix 5.1). It is widely understood that iteroparity helps stabilize populations, yet it is worth noting that bivalves, among marine species, are particularly long-lived. The ocean quahog, Arctica islandica, comprising 25% of total benthic biomass on Georges Bank and by far the most abundant mollusc (Theroux and Grosslein 1987), lives in exploitable numbers past the age of 100 (Murawski et al. 1982).

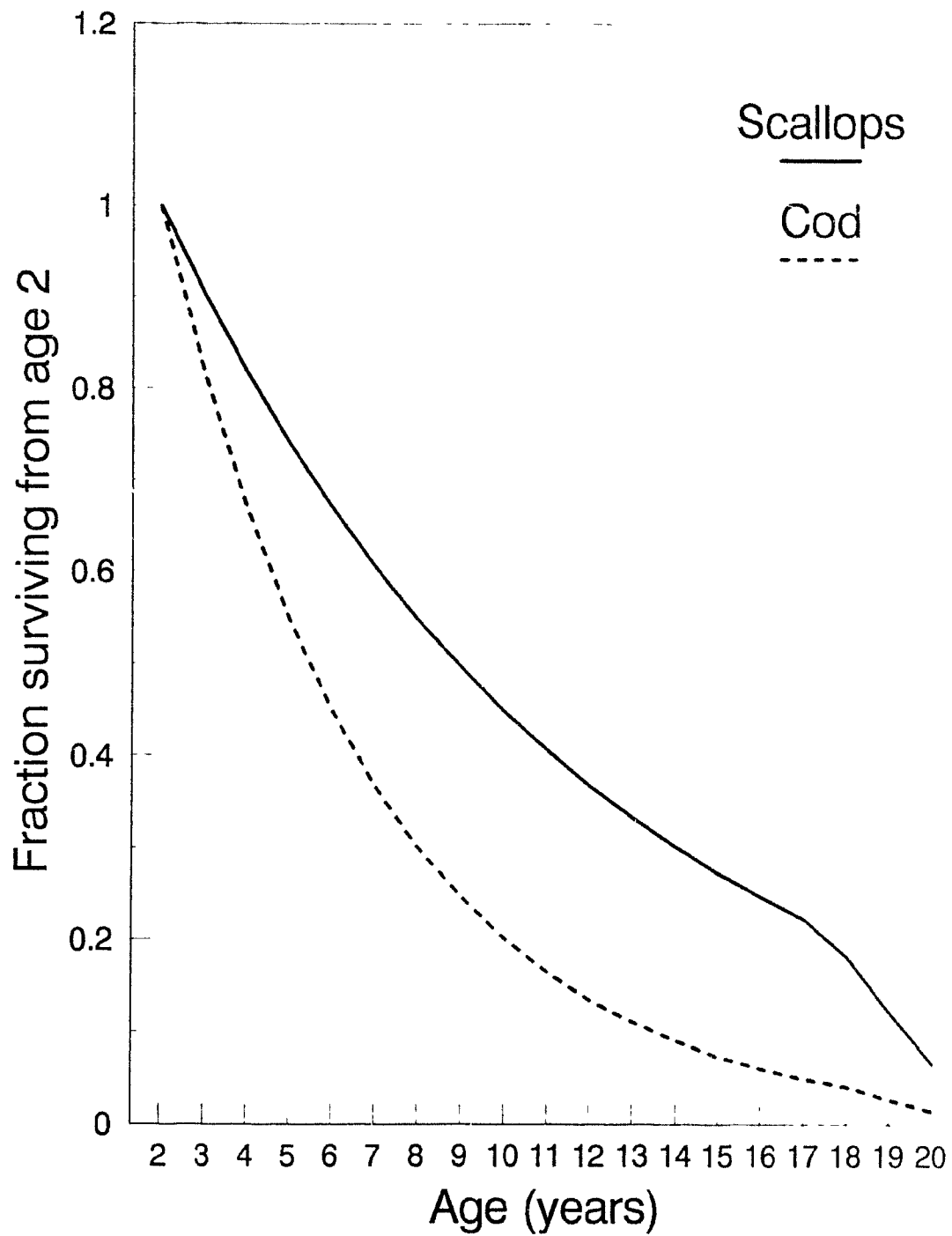


Figure 5.1. Scallop and cod survival probability from age 2 onward: a comparison.

Fecundity

Scallops produce far more eggs than cod. A comparison of age-specific scallop egg production employed in Chapters 1 and 2 with fecundity measured by May (1967) for Newfoundland cod is illustrated in Figure 5.2. An age 10 cod produces about 2 million eggs at yearly spawning, the same aged scallop about 200 million. Scallop eggs are much smaller upon release, about 64 to 72 microns (Culliney 1974, Langton et al. 1987, MacDonald and Thompson 1986a), compared with cod eggs of about 1.5 mm (May 1967). Thus, considering both fecundity and survival to each spawning age, it is calculated in Appendix 5.1 that a female scallop spawns 1.3 billion eggs, a codfish 5 million, in an average natural lifetime. On average only one of these will reach age 2. Per gram of whole body weight, a female scallop produces 3.4 million eggs and cod 2100.

Scallops, like most bivalves, cannot migrate (Baird 1954, Posgay 1963, Melvin et al. 1985) as fish do, and so rely to a much greater extent on chance to transport their larval spawn to favorable settlement locations. This may, in part, explain the evolution of a more "r-selected" life history strategy, scallops producing 250 times more eggs in a lifetime than cod, and over 1600 times as many eggs per gram of body weight.

By this strategy, population stability is achieved. In

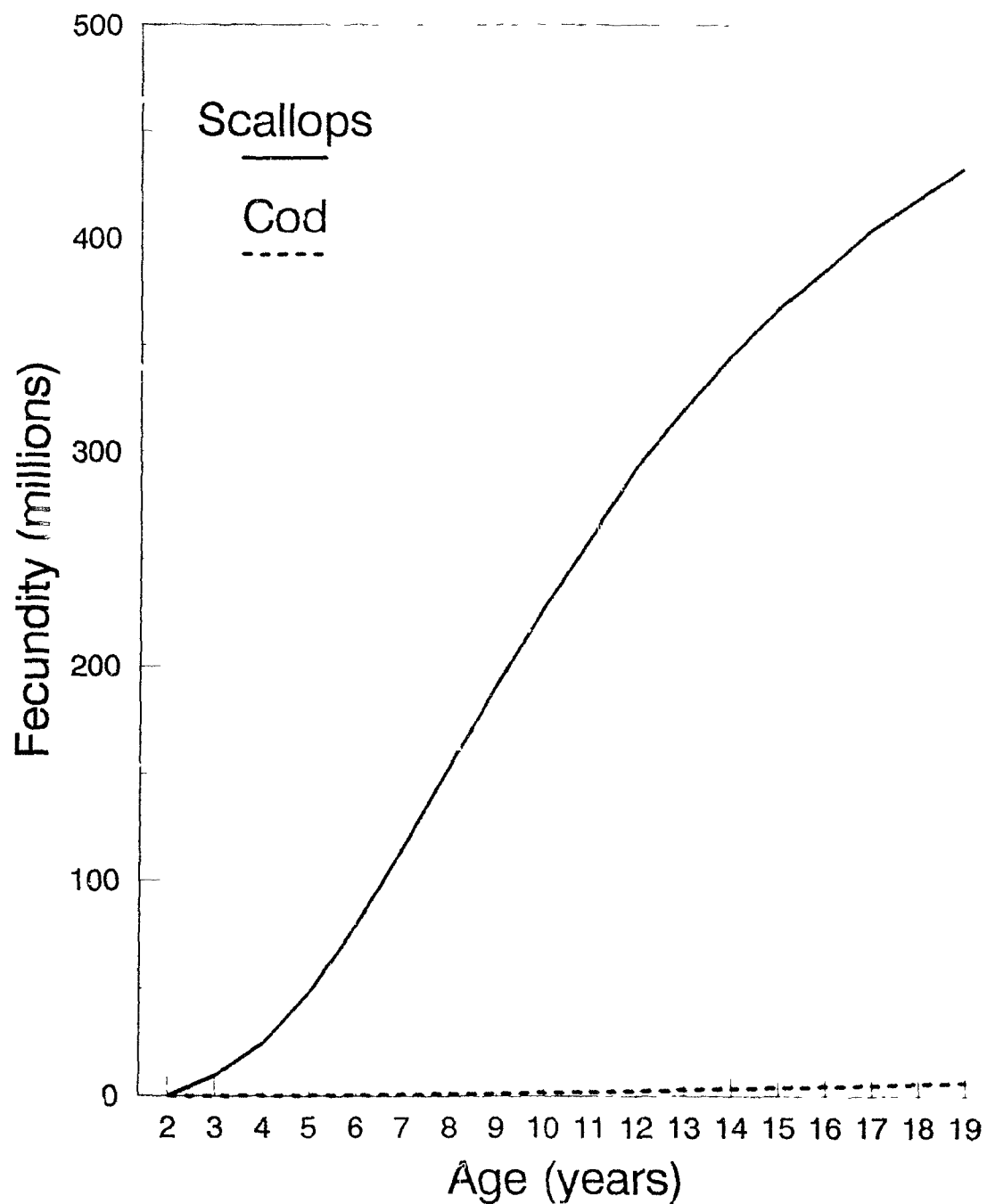


Figure 5.2. Eggs per female. Newfoundland scallops from Sunnyside, 10 m (MacDonald and Thompson 1985b) and Newfoundland cod (May 1967).

years when the environment is adverse, recruitment can fail, and the population will persist. Because of long lifespan, negligible numbers of offspring may reach maturity even for a number of consecutive spawning seasons and in the subsequent year, once the marine environment is again favorable for reproduction, the high fecundity of the older scallops assure population survival. The huge numbers of spawned eggs also act to spread scallop spat over a wide area, filling the water column with between 500,000 and 5 million eggs per m^2 each year (Table 1.4), to procreate the one egg per lifetime which survives to become a reproducing descendant. The repeated, abundant, and wide dispersal of spawn may be due to the fact that scallops, as larvae, and particularly as juveniles and adults, have far less control over their physical location in the marine habitat than do less fecund species, including nearly all fish.

Yet high fecundity can also yield a succession of very large year classes. Huge upward variations in recruitment can therefore be as destabilizing as widespread multi-year failure. Examining CPUE in Figure 3.1b during the early years of the fishery, 1944-1958, reveals a population which is remarkably steady. A third element of reproductive strategy is needed to achieve the stability observed in the natural population.

Density Dependence

In a steady state population, the total lifetime egg production of an average female equals the number of eggs needed to produce a single female replacement. This mathematical fact, formally reproven in Appendix 5.2, is simple and widely known (e.g. Begon et al. 1986) but its power has, perhaps, been underutilized.

Assuming two steady state populations, we may compare eggs per recruit in a natural population with the same measure in the present-day fishery. The calculation, detailed in Appendix 5.1, of total lifetime egg production equal to 1.34 billion, constructs the age distribution of scallops which suffer only natural mortality, estimated for scallops at $M = 0.1$, and so applies to an unexploited population living a natural lifespan.

Applying this mathematical relationship of Appendix 5.2, and using the time-averaged values for total recruitment and egg production from Chapter 1, we can directly calculate this same ratio, the reciprocal of the survival probability of each egg, in the present-day fishery:

Lifetime egg production of an average female in the fished population

$$\begin{aligned}
 &= \frac{\text{Total average yearly population egg production}}{\text{Total average yearly recruits (to age 2)}} \\
 &= \frac{56 \times 10^{15} \text{ eggs}}{13,700 \times 10^6 \text{ recruits}} \\
 &= 4,090,000 \text{ eggs/recruit}
 \end{aligned}$$

for all of Georges Bank.

Thus, under exploitation, scallop eggs recruit at an average rate 328 times more successfully. Comparing the early development phase of the fishery and recent years (Figure 3.1), average total population biomass, as CPUE, has remained largely unchanged. The greatly reduced adult densities in the exploited population, where adults are continuously removed at an early age in their reproductive lives, must permit dramatic increases in recruits per egg.

The one critical assumption is that both populations are at a steady state, differing in age-structure. In the natural population, where we are free to average over long times, the population was persistent for many generations implying some form of stability and an approximate steady state. This assumption is directly substantiated in CPUE data from the early years, 1944-1958. In the fishery, a steady-state age structure is less reliably assumed because of the cycle; the population and its age-structure are not

stable. But as Volterra (1927) demonstrated for a 2-variable predator-prey system, where the total population numbers averaged over one cycle are identical to the steady state values about which the two populations oscillate, so also would we expect, in the absence of detailed modeling, that the steady-state age-structure be approximated by the time averages. The further extension of this assumption to the Georges Bank scallop fishery, where age-structure, realistic levels of recruitment variability and density dependence were incorporated (Chapter 4), prove that it remains a very good approximation.

To assess the chance that recruits per egg is significantly lower in the natural population, we may take explicit consideration of the uncertainties for R and S from Chapter 1. In the fished population, taking the lowest likely estimate for recruits and the highest for egg production we obtain a minimum likely increase of 112. Even without a perfect steady state, an increase in eggs per recruit by a factor of 3 or 4 in the exploited compared with the natural population would have been significant, since even if the uncertainty bars above and below the mean were the same size as the mean itself, anything above a factor of 2 would lie outside this uncertainty. A factor of over 300, with a minimum of two orders of magnitude seems incontrovertible. Moreover, if females of age 3 and 4 are not producing viable spawn, the success rate of viable eggs roughly doubles in the fished population but is not

significantly affected in the natural population, implying a 600-fold increase in recruit per egg under exploitation. Density dependence is thus revealed as the third element maintaining stability in the face of strong environmental variability.

Density Dependence: Survey Data

The above method of detecting density dependence averaged the available survey data from 1977 to 1988 to compare the present stock with a natural population. One may also inquire whether any density dependence can be discerned within the (recent) survey data, despite heavy fishing. Since an increasing trend of recruitment with stocksize was demonstrated in Chapter 2 for the full range of stocksizes measured during those years, a strong Ricker-type decline in recruitment with stocksize is ruled out. However, an increasing stock-recruitment relationship may exhibit mild density dependence as a second order effect, revealed by a convex curvature. Taking the most intuitive approach, we consider the correlation of recruits per egg, $R/S = b$, with biomass density. If higher stock densities are inhibiting recruitment, as they were shown to do comparing R/S in the fishery with the presumably much higher-density and older natural population, this would be

expressed by a negative correlation between $\{b(IY)\}$ and $\{BIOMASS(IY)\}$, the latter defined in Chapter 1.

These two time series are presented for comparison in Figure 5.3, their cross-correlations in Figure 5.4.

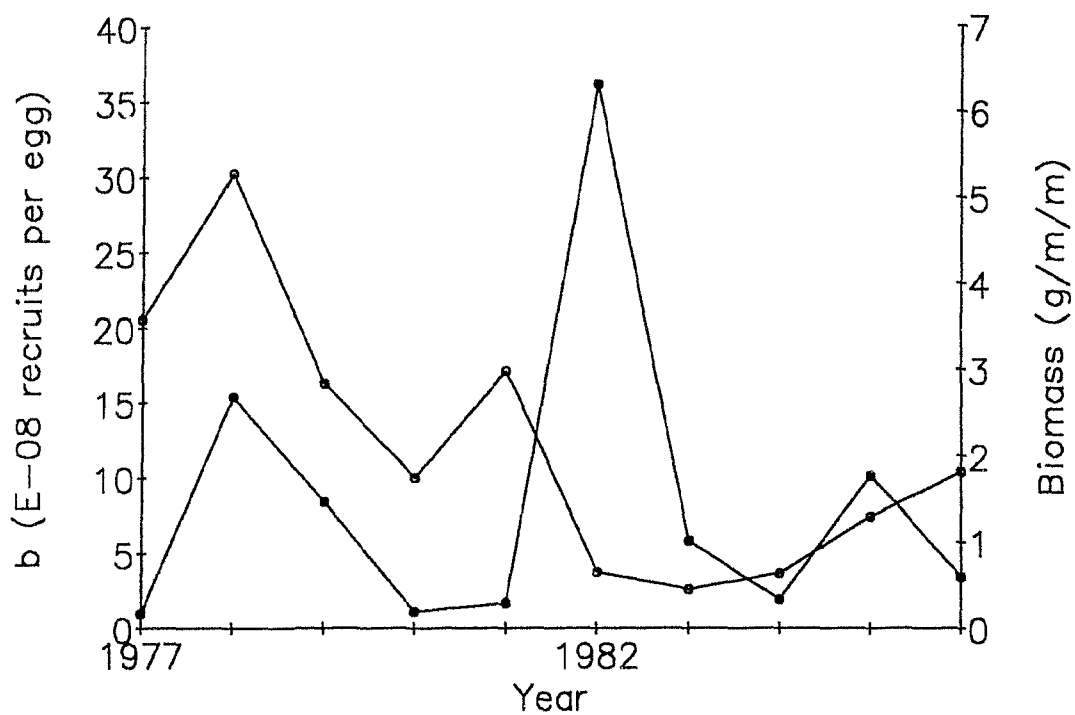


Figure 5.3. Time series for b, recruit per egg (solid circles), and biomass of scallops, 40 mm and up (open circles), on the Northern Edge and Northeast Peak from 1977 to 1986.

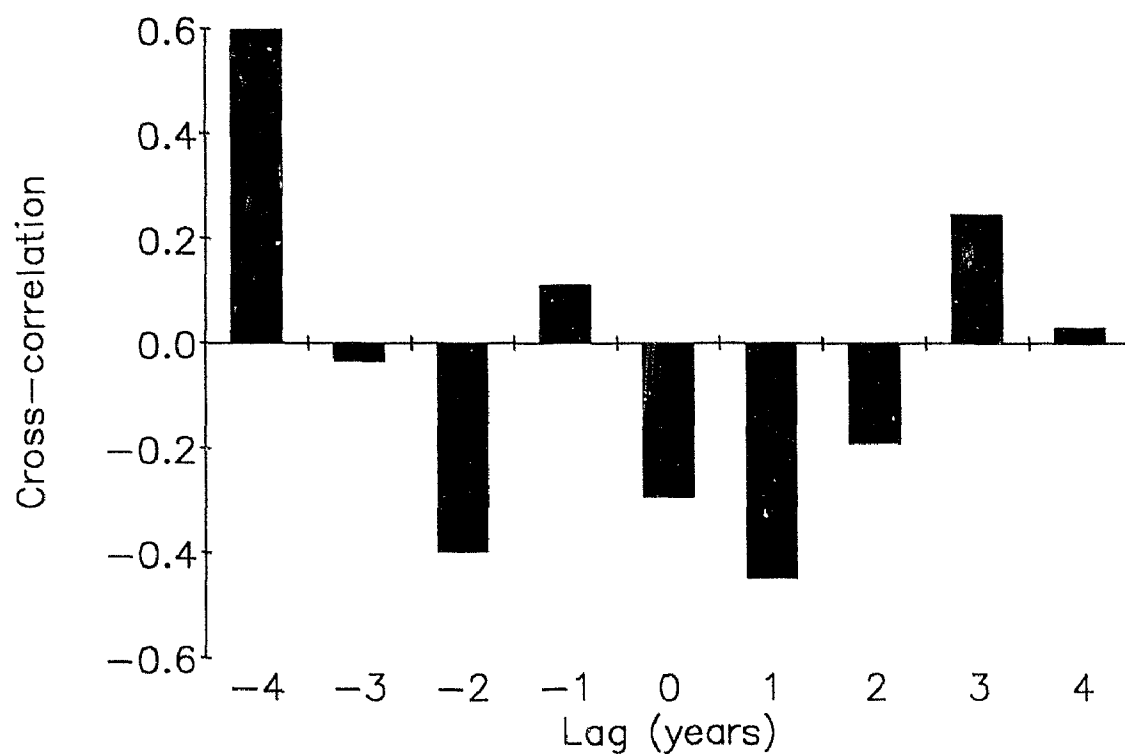


Figure 5.4. Cross-correlations of the time series in Figure 5.3, $\text{BIOMASS}(IY+K)$ lagged by K with respect to $b(IY)$.

Evidence of density dependence over the range of densities seen in this intensively harvested stock is not strong, but the cross-correlations are negative for lags 0, +1 and +2. This implies that when biomass was higher than average, recruitment per egg of year classes that were eggs of age 0 and juveniles of age +1 and +2 was lower than average. This is what we would anticipate where density dependence is acting, but relatively weakly. The negative correlation at lag 0 implies that the overall increasing stock-recruitment trend is indeed curved downward. The negative correlations at +1 and +2 may further suggest that this density dependence also acts at the post-settlement stage.

A more direct estimate of this potential curvature in the stock-recruitment data, by simply fitting these 10 points to a second order polynomial, was also attempted. However, in every instance, even when the fitted continuous line was fixed at the origin, the algorithm broke down and gave a negative slope. The unusually high dispersion of recruitment points makes this understandable: it simply asks too much to ascribe a curvature to a set of data points whose y-axis variable has a standard deviation considerably greater than its mean.

Dynamics: The Cycle

Strong density dependence in the natural population provides an explanation for two notable differences between the dynamics observed in the Georges Bank scallop cycle and that predicted by a Schaefer model. It was these two discrepancies which initially motivated the investigation of density dependence in this population.

First it may be noted (Figure 3.1b) that catch per unit effort, the commercial measure of abundance, does not drop off with the arrival of intense fishing. Over the years 1944 to 1958, CPUE averaged 0.729, and over the years 1958 to 1987, it rose slightly to 0.773. Compensatory increases in recruitment when adult populations declined due to fishing would account for this unusual population response.

Secondly, density-dependent recruitment provides an explanation of why stocksize should have increased dramatically at the outset of the cycle, producing the CPUE peak of 1960-61. Survey height-frequency distributions from early cruises reported by Posgay (1956) reveals that the natural stock, including many older scallops, was still largely intact. Egg production must still have been considerably higher compared to the present more heavily fished age distribution.

But more importantly, since adult scallops were being removed much more rapidly due to the rise in effort up to 1956, more space might have been opened up on the bottom

than before, allowing unusually high recruitment. This would be around 1954-58, during the later years of this development phase of the fishery. Serchuk (1984) designated this 1960-61 peak as a large 1955 year class, Mohn et al. (1986) as a large 1957 year class, coinciding closely with the effort peak of 1956. In fact, the biggest share of this rise was Canadian effort (New England Fishery Management Council 1982) which, because of proximity to the south shore of Nova Scotia, has always been directed toward the beds on the Northern Edge and Northeast Peak. Because these populations are the most dense, and because this habitat is the most favorable, reduced density due to steadily rising effort would be expected to generate higher recruitment--precisely in this region, and precisely at this time, when effort there was rising most rapidly.

Relatively constant CPUE from 1954-1958 probably reflects steady depletion of the natural beds during this development phase of the fishery, a view well substantiated by early scallop survey height-frequency data available from the late 1950's (unpublished data, Northeast Fisheries Center, Woods Hole, MA). But uniform CPUE, in that case, implies a steady bottom density in both time and space, and suggests that beds of the unfished population, presumably the bulk of the harvest in those early years, were characterized by a relatively constant meat weight (i.e. biomass) density. The subsequent dramatic rise in CPUE, peaking in 1961, is thus all the more difficult to explain

without postulating unprecedented increases in recruitment occurring during the peak in effort around 1956. The very large increases in recruit per egg, shown to characterize the present population compared with its unexploited age-structure would explain this dramatic rise in recruitment.

Without invoking strong density dependence, it is hard to imagine how stock abundance could suddenly rise upon impact by a rapidly developing fishery. The pure Schaefer model, with logistic stock growth, predicts a decline in stocksize with rising effort (although total catch increases up to maximum sustainable yield). Strong density dependence, accompanied by higher egg production, provides one mechanism which resolves this discrepancy. At the same time it provides a plausible explanation of the observed transition resulting in the onset of the cycle, an aspect of the dynamics not addressed by the Schaefer model itself.

Discussion

A fishery can therefore serve as a large inadvertent manipulation experiment. Because adults were removed from the population at a greatly increased rate, we observe the ability of recruitment to increase correspondingly, maintaining the population at a (variable but) stable size.

Some scallop populations are not persistent in the face of intense fishing. The scallop beds in Mahone Bay, for

instance, yielded commercial quantities of biomass in the early part of this century and then disappeared entirely (Sinclair et al. 1985).

The conclusions derived thus far are based on evidence gathered and analyzed at the population level. But the processes controlling reproduction are based on physiology and behavior. Feeding, gamete development, and spawning are physiological processes; density dependence and fertilization involve behavioral interactions among individuals in a bed. Studies on this level have shown that among other unexploited bivalve populations, density dependence inhibiting growth (Peterson 1982) or recruitment (Luckenbach 1984) is not uncommon.

The extensive literature on Placopecten may be used to help understand the interactions among individuals which regulate recruitment as a function of density. A unifying theme is the transition that appears to occur around age 5 affecting energy production partitioning, behavior, predation susceptibility, and perhaps also gamete viability.

MacDonald and Thompson (1985a, 1985b, 1986a, 1986b, 1988) and MacDonald (1988) showed for several inshore populations, at different sites and depths, and in different years, that somatic growth, apart from gonad, increased up to age 5 or in a few cases to age 4, and declined every age thereafter. The only exception were scallops suspended in nylon bags off the bottom, a common practice in mariculture, which developed more rapidly but followed the same somatic

growth pattern. Gonad growth, on the other hand, was considerably slower than somatic growth at ages 2 to 5, but typically surpassed it around age 6, although in less productive habitats not until as old as age 10, presumably because reproduction held a lower priority in these nutrient-poor or temperature-limited environments.

From age 5 on, somatic growth dwindled toward zero and egg production rose rapidly, continuously increasing up to the maximum ages measured, around 19. Most variation observed for scallops in different habitats, along gradients from favorable to unfavorable (e.g. from shallow to deep) occurred in the amount of production allocated to gametes. When food is available, scallops can direct relatively large fractions of energy toward high fecundity. In years when primary production and temperature are not favorable, body weight is maintained but less is diverted into reproduction. The long lifespan of sea scallops allows such reproductive flexibility.

The second major physiological transition at age 5, as yet hypothetical, is that scallops are not fully mature until this age, of size around 100 mm. The increases with age of stock in stock-recruitment correlations (Chapter 2) are indirect evidence for this. An additional supporting observation is the pattern of energy partitioning discussed above. Scallops, at age three and four, still channel most of their production to soma, and above these ages most and eventually almost all energy is diverted towards gamete

production. This may imply that the reproductive physiologies of 3 and 4 year old scallops are not fully developed, and that part of the rapid somatic growth at these ages is directed to that end. It is also compatible with a reproductive strategy based on long life and extraordinarily high fecundity. After age 5, on average, 8 seasons of spawning await a scallop in an unfished population. About 98% of the spawned gonad biomass, whether viable or not, is produced in an average lifetime after age 4; 1312×10^6 eggs for ages 5+; 28×10^6 eggs for ages 3 and 4. For such a fecund and long-lived species, the gamete producing mechanism may take more than one year to fully mature.

The third major life-history change occurs in scallop behavior. Independent observations by divers (Caddy 1968, M.J. Dadswell, Acadia University, Wolfville, Nova Scotia, pers. comm.) confirm that scallops can be divided into two basic types: "sitters" and "swimmers". The swimmers include basically all the smaller-sized scallops, below about 100 mm (Caddy 1968). Upon approach, they will nearly all swim away, 6-8 feet being a typical flight distance (Caddy 1968). Above this age scallops become sitters. They maintain a small depression in the bottom from where they will not flee upon approach.

Elner and Jamieson (1979) demonstrated that predation by lobster (Homarus americanus) and rock crab (Cancer irroratus) was highly size dependent. This was confirmed in

field enclosures by Jamieson et al. (1982), who observed that while juvenile scallops (40-55 mm) were highly susceptible to predation, medium-sized scallops (80-110 mm) were untouched by crabs. Only a small number of the medium-sized scallops were consumed by lobsters when that predator's density was elevated well beyond natural levels, and scallops were chosen only 25 days after all horse mussels, Modiolis modiolus, were removed and even after considerable cannibalism among the adult lobsters themselves was recorded. This confirms the prevailing view (New England Fishery Management Council 1982) that predation on adults, again above this critical size of around 100 mm, is not significant. Volkov et al. (1982) in a large-scale study of the closely related Japanese scallop, Patinopecten yessoensis, found that juveniles, at artificially elevated densities, actively and probably randomly dispersed, followed and presumably hastened by relatively dense concentrations of predatory starfish, Distolasterias nipon. Thus predation susceptibility explains why juveniles swim, as an escape mechanism, unlike adults.

This behavior may also allow inadvertant territoriality, since mature scallops, after swimming randomly about on the bottom for most of 4 years finally settle in one location and stay there, precluding subsequent settlement by the younger, actively motile juveniles.

Scallops can plainly sense the presence of predators such as starfish, actively responding to their approach by

swimming (M. Barbeau, Department of Biology, Dalhousie University, Halifax, Nova Scotia, pers. comm.). They have a crude visual sense (Land 1984), and a sense of smell (Barnes 1974), and must therefore be able to sense the presence of one another. They do appear to actively regulate their positions with respect to one another on the bottom (M. Barbeau, Department of Biology, Dalhousie University, Halifax, Nova Scotia; M.J. Dadswell, Acadia University, Wolfville, Nova Scotia, pers. comm.), so some active or passive form of territorial behavior which gives rise to density limitation is possible.

Since the juveniles swim about randomly, and since adults are sedentary, territoriality would not be expressed by preventing juveniles from "passing through"; but rather by established adults somehow precluding further settlement in their immediate neighborhood.

Active density regulation is also reflected in the pattern of spatial distribution on the bottom. Scallops tend to form themselves into discrete beds of relatively uniform density, around $1-4 \text{ m}^{-1}$ (MacDonald and Thompson 1986b, Naidu 1969, Caddy 1970, Caddy 1968). They must be relatively closely aggregated for reproduction since fertilization occurs in the water column. On the other hand, excess fecal accumulation in the sediments may fix a maximum tolerable density.

Lab studies by Wildish et al. (1987, Wildish and Kristmanson 1988) showed that the mechanics of filter

feeding require flume or tube current velocities not exceeding $10\text{--}20\text{ cm s}^{-1}$, optimal being around 5 cm s^{-1} , apparently because pressure differentials between food intake and outflow become disrupted above these limits, yielding slower growth. Yet scallops in the Bay of Fundy, the second largest population of Placopecten, experience maximum depth integrated velocities exceeding 100 cm s^{-1} (Wildish and Kristmanson 1988). On Georges Bank, the fastest currents occur on the Northern Edge, precisely where scallops are most abundant. Divers in inshore waters also report that scallops tend to be found in locations, at the narrows of bays or inlets, where currents are most rapid (T. Kenchington, Halifax Fisheries Laboratory, Canadian Dept. of Fisheries and Oceans, P.O. Box 550, Halifax, Nova Scotia, pers. comm.). Furthermore, this corroborates the findings of aquaculturists who observe rates of growth significantly faster than any known natural populations when scallops are suspended even in very high densities off the bottom (MacDonald 1986, Dadswell and Sinclair 1989). Like their abundance in tidal currents that are too fast for optimal feeding, this is explained if fecal deposition in the sediments rather than competition for food is the limiting process in scallop growth. Cranford and Grant (1990) have suggested that scallops may feed on stirred up bottom sediments. Their lab studies confirm that phytoplankton is the primary food source, but that scallops do sometimes absorb resuspended sediment.

If juvenile scallops, at the age of settlement and below, are more negatively affected by higher concentrations of fecal accumulation than are well-settled adults, this would provide a second mechanism for passive density limitation. Specifically, if the tolerance of scallops to waste increases with age, particularly at the critical transition age of around 5 years when scallops settle in one location, then the exclusion of new settlers in well-established beds of older scallops would occur without the need for active territorial behavior more typical of terrestrial mammals and birds and some shallow water fishes. Such a mechanism, compatible with observations of scallop behavior and physiology, would produce density dependence as a natural outcome.

These two hypotheses to explain density dependence, active territoriality and fecal accumulation, could be amenable to direct lab or field testing. Do scallops actively regulate their spatial distribution, in particular with respect to one another on the bottom? What happens if they are redistributed by currents or human hand to locations farther apart or closer together than their natural density? Are currents necessary for fecal evacuation? How does the fertilization success rate depend on density? And most importantly, is the recruitment rate of juveniles affected by the presence of well-established adults at their normal densities of 1 to 4 m⁻² or higher?

Appendix 5.1. Lifetime Fecundity: Scallops and Cod

Average steady state lifetime egg production of scallops and cod which reach age 2 is estimated from two sets of parameters, natural mortality, $\{M(IA); IA = 2 \text{ (to } 3), 3 \text{ (to } 4), 4 \text{ (to } 5), \dots, 19 \text{ (to } 20)\}$ and fecundity, $\{EGGS(IA); IA = 2, 3, 4, \dots, 20\}$.

The calculation assumes, lacking more detailed information, that cod, like scallops, have a maximum lifespan of 20 years, although few have been observed recently above 16 (Baird and Bishop 1989) in the Newfoundland stock. The same pattern of senescence is postulated for both, the natural mortality with age presented in Table 5.1. Fecundity for cod is calculated directly from the formula of May (1967),

$$EGGS(AGE) = 21510 * AGE^{1.95}$$

The survival probabilities, $\{L(IA)\}$, of a cod or scallop reaching age IA , of those which reach age 2 (Figure 5.1), follow from the natural mortalities,

$$L(IA) = L(IA-1) * \exp[- M(IA-1)],$$

Table 5.1. Natural mortalities employed in Appendix 5.1 and Figure 5.1, assuming a lifespan of 20 years.

Age	Natural mortality	Natural mortality
IA	IA to IA+1	IA to IA+1
	Scallops	Cod
1	0.1	0.2
2	0.1	0.2
3	0.1	0.2
4	0.1	0.2
5	0.1	0.2
6	0.1	0.2
7	0.1	0.2
8	0.1	0.2
9	0.1	0.2
10	0.1	0.2
11	0.1	0.2
12	0.1	0.2
13	0.1	0.2
14	0.1	0.2
15	0.1	0.2
16	0.1	0.2
17	0.2	0.2
18	0.4	0.4
19	0.6	0.6
20	infinite	infinite

for IA from 3 to 20. $L(2) = 1$, by definition.

The formula for average lifetime egg production (often called the "basic reproductive rate"), employed here for both cod and scallops, is

$$\sum_{IA=2}^{20} L(IA) * EGGS(IA).$$

Extending this, the formula applied to calculate lifetime eggs per gram of body weight is

$$\sum_{IA=2}^{20} L(IA) * EGGS(IA) / WG(IA),$$

where $\{WG(IA)\}$, the body weight in grams, is given by 8.3 times the meat-weight (i.e adductor muscle) for scallops, taken from the weight-at-age formula of Serchuk et al. (1979). Cod weight-at-age (like fecundity), is taken from the Newfoundland stock (Baird and Bishop 1989), NAFO districts 2J3KL, which, like Georges Bank scallops, comprise the single largest population(s) in the Northwest Atlantic.

The average number of spawning seasons, of those which reach age 5, is calculated as

$$\sum_{IA=5}^{20} [L5(IA) - L5(IA+1)] * (IA-4).$$

Appendix 5.2. Steady State Population Reproduction

We now prove that in a steady state population the numbers of eggs produced by an average female in her lifetime, from age 2 on, is equal to the ratio of total eggs produced in any given year, divided by total age 2 recruits. This relationship is not mathematically new, but worth proving here for the specific notation of Georges Bank scallops as calculated in Appendix 5.1. It differs from the manner that it is more traditionally expressed by defining the youngest class at age 2, rather than age 0. This is advantageous not merely because age 2 recruitment is far easier to measure, individuals being near fishable size, but in addition, the estimates of average survival, $Nss(IA)/Nss(2)$, from age 2 upward, are far more reliable than from age 0, since eggs and larvae are subject to enormous environmental variability and survive with such exceedingly low probability.

This choice of age 2 rather than age 0 as the lowest age class to be explicitly included in the population-at-age vector, is subject to the constraint that this earliest age be less than or equal to the lowest age of viable egg production, i.e. in a scallop population, as long as one year olds are not mature. It has the third advantage of being more demographically meaningful. The ratio

$$\frac{\text{Total yearly average number of individuals of age 0}}{\text{Total average yearly egg production}}$$

is tautologically equal to 1 in a steady state, of interest only if the population is changing in total size. But when this quantity of interest is chosen instead as

$$\frac{\text{Total yearly average number of individuals of age 2}}{\text{Total average yearly egg production}}$$

it becomes a more useful measure, and may be applied in studying density dependence, an advantage not obtained in its traditional form.

For a steady state population, broken down by age, $\{N_{SS}(IA), IA=2,20\}$, the total yearly egg production is

$$S_{SS} = \sum_{IA=2}^{20} N_{SS}(IA) * EGGS(IA).$$

Steady state recruitment to age 2 is assumed, and taken as the time-average

$$R_{SS} = \bar{R} = N_{SS}(2).$$

Thus the number of eggs per recruit is

$$\frac{S_{SS}}{R_{SS}} = \frac{\sum_{IA=2}^{20} N_{SS}(IA) * EGGS(IA)}{N_{SS}(2)}$$

$$\frac{S_{SS}}{R_{SS}} = \sum_{IA=2}^{20} \frac{N_{SS}(IA)}{N_{SS}(2)} * EGGS(IA).$$

Assuming one year olds do not produce eggs, the proof is complete since the survival probabilities of individuals

which reach age 2, $L(IA)$, equals $N_{SS}(IA)/N_{SS}(2)$ by definition, and therefore the right hand side is the lifetime egg production of an average female.

The great power of this relationship is that, assuming a steady state, it permits estimation of the most basic ratio describing reproduction, the survival rate from egg to recruit, employing only adult population parameters. These reflect life-history strategy, how many eggs are spawned and for how many seasons before senescence. Expressed at the level of the individual, they are more easily measured. And because they have a strong genetic component, the results may be interpreted to apply quite widely, if considered over long enough times that environment is averaged out. The ratio to which it is equal, namely R/S , is measured at the population level, requiring yearly trips in a research vessel and a crew on the open sea. A link between these two levels of the biological hierarchy is established by this mathematical equality.

CONCLUSION

Conclusion

Identifying the dynamical mechanism which drives the Georges Bank scallop population may be helpful in managing the fishery. In particular, management strategies may be adopted to stabilize the cycle, inducing a more stable financial base for the fishing communities that rely on this \$130 million a year resource.

A number of management options were explored using a continuous-time Monte Carlo birth and death formalism for the entry and exit of vessels and harvest in a Schaefer dynamical model. Ultimately, it appeared that the best strategy for damping the cycle, under the assumption that only effort can be directly controlled, is simply to fix effort at some unchanging value. Then, the dynamical question of how to vary yearly incentives or controls, for example by including a yearly licence fee or a catch limit, reduces to the same solution recommended by the classical theory of fisheries economics. In a cycling system managers have two goals, namely (1) to maximize catch, and (2) to stabilize the supply. The simulations, which tested a wide range of possible management policies, ultimately found that a fixed level of effort stabilized the Schaefer cycle most directly. This is not surprising, in hindsight, but significant. If we choose a fixed level of effort to achieve MSY or MEY, or optimize our social and economic

rents measured by any other criterion, it would also achieve our second dynamical objective at the same time, and stabilize the predator-prey cycle.

Since 1984, cooperation among the Canadian firms which operate scallopers on Georges Bank, and the Canadian Department of Fisheries and Oceans have begun to restrict catch with Enterprise Allocations, a catch limitation, and coordinated fleet size reductions, removing older less efficient vessels (Robert and Black 1990). Effort, measured as hours of bottom drag time has indeed begun to stabilize since that time (Figure 3.1b). A prediction follows.

The simulations reported above suggest that holding effort steady will, after a time, stabilize a Schaefer cycle. If the Georges Bank scallop cycle is driven by a Schaefer mechanism, then that hypothesis yields the prediction that, due to this management intervention, the cycle, in particular stocksize, will stabilize in the next several years. Robert and Black (1990), in the most recent stock assessment, noted a stabilizing trend since 1985, observing lower variation in catch rates and recruitment, and ascribed it to the the new management regime.

The predictions of the Schaefer model also appear to be born out from the perspective of the classic equilibrium paradigm: the level of effort to which the Canadian fishery appears to be stabilizing is above the average of the previous 30 years since the cycle began. Accordingly, catch is stabilizing at a lower than average level, although not

as low as during a trough of the cycle. Furthermore, the demonstration of a stock-recruitment relationship (Chapter 2) substantiates these equilibrium considerations.

Furthermore, the evidence (Chapter 2, 5) that scallops of age 3 and 4 are not yet fully mature, if proven correct, would also substantiate the Schaefer cycle hypothesis. If most scallops do not reach maturity due to fishing, small decreases in effort would bring about relatively large increases in viable egg production. Thus the effect of changing effort (slightly more than doubling from trough to peak) on egg production would be strongly amplified (factor of 20 from trough to peak), and even if recruitment were weakly proportional to egg production, the effect of changing effort on recruitment would still be very significant.

Strong evidence for Schaefer dynamics in this fishery (Chapter 3), together with evidence of recruitment overfishing (Chapter 2), corroborate the above observations of recent long term steady state levels of catch and effort, suggesting that the recommendations of the classic equilibrium Schaefer model could lead to substantial increases in annual harvest and, at the same time, allow a stable resource.

The discrete model constructed for validation may also be useful in other fisheries management applications, in particular, in a dynamical yield-per-recruit analysis. At least three independent equilibrium yield-per-recruit

analyses (Posgay 1958, Serchuk et al. 1979, Sinclair et al. 1985) have indicated that Georges Bank scallops are harvested at too young an age. Recruitment dynamics could be included in such analyses, in the tradition of Beverton and Holt, including also its log-normal stochastic variation. Density-dependence, not previously considered, would be crucial in this analysis because it is the only factor which argues against leaving adults on the bottom for a year or two of additional growth and spawning.

The robustness of predator-prey cycles proved to be a theoretical contribution of great benefit in this study. A pure Schaefer model has well-defined properties because it undergoes no bifurcations. The complexities encountered in most dynamical systems are therefore mathematically excluded, making it eminently structurally stable. Furthermore, because there is one globally stable steady state, inaccuracies in parameter estimation will have no major effect on the qualitative dynamics of interest.

For more complicated elaborations of the pure Schaefer model, I encountered no deviations from this general rule. In a wide assortment of predator-prey class of models, spatial and non-spatial, with or without age-structure, with markovian birth and death or deterministic boat dynamics, with recruitment sampled stochastically from a number of different distributions and subject to a range of forms of density dependence including the logistic, Beverton-Holt and Ricker relationships, and despite a vast array of model

management policies devised specifically with the intent of stabilizing the cycle, predator-prey oscillations were invariably the observed dynamical outcome. What varies is whether the solution spirals towards or away from the steady state, i.e. whether the steady state is stable or unstable, but it is nearly always oscillatory, as noted in the Introduction. In a real Schaefer system, the robustness of this cycle mechanism renders it unusually amenable to the methods of dynamical systems modeling and have certainly helped to make its identification in this study so unambiguous.

The dynamical interactions in a real fishery are commonly more complex than those observed in Georges Bank scallops, because usually more than one process is acting at a time. The Georges Bank scallop fishery is particularly valuable for dynamical study because the cycle appears to be dominantly influenced by one process alone, which largely explains all the dynamical features observed.

A useful methodological contribution in this work is the application of qualitative taxonomic criteria to assess hypotheses for the cause of a population cycle. They are intuitive, based on our understanding of how each hypothesis would act. As a result, they are robust, because they are derived from the mechanism of cycle cause rather than (or in addition to) the solution of a deterministic model, and thus would presumably hold true independent of the mathematical

model employed. The fact that these criteria are intuitive can be viewed as a additional practical advantage.

In the stock-recruitment analysis, a second methodological consideration proved useful. Size, rather than age, was used as the independent variable. This has a number of advantages:

(1) First, and most important I believe, the surveys measure population with size as the independent variable, the original samples yielding stratified numbers per tow in each 5 mm shell height class. Associating an age with size is very uncertain, since no widely accepted aging technique has been found and growth is known to be quite variable in this species. Some information is probably lost in this step of a conventional age-based method such as virtual population analysis (VPA). I suspect that recruitment time series from a VPA, SPA or other form of cohort analysis are characterized by significant false autocorrelation, potentially, from two causes:

(i) The aging of size-based data tends to smear the apparent width of large recruitment year classes, ascribing some of the larger individuals from the large year class peak to the age class above, and some of the smaller individuals to the age class below. This would give the appearance of 3 or perhaps as much as 5 years of steadily rising and then steadily falling recruitment when, in truth, there was just one large recruitment event. Two aspects of scallop (and fish) growth amplify this smearing effect:

growth slows as the individuals become older, so the means of each peak in a size frequency distribution get closer and closer, while the variance of size is expected to increase with age, resulting in more and more overlap among cohorts.

(ii) Second, this smearing effect may be amplified by smoothing among age classes of each cohort in the mathematical calculation of the VPA matrix which, for instance, usually assumes a fixed natural mortality.

This false autocorrelation may make VPA less useful for analyzing stock-recruitment relationships than is the more simple and direct method applied here, which obtains recruitment as a simple sum of survey numbers. This simple approach does require some association of size with age in choosing the size range over which to sum. With Georges Bank scallops, we sought to avoid overlap in the age 2 year-classes evident in the height frequency diagrams of Figure 2.1. This size range can be chosen conservatively (i.e. on the narrow side), to largely preclude the problem of false-autocorrelation by avoiding the two potential causes described above.

(2) For the estimate of total egg production, no aging is needed. Moreover, the measure of stocksize (total egg production) may be more accurate using the simpler size-based method because the original data of population numbers at size are probably more accurate than VPA-derived population numbers at age which are derived from the population-at-size data. (This assumes that information is

only lost in the VPA calculation, which might not always be true if the smoothing of the VPA eliminates measurement noise.)

(3) Furthermore, it is possible that size (particularly adductor muscle size) may be better correlated with eggs-per-female than age, because in scallops, the adductor muscle stores all the glycogen which is shunted into the gonad before spawning, when the adductor muscle shrinks as the gonad swells. However, it remains to be established whether fecundity is better correlated with age or with the survey measure of size in each fishstock, including Placopecten.

One possible line of future research might be to investigate these potential liabilities of VPA in analysis of stock-recruitment relationships.

A formal analysis of the effect of false-autocorrelation might be obtained by performing the full process of sampling and VPA numerically on a large set of simulated data. From this simulated population, samples can be drawn in a way which mimics the method of fisheries surveys. After subjecting these samples to the same aging and VPA analysis applied to real data, the VPA-derived recruitment time series can be compared with the "true" recruitment obtained directly from the original simulated population. In particular, autocorrelation analysis and stock-recruitment correlations before and after VPA can be

calculated to assess whether VPA does, in fact, create false autocorrelation and obscure stock-recruitment relationships.

Other lines of research in the Georges Bank scallop fishery may be fruitful. The first would be a closer analysis of price. At present, Canadian time-series data show that landed sea scallop price does cycle. There is, however, little or no lag in the changes in price following (inverse) changes in catch. Price follows a strict law of supply. Without a time delay, the price mechanism is an unlikely fourth possible cause of the cycle. However the dynamical relationship between price and effort is identical in general form to the relationship between effort and stock abundance, namely it is a predator-prey relationship where, again, effort is the predator, but price takes the role of prey. Detailed cross-correlation analyses of price with catch, effort, stock, and recruitment, and dynamic analysis, including modeling, of this 3-variable interaction (effort, stocksize and now price) could be of interest.

A second line of research could analyze and compare the causes of the apparant 10-year cycle in the Digby scallop fishery (Dickie 1955, Caddy 1979) with that of Georges Bank. The Digby cycle is not as regular, but has been continuing for a considerably longer period of time, and substantial evidence (Caddy 1979) suggests that forcing rather than a predator-prey interaction is the most likely cause. Recent reconsideration of this cycle, shows that the phase at which peaks in Digby scallop abundance occur match precisely the

predictions (Loder and Garrett 1978) of an 18.6 year lunar forcing. Peaks should occur at the time when the forcing cycle passes through its mean, and this is what is observed. Because any cycle passes through the average or steady state value twice in the course of one cycle, the 18.6 year lunar forcing would predict a 9.3 year period for the population.

Work on these latter two projects is at present underway.

I conclude with the caveat of realism to users of this work: The system under investigation, the Georges Bank scallop fishery, is more complex than any of the models here applied to represent it, can fully symbolize. This enhances the value of this prediction to test the outcome of the analysis: If CPUE does stabilize with the application of this new management regime, the confidence in these conclusions would be greatly strengthened.

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