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Canadian Atlantic Fisheries
Scientific Advisory Committee

Comité scientifique consultatif des
pêches canadiennes dans l'Atlantique

CAFSAC Research Document 89/22

CSCPCA Document de recherche 89/22

Less Leslie Please

by

R.J. Miller and R.K. Mohn
Halifax Fisheries Research Laboratory
Department of Fisheries and Oceans
Scotia-Fundy Region
P.O. Box 550
Halifax, N.S.
B3J 2S7

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ABSTRACT

The Leslie method has been popular for estimating sizes of Atlantic snow crab stocks for the past decade. The data requirements are modest, the calculations easy to perform, and the outputs are in demand by fisheries managers. However, the target population and fishing effort will likely change over a fishing season, violating important assumptions of the Leslie method. These assumptions were investigated by reviewing the literature on catchability of decapods, and by simulating the violations. In addition to violating assumptions, the necessary extrapolation of regressions beyond the limits of the data often gives very wide confidence limits on biomass estimates, and data points from the beginning and end of the season have greater influence on biomass estimates than points from the middle of the season.

Petersen tag-recapture studies have been used to verify the accuracy of Leslie estimates. However, assumptions that catchability is the same for all individuals, that the stock is closed to immigration and growth, and that landings are correctly reported are common to both methods. Violations of these assumptions would bias stock size estimates in the same direction.

A seasonal mean catch per unit effort used as an index of stock abundance is an alternative to Leslie analysis. Simulations showed this method to be as accurate or more accurate than Leslie for most likely scenarios.

RESUME

La méthode de Leslie a été couramment utilisée pour évaluer l'ampleur des stocks de crabe des neiges de l'Atlantique pendant la dernière décennie. C'est une méthode qui fait appel à des besoins en données modestes et à des calculs faciles, et dont les résultats sont en demande parmi les gestionnaires des pêches. Toutefois, la population-cible et l'effort de pêche changent vraisemblablement durant la saison de pêche, ce qui fausse certaines hypothèses fondamentales de la méthode en question. On a donc examiné de près ces hypothèses en simulant les déviations et en étuidant la documentation existante sur le potentiel de capture des décapodes. Or, il est apparu qu'en plus de fausser les hypothèses, l'extrapolation nécessaire des régressions au-delà des limites posées par les données aboutit souvent à une marge de confiance très large dans les estimations de biomasse; en outre, les données du début et de la fin de la saison ont plus d'influence sur ces estimations que les données de la mi-saison.

On s'est servi d'études des recaptures de crabes porteurs de la marque Petersen pour vérifier l'exactitude des évaluations obtenues selon la méthode de Leslie. Toutefois, ces deux méthodes ont comme hypothèses communes que le potentiel de capture est le même pour tous les spécimens d'un stock, que le stock n'est pas sujet à immigration et croissance et que les débarquements sont correctement déclarés. Toute déviation à ces hypothèses, dans quelque sens que ce soit, fausserait dans le même sens les estimations sur l'ampleur des stocks.

Un méthode autre que celle de Leslie fournit un indice de l'abondance d'un stock; il s'agit de la prise moyenne saisonnière par unité d'effort. Dans les simulations des scénarios les plus probables, cette méthode s'est avérée aussi exacte, sinon plus, que celle de Leslie.

INTRODUCTION

The Leslie method has been used to estimate stock size of the Atlantic snow crab (*Chionoecetes opilio*) fishery since 1978 (Bailey 1978), including 24 times from 1984 to 1988 (Anon 1984, 1985, 1986a, 1987, 1988). The data requirements are modest, the calculations easy to perform, and the outputs are in demand by fisheries managers. Data requirements are mean catch per trap (or any other index of abundance) and fleet landings for several time intervals throughout the fishing season. The catchability coefficient (the fraction of the stock taken in a single trap haul), the size of the fishable stock at any time during the season, the exploitation rate, and recruitment between the end of one season and the beginning of the next can all be calculated. This is an impressive yield of information from such modest inputs.

In this discussion paper we review the sources of bias and consider their effects on biomass estimates. We conclude that the target population and the fishing effort will likely change over a fishing season, violating important assumptions of the Leslie method. Finally, an index based on mean catch per unit effort over a long time interval, is suggested as an alternative to the Leslie method.

METHODS

Five assumptions of the Leslie method are reviewed, and examples of violating these assumptions have been taken from the literature on several decapod species. Studies on decapods other than Chionoecetes were included to supplement the literature on snow crab biology and fisheries.

Some violations of assumptions have been simulated and the resulting bias in population size estimates calculated. Each simulation had 10 equal time periods, representing constant season length, with equal fishing effort applied in each. Approximately 60% of the population was removed by fishing. The population biomass was either 100 at the start of the season, or summed to 100 with additions from recruitment during the season. Data points for the Leslie regression were mean catch per unit effort (CPUE) for a time period plotted against the cumulative catch at the middle of the period, as suggested by Ricker (1975).

ASSUMPTIONS OF THE LESLIE METHOD

1. Catchability of the fished population is constant among individuals and is constant over a fishing season. It is unlikely that this assumption can be met for any decapod species.

Smaller individuals are frequently underrepresented in trap catches. This has been demonstrated for American lobster (Smith 1944, Ennis 1978 and pers. comm.), Cancer sp. (Carroll 1982 and pers. comm.; Miller, in press), and crayfish (Morrissy and Caputi 1981). Within size ranges completely retained by the traps the smallest increase in catchability for larger animals was at least double, and was as high as a factor of 12.

For many decapod species mature females have lower catchabilities than males (e.g. Branford 1979; Morgan 1979; Howard 1982). However, this selectivity is not a problem in snow crab fisheries since females are not landed.

Two studies compared Leslie and DeLury (this method has the same assumptions, inputs, and outputs as the Leslie method) estimates to known abundance of decapods using short term fishing experiments. Morrissy (1975) fished for crayfish with fast fishing hoop nets set 10 times per night in a small pond. After fishing, the population was censused by draining the pond. The Leslie method underestimated the population numbers by 61%, 47%, and 54% in December, February, and April respectively. Morgan (1974a) trapped spiny lobster for 6 days in 34 of 38 successive months. When the DeLury method was applied to each data set, it underestimated density by an average of 75%. This was compared to tag-recapture estimates corrected for the higher catchability of tagged animals. In both studies the large underestimates were attributed to low catchability of some components of the stock. That is, the catch per trap decreased faster than the stock size because the most vulnerable animals were caught first.

Figure 1 represents a hypothetical case of a stock with three equal sized component of different catchabilities, $q = 0.05$, 0.1, and 0.2. Total stock biomass was estimated by Leslie at 85, a 15% underestimate. To obtain underestimates as large as those reported by Morrissy (1975) and Morgan (1974a), large portions of the stocks must have been nearly uncatchable.

The above discussion dealt with different catchabilities among individuals. The same individuals can also change catchability during a fishing season.

In the laboratory Chionoecetes opilio did not feed for 3-6 weeks before molt and 3-4 weeks after molt (O'Halloran and O'Dor 1988). Spiny lobster in premolt condition were only one third as catchable as those not in premolt condition (Morgan 1974b). For the same species Chittleborough (1970, 1975) observed decreased feeding and catchability during premolt and a rapid increase shortly after molting. Reduced CPUE was associated with molting in fisheries for Cancer pagurus (Hancock 1965) and Jasus lalandei (Newman and Pollock 1974).

Catchability often increases with temperature because activity and appetite increase, as does diffusion of the bait molecules (Morrissy 1975). In the laboratory, food consumption by C. opilio was 80% higher at 3^{o} and 130% higher at 6^{o} than at 0^{o} (Foyle 1987). Although this is a stenothermal species, it experiences bottom temperatures ranging -1 to 5^{o}C and commonly from -0.5 to 3^{o}C in the southern Gulf of St. Lawrence (Brunel 1960; Foyle 1987).

Figures 2, 3, 4, and 5 illustrate the effects of changing catchability within a season on population estimates. Both a stepped decrease (from $q=0.12$ to $q=0.08$) and gradual decrease (from $q=0.15$ to $q=0.06$) produced moderate underestimates of 21% and 26% respectively. However, both a stepped increase (from $q=0.08$ to $q=0.12$) and a gradual increase (from $q=0.06$ to $q=0.15$) gave population estimates of 208 and 1470 respectively, very large overestimates. Braaten (1969) has also shown that a stepped decrease in catchability gives a small bias and a stepped increase a large bias using the DeLury method.

2. The fishing effort is uniformly distributed over the area occupied by the stock. This assumption can be reasonably met for a small experimental area where the traps are distributed over the entire area every time they are fished. Small redistribution of the target species or of the traps from one fishing time to the next will expose most of the target animals to trapping. This assumption will rarely be met for fisheries where the fishing vessels are much more mobile than the target animals, and the fleet is not large enough to fish all fishable concentrations simultaneously, as is typical of benthic invertebrate fisheries.

Mohn and Elner (1987) simulated the fishing behavior of a fleet of crab vessels. Each vessel randomly chose among three levels of crab concentration, fished the concentration down to 60% of the average catch for the rest of the fleet, then randomly chose another concentration. A Leslie analysis of the fleet performance underestimated actual abundance by 43%. The underestimate may have resulted from areas of high concentration being fished hard first and areas of low concentration being fished little and last. These authors and Bailey (1983) also described other possible scenarios of fleet behavior. If vessels moved as a group between areas of equal concentration, CPUE could remain nearly constant and abundance would be greatly overestimated as simulated in Fig.6. If an area of high concentration was located late in the season the slope of the Leslie regression could even be positive. If concentrations are fished in order of increasing distance from port, CPUE and estimated population size would reflect the order in which different densities were encountered.

3. The quality of the fishing effort is constant over the time of fishing. Such factors as soak time, bait type and amount, and trap design can be controlled in experimental fishing, but not in a fishery. If they vary randomly over the season they will not bias population estimates, but if they change in a systematic way over time they can introduce bias. For example, if crabs are more attracted to fresh than salted bait, a change to salted bait during the season would lower catchability, and the estimated population size (e.g. Fig. 2). On the other hand, lower catch rates late in the season may cause a switch to longer trap soak times (e.g. Gotshall 1978, for *Cancer magister*) and an effective increase in catchability (e.g. Fig.4). Failure to meet this assumption has the same consequence as failure to meet the first assumption, that is change in catchability during the season. However, in this case the cause is changing fishing methods compared to a change in biological parameters among the target animals in the first assumption.

4. The fished population is closed to immigration, emigration, natural mortality and growth. This assumption might be satisfied in fishing experiments lasting days or weeks, but is difficult to satisfy using data collected over a fishing season. Immigration and growth would lead to overestimates in initial biomass, emigration and natural mortality would lead to underestimates. Mohn and Elner (1987) described a simple method to accommodate growth when it occurs for a known time early in the fishing season. A plateau on the left side of the curve results from biomass gain from growth balancing biomass loss from fishing. A new ordinate is erected at the curve inflection, and the regression and B_0 calculated for the right hand portion. This is presumably the time after growth has stopped. The cumulative catch before the inflection is added to B_0 for a total

available biomass. However, this method is not applicable if growth occurs throughout the season, at the end of the season, or for an undefinable portion of the season. Figs. 7 and 8 illustrate recruitment of 20% of total biomass at the beginning and at the end of the season respectively. Both cases produce a modest overestimate of total biomass.

5. Landings and catch per unit effort are correctly reported. Bailey (1983) has given a good explanation of this problem for snow crab. The stock size will be underestimated in proportion to the underreporting of landings if the fraction unreported is constant throughout the season. If the fraction unreported varies the resulting underestimate will depend on amount and timing during the season. Avoiding taxes and quota restraints are incentives to underreport. Underreporting the number of trap hauls will inflate CPUE, but this will affect the stock size estimate only if the underreporting varies throughout the season. A legal limit on number of traps is an incentive to underreport the number used.

CAN LESLIE BE CURED?

Unfortunately, a changing slope does not alone allow one to distinguish among alternative causes. A slope which becomes less steep over time can be caused by increasing catchability, fleet movement to areas of higher concentration, increased quality of effort, immigration, or growth. Conversely, a slope which becomes steeper with time can be caused by decreasing catchability, fleet movement to areas of lower concentration, decreased quality of effort, emigration, or mortality. Even when the slope does not change and the regression line is a very good fit to the points, as in Figures 1 and 3, the estimate of stock size can be biased. Without knowledge of cause, bias in fishable biomass cannot be corrected. Points on Leslie plots which deviate from a uniform declining slope are routinely excluded for a variety of reasons (Bailey 1978; Methot and Botsford 1982; Taylor and O'Keefe 1983; Mohn and Elner 1987). However, one wonders if points which fit the model are questioned. An interpretation that the model is not useful for determining stock size deserves more frequent consideration.

Extrapolation of the Leslie regression and a disproportionately large influence of end points are further weaknesses of the Leslie method. Extrapolation is often responsible for very wide confidence limits on B_0 (the intercept on the X axis). Points on the end of the regression line have more influence on the slope of the line than do points near the middle, and thus more influence on the extrapolated X intercept.

A tag-recapture (Petersen) method of estimating C. opilio stock size has been used in conjunction with the Leslie method as a check on the accuracy of the latter (Bailey 1978; Bailey and Coutu 1987; Elner and Robichaud 1980, 1981, 1984; Taylor and O'Keefe 1981, 1983, 1984). Unfortunately, the assumptions that catchability is the same for all individuals, that the stock is closed to immigration and growth, and that total landings are correctly reported are common to both methods. Since violations of these assumptions would bias stock size estimates in the same direction for both methods, bias would not be detected. Morgan (1974a) found that the Petersen method underestimated abundance of spiny lobster by 44%. The proportion of marked lobsters in trap catches was higher than the proportion seen on the fishing ground by diving. He attributed this difference to preselecting the most catchable lobsters by marking animals caught by traps.

Additional assumptions applying to the Petersen method only are also possible sources of bias. Marked and unmarked animals have the same natural mortality (i.e. marking does not affect survival). All marked recoveries are noticed and reported. Marked animals become randomly mixed with the unmarked.

ALTERNATIVES

We have seen that using the Leslie method on fishery data assumes that qualities of the target species and of the fishing effort do not change throughout the season. These are ambitious assumptions.

Alternatively, catch per unit effort alone, averaged for all or part of the season, might be used as an index of relative abundance from year to year. This would be calculated as total fleet catch divided by total fleet effort, or CPUE at weekly intervals weighted by effort in each interval. These data could be further refined by using only CPUE of the recruit molt class, or from near the end of the season as a relative measure of stock size remaining. Or if practical, the biologist could obtain better data on CPUE by fishing standard gear in a standard manner at particular times and locations each year. Any of these alternatives assume that catchability, crab distribution, fishing effort, etc. follow the same temporal pattern from year to year. But, they avoid the more forbidding assumptions that catchability is the same for all individuals for all of the fishing season, and that quality and distribution of fishing effort does not change over the season.

Table 1 compares results of Leslie analysis and mean CPUE for a variety of scenarios. Conditions are as described for the above simulations: the stock biomass starts at 100 or sums to 100 with recruitment, an equal unit of fishing effort is applied for 10 time periods, and approximately 60% of the stock is removed by fishing.

For the standard run, with q constant at 0.1 and no recruitment, B_0 is correctly estimated at 100 and the mean CPUE is 6.3. If q is a constant 0.12 or 0.08 throughout the season B_0 is again exact at 100, but mean CPUE over and under estimates the standard by about 12%. A stepped decrease in q underestimates B_0 by 21%, and a stepped increase in q overestimates B_0 by 108%. In both these cases the estimated q's are outside the range of the two q's used in the simulation. In both cases mean CPUE agrees exactly with the standard. When q increases and decreases gradually throughout the season B_0 is considerably in error, and again the estimated q's are outside the range of actual q's. Mean CPUE's are only a few percent higher than the standard. With recruitment early in the season B_0 is overestimated by 24%, but mean CPUE is nearly the same as the standard. With recruitment late in the season both methods are close, B_0 is 12% over and mean CPUE 14% under the standard. When three equal sized patches are fished in succession, B_0 is grossly overestimated and mean CPUE is underestimated by 12%. When the population has three equal sized components of different catchabilities B_0 is underestimated by 15% and mean CPUE is correct. In conclusion, the only cases where mean CPUE is not as good as, or considerably better than Leslie , are where q differs from the standard and is constant over the season. We suspect these are the least likely of all the cases considered.

The mean CPUE method uses no extrapolation, and data from the beginning or end of the season do not have a larger influence on the result than do data from midseason. If each time period has equal fishing effort, as in the simulations, each data point has equal weight. If effort is low at the beginning or end of the season, as is often the case, and each CPUE measure is weighted by fishing effort, the end points will have less influence than midpoints on the mean CPUE.

Leslie analyses are typically used in assessment of snow crab fisheries to set a TAC which will give a target exploitation rate. Management by TAC is intended to provide stable landings and reasonable catch rates (Bailey and Elner 1989). The fishable biomass for the coming year is based on hindcasting of the previous year's fishable biomass (B_0) (e.g. Bailey 1978, Elner and Robichaud 1981, Taylor and O'Keefe 1981). For example, if B_0 for 1988 was 1000t, and the target exploitation rate was 60%, the 1989 TAC would be set at 600t.

Notwithstanding the security of calculating a TAC as above, the usual target of 50-60% exploitation rate was a 'trial and error' 'seat of the pants' guideline based on experience of stable landings in a single northwestern Cape Breton stock when this strategy was applied. However, CAFSAC advised that the 50-60% exploitation strategy has proven unsuitable for many areas (e.g. Anon 1986b).

'Seat of the pants' criteria could also be applied to a target mean CPUE. If the seasonal mean CPUE was higher in 1988 than in 1987, a proportionately higher TAC could be set for 1989. Or, if one had confidence in a mean CPUE for part of the season, a high mean for the end of 1988 or beginning of 1989 would be reason for an increased TAC in 1989. Or, one might wish to set the TAC low enough to ensure a range of size (and age) frequencies in the catch.

Both Leslie and mean CPUE methods assume a correlation between CPUE and fishable stock density. Remarkably, this has rarely been tested. Morgan's (1974b) data for spiny lobster was highly correlated ($R^2 = 0.74$). However, his abundance estimates, based on mark-recapture, and CPUE were not independent because they came from the same trap catches. No correlation ($R^2 = 0.1$) existed between density of snow crabs, based on bottom photography, and trap catches for four areas, although the range of crab densities was not large (Miller 1975). Morrissy and Caputi (1981) obtained a high correlation ($R^2 = 0.83$) between observed density of crayfish in farm ponds (measured by seining) and density predicted from trap catches. However, their predictive equation was the result of an elaborate curve fitting exercise. It included independent variables for temperature, animal length, a coefficient of variation for animal weight, and turbidity. Four other independent variables were tried and discarded, as were data for 2 of the 12 ponds.

In conclusion, Leslie analysis is not a reliable estimator of stock abundance because assumptions are frequently violated and some biases cannot be diagnosed from data inputs. A mean CPUE as an index of abundance has fewer assumptions, but correlation between these variables need to be established for snow crab. An alternative management strategy not requiring an estimate of abundance could be simply a biologically safe minimum size and no TAC.

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Table 1. Summary of Leslie and mean CPUE simulations.

Conditions	Starting B	Leslie B_0	Leslie q	mean CPUE
Standard, q=0.1	100	100	0.10	6.3
q = 0.12	100	100	0.12	7.0
q = 0.08	100	100	0.08	5.5
Stepped decrease in q[1]	100	79	0.16	6.3
Stepped increase in q[2]	100	208	0.04	6.3
Gradual decrease in q[3]	100	74	0.21	6.5
Gradual increase in q[4]	100	1470	0	6.6
Early recruitment, q=0.1[5]	80	124	0.07	6.2
Late recruitment, q=0.1[6]	80	112	0.07	5.4
Patch fishing, q=0.1[7]	100	3605	0	5.5
Population components with q = .05, 0.1, and 0.2[8]	100	85	0.13	6.3

[1]q=0.12 for first 5 time periods and q=0.08 for last 5 time periods.
[2]q=0.08 for first 5 time periods and q=0.12 for last 5 time periods.
[3]q decreases from 0.15 to 0.06 in 10 steps of 0.01.
[4]q increases from 0.06 to 0.15 in 10 steps of 0.01.
[5]7, 7, and 6 units of biomass are added during time periods 2,3, and 4
[6]7, 7, and 6 units of biomass are added during time periods 8, 9, and 10.
[7]Three biomass patches of equal size are each fished down 60% in turn.
[8]Three biomass components of equal size, but with different catchabilities, are each fished simultaneously.

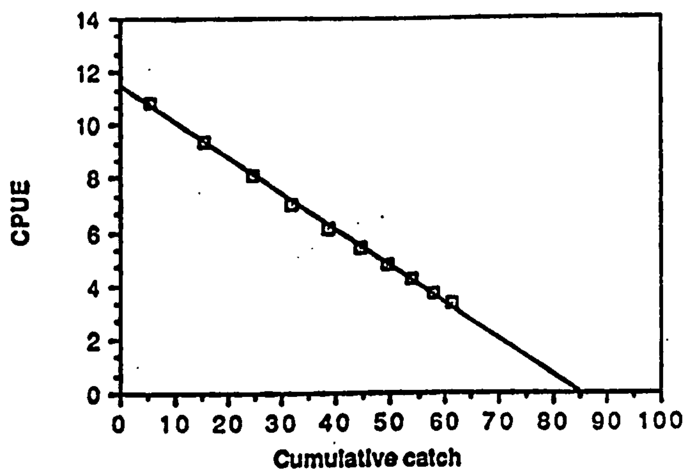

Fig. 1. Leslie regression on a stock of three equal sized components with catchabilities of 0.05, 0.10, and 0.20.

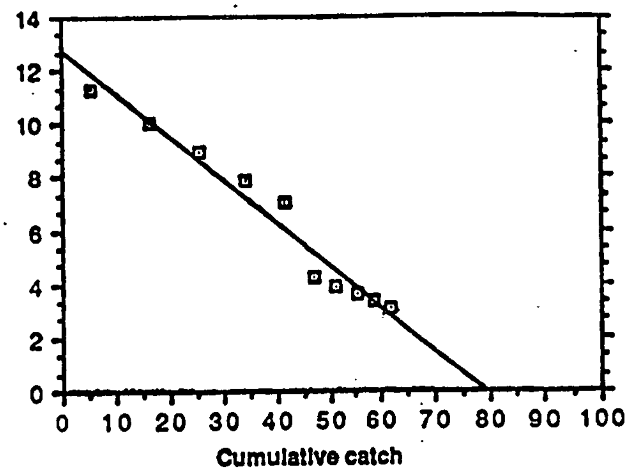

Fig. 2. Leslie regression on a stock with a stepped decrease in catchability, from q=0.12 to q=0.08.

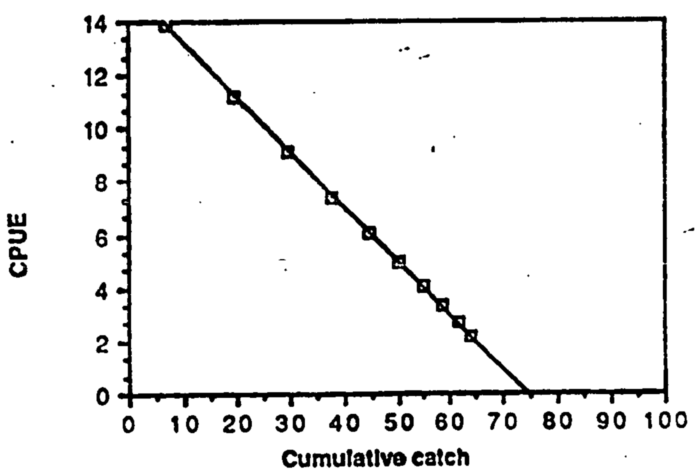

Fig. 3. Leslie regression on a stock with a gradual decrease in catchability, from q=0.15 to q=0.06.

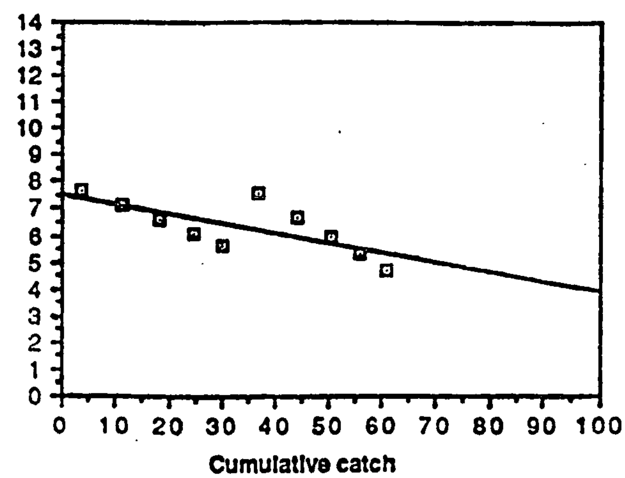

Fig. 4 Leslie regression on a stock with a stepped increase in catchability, from q=0.08 to q=0.12.

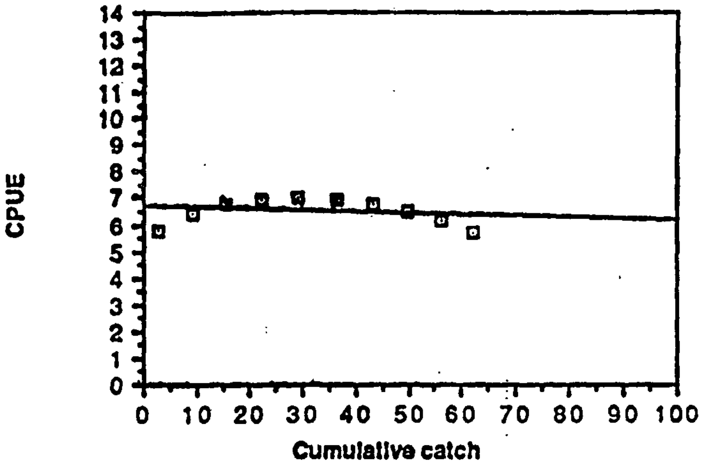

Fig. 5. Leslie regression on a stock with a gradual increase in catchability, from q=0.06 to 0.15.

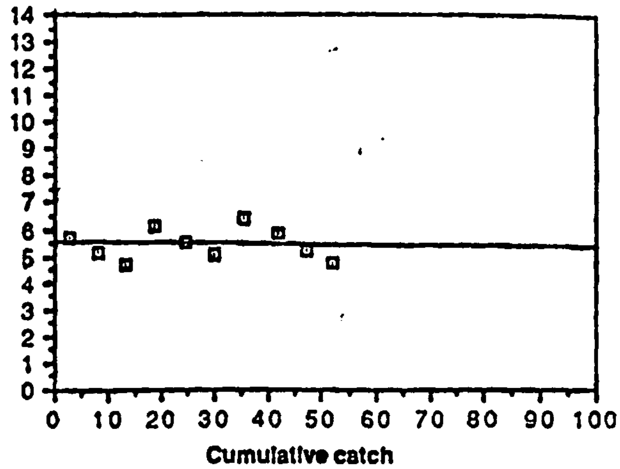

Fig. 6. Leslie regression on a stock with three equal sized components fished in turn, q=0.10 for all components.

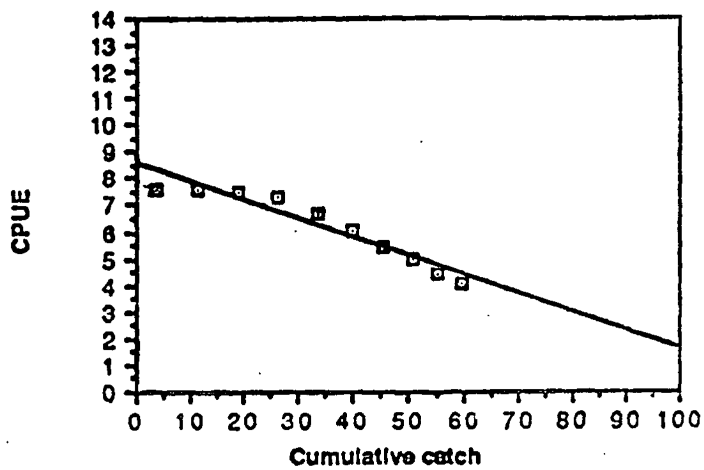

Fig. 7. Leslie regression on a stock with biomass 80 at the start of fishing, but with additions by recruitment of 7, 7, and 6 units of biomass during periods 2, 3, and 4.

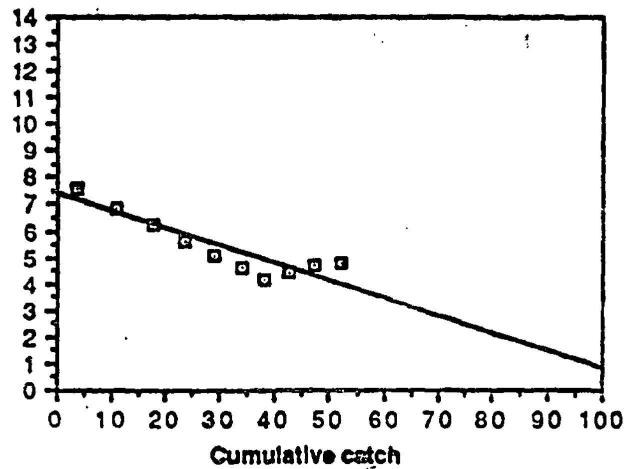

Fig. 8. Leslie regression on a stock with biomass 80 at the start of fishing, but with additions by recruitment of 7, 7, and 6 units of biomass during periods 8, 9, and 10.