A Simple Mechanism that Causes Collapsing Stability Regions in Exploited Salmonid Populations

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Depensatory predation mortality on salmon when added to a Ricker production model can create a system with at least two stable equilibria and two domains of attraction. The behavior of such a fish system is different from a single equilibrium situation and a simple mechanism is described through which commercial exploitation changes the ability of such multiple-equilibrium fish populations to respond to perturbations in survival rates. Furthermore, it is shown that this change in size of stability regions is proportional to the exploitation rate and that classically defined maximum sustainable yield (MSY) exploitation rates are inevitably close to the rates that would cause a drastic decrease in the population. The uncertainties inherent in environmental effects on survival and in achievement of desired exploitation rates precipitate the need to back away from the usual MSY exploitation rates and set up (through enhancement) a system of stocks whereby feedback information is provided to the manager. This approach of adaptive management seeks reasonable yields while gaining information about the state (or changes in state) of the system. Some applications of catastrophe theory are discussed, especially with reference to harvesting multiple-stock salmon systems.

Key words: stability, resilience, exploitation, salmon, depensation, multiple equilibria, adaptive management, enhancement, catastrophe theory

La mortalité par prédation dépensatoire sur le saumon, ajoutée à un modèle de production de Ricker, peut créer un système possédant au moins deux équilibres stables et deux domaines d'attraction. Le comportement d'un tel système pour les poissons diffère d'une situation à un équilibre, et nous décrivons un mécanisme simple en vertu duquel l'exploitation commerciale change l'aptitude de telles populations de poissons à équilibre multiple à répondre aux perturbations des taux de survie. De plus, nous démontrons que ce changement dans l'étendue des régions de stabilité est proportionnel au taux d'exploitation, et que les taux d'exploitation classiquement définis comme rendement maximal soutenable (RMS) se rapprochent invariablement des taux qui causeraient une diminution dramatique dans la population. A cause des incertitudes inhérentes aux effets de l'environnement sur la survie et à la poursuite des taux d'exploitation désirés, il devient de plus en plus urgent de s'éloigner des taux d'exploitation correspondant au RMS usuel et d'établir (par revalorisation) un système de stocks selon lequel le gestionnaire recevra un retour d'information. Cette approche de gestion adaptive cherche à obtenir des rendements raisonnables tout en apprenant davantage de l'état (ou changement de l'état) du système. L'auteur examine certaines applications de la théorie de la catastrophe, surtout en rapport avec la récolte de systèmes de saumons à stocks multiples.

HOLLING (1973) argues from theoretical and empirical grounds that it may prove useful if ecologists modify their viewpoint of stability of ecological systems. Historically, the main focus of attention has been on equilibria, but we know that in the real world, equilibria are rarely, if ever, achieved. Natural systems are constantly subjected to fluctuating conditions that cause changes within the system. Often these fluctuations exceed the limits of a system's ability to respond and the system becomes distinctly different in character through extinction or drastic long-term changes in abundance. Holling concludes that we should concentrate on these limits to system response, rather than on equilibria.

Those natural systems that can cope successfully with wide ranges of fluctuations in state

variables, driving variables, or parameters are more "resilient" than systems with narrower tolerance ranges (Holling 1973). There are numerous mechanisms affecting a system's resilience: for example, shapes of reproduction and survival functions, types of dispersal characteristics, and existence of areas of inaccessibility to predation (refugia). Holling (1973) suggests that one effect of man's activities may be to reduce the resilience of ecological systems by shifting the boundaries or limits of stability and Ricker (1963) investigates an example of changing stability bounds caused by shifts in fish population age structure.

This paper describes another simple man-induced mechanism that reduces the size of stability domains in commercially exploited salmon populations, and the management implications of this mechanism are explored in depth.

Background

Ricker (1954) noted when he introduced the stock–recruitment concept that the existence of depensatory mortality processes (defined by Neave (1953) as processes causing higher percentage mortality at low prey population densities) might result in the replacement line crossing the recruitment curve in three places; instead of one equilibrium, there would be three (Fig. 1). Two of these equilibria (points A and C) are stable, that is, the spawning population tends to move toward

FIG. 1. A recruitment curve showing the effect of depensatory mortality (after Ricker 1954, fig. 30). See text for explanation.

one or the other value. Point B, on the other hand, is a transient or unstable equilibrium; the population moves away from this level. Thus, the spawning population size corresponding with point B forms the boundary (X_0) between two different domains of attraction. Spawning populations in any one domain tend to remain there unless pushed across this boundary. The evidence for existence of more than one equilibrium or domain of attraction in real fish populations comes from two sources: data showing temporal changes in fish populations and knowledge of the form of the processes that cause these changes.

First, there are numerous examples of populations that dropped to very low levels and that failed to recover to former high levels, even after the causes of the stock collapses were removed (see Beeton 1969; LeCren et al. 1972; Holling 1973). Such examples suggest the existence of upper and lower domains of attraction for these populations.

Perhaps one of the best illustrations of the existence of multiple equilibria or domains of attraction comes from the history of the pink salmon (*Oncorhynchus gorbuscha*) on the Atnarko River in British Columbia. The odd-year population (total catch plus escapement) on this river dropped from a high of about 2.5 million in 1961 to about 80,000 in 1967 due to a combination of overexploitation and poor weather conditions (F. E. A. Wood and R. Hilland, Fisheries and Environment Canada, unpublished data). The population has remained at this very low level for five consecutive cycles (Fig. 2), despite the fact that the exploitation rate has dropped considerably and that environmetnal conditions have been relatively good. It is notable that the even-year Atnarko pinks, which spawn in the same area, have remained high during the past five cycles, showing that the low odd-year population is not being held down by major alterations in spawning habitat conditions. The mechanism that keeps the odd-year cycle population small is not known; it could be the interaction between odd- and even-year cycles through adult predation on outgoing young or through deterioration of spawning grounds by masses of dead even-year eggs. However, the exact mechanism is not important for the purpose of this paper. What is significant is the apparent existence of two distinct domains of behavior, one for small population sizes and one for large populations.

Next, Paulik (1973) and Holling (1973) illustrate how multilife stage, density-dependent processes such as predation can result in recruitment curves that cross the replacement line at several points. There is extensive evidence in the salmonid
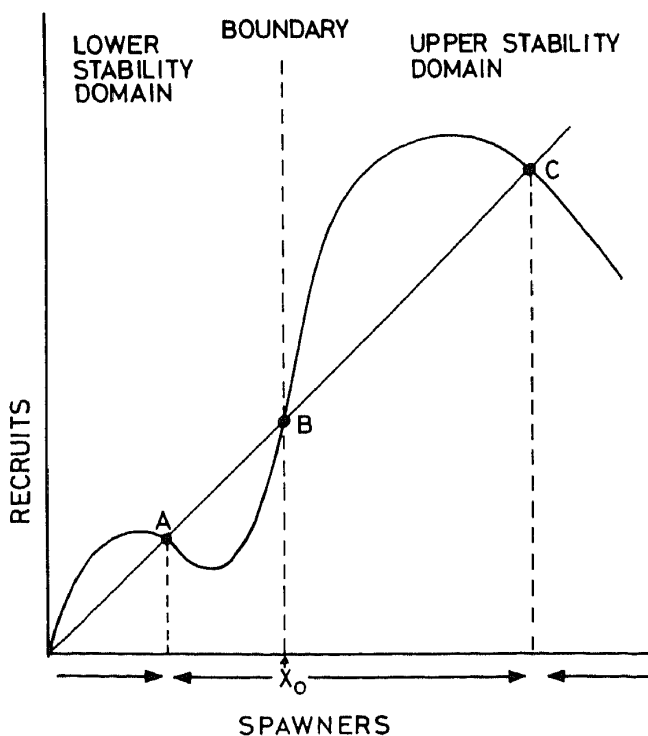
ODD-YEAR PINK SALMON

— total area 8
-- Atn arko R. only

DATA FOR THE LOW RUNS:

year	area 8	Atnarko R.
1967	110,235	81,559
1969	78,869	31,038
1971	291,720	55,635
1973	229,842	62,233
1975	345,783	39,300

EVEN-YEAR PINK SALMON

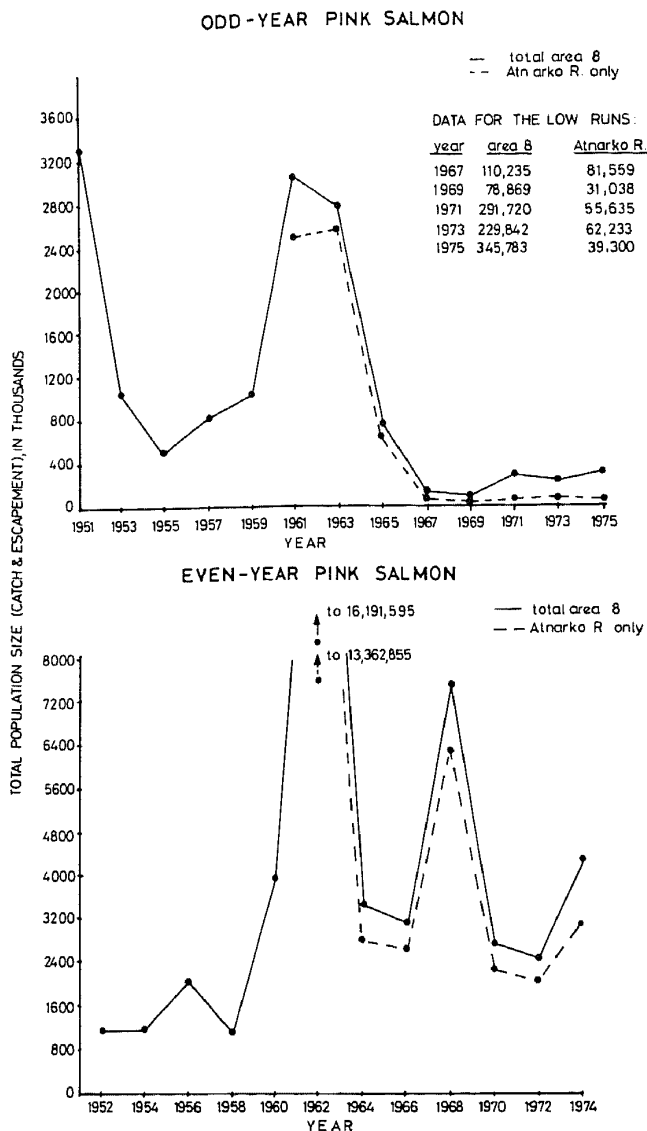to 16,191,595   — total area 8
to 13,362,855   — — Atnarko R only

FIG. 2. Total population data (catch plus escapement) for the pink salmon (*Oncorhynchus gorbuscha*) of the Atnarko River, B.C. and total Area 8 pinks (which includes Atnarko River). Note that while Atnarko River data have been separated only since 1961, this stock has constituted most of the total Area 8 population, which has been counted back to 1951.

literature showing that predation mortality on young salmon can be as high as 65–85%, with the highest percentage mortalities occurring at low prey population densities (Hunter 1959; Neave 1953; Ricker 1962). As will be illustrated later, this magnitude of depensatory mortality, when combined with the other sources of mortality, can be sufficient to create the multiple-crossover phenomenon discussed by Paulik and Holling, at least for some exploited systems if not for unfished situations.

Thus, the theoretical and empirical evidence implies that some, but not all, fish populations may have recruitment curves with two or more

potential equilibria, and therefore more than one domain of attraction. Clearly, fisheries managers dealing with such multiple-equilibrium situations would like to keep populations in the upper domain by avoiding the boundary shared with the lower domain. If the boundary were static, this task might be relatively simple, but this boundary shifts in response to man's interventions as well as environmental changes. Ricker (1954) noted that as the exploitation rate on a population increases, the slope of the new replacement line increases accordingly (Fig. 3), and that even if there is not more than one equilibrium when the stock is unexploited there could be two or more when there is harvesting. Note that recruits here mean recruits before harvest. The critical implication for management is that the spawning or boundary population size below which the stock drops into the lower region of stability increases from X_0 to X_0' when the exploitation rate is increased to 30%, for example.

This paper investigates the management consequences of changes in exploitation rate and subsequent shifts in this boundary and in sizes of stability domains. In addition, some effects of altering reproduction parameters (through enhancement, for example) will be discussed.

The Model

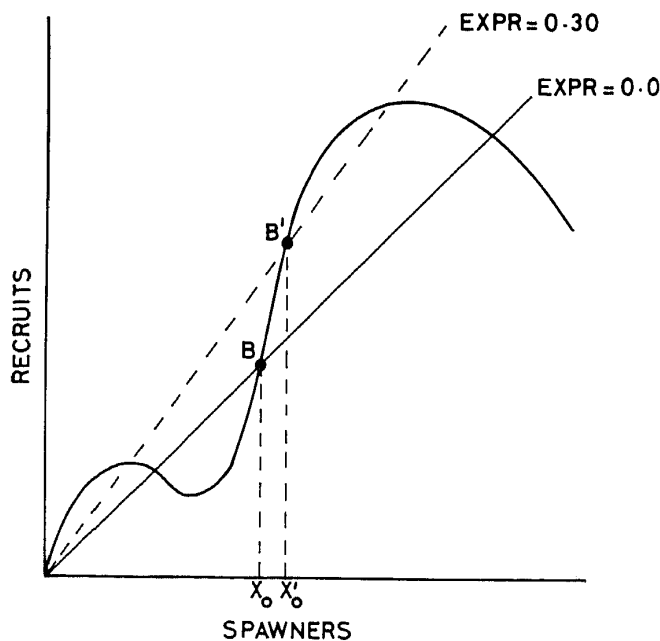The theoretical species used for this study resembles pink salmon, which has a simple age

FIG. 3. Same recruitment curve as in Fig. 1. When the exploitation rate on the recruits (EXPR) is raised from 0 to 30%, the slope of the replacement line changes accordingly. The location of the transient equilibrium changes from B to B', and the boundary population size changes from X_0 to X_0'.

structure and discrete generations. Offspring (fry or smolt) production is assumed to be described by a Ricker stock–recruitment curve, an assumption supported by some salmon data (e.g. Skud 1973). Losses to predation on the downstream migration, in the rearing lake, in the estuary, or in the ocean are removed from the resulting offspring population to give net recruits, or returning adults. It is assumed that a constant proportion of the offspring surviving predation will return as adults. It can be shown that the general conclusions of this study would be the same if a Beverton and Holt model (1957) had been used instead of the Ricker model, as long as depensatory mortality due to predation had been added in the same way.

The basic model used was:

(1) $R = S \exp [A(1 - S/E)]$

(2) $N = R - [(B \cdot R^2)/(P^2 + R^2)]$

where R = number of offspring before predation losses, S = number of spawners, A = the reproduction parameter of the Ricker model, E = the unfished equilibrium population size, before effects of predation are added, N = net number of recruits after predation losses but before harvest, B = the maximum number of fish that could be removed by the total predator population (maximum ration per predator times number of predators), P = the number of prey that results in $B/2$ prey lost to predation.

Predation can be measured in terms of the functional response, defined by the number of prey eaten per predator per unit time as a function of the number of prey available. Holling (1965) describes several basic forms for this relationship and two are relevant to the present situation. The so-called Type II functional response (Curve a in Fig. 4) describes the situation for predators that do not have learning characteristics. The number eaten increases with increasing prey numbers, but begins to asymptote as the predator begins to reach its capacity for processing prey (due to limited handling time). Thus, above a certain number of prey, each predator can only take a maximum number of prey. The Type III or S-shaped functional response (Curve b in Fig. 4) is characteristic of predators that learn. At low prey numbers, the predators may need some experience before "switching on" to the prey, but once this has occurred the number eaten increases more rapidly with increasing prey than in the Type II response. However, these predators are subject to the same handling time limitations and an asymptote is soon reached.
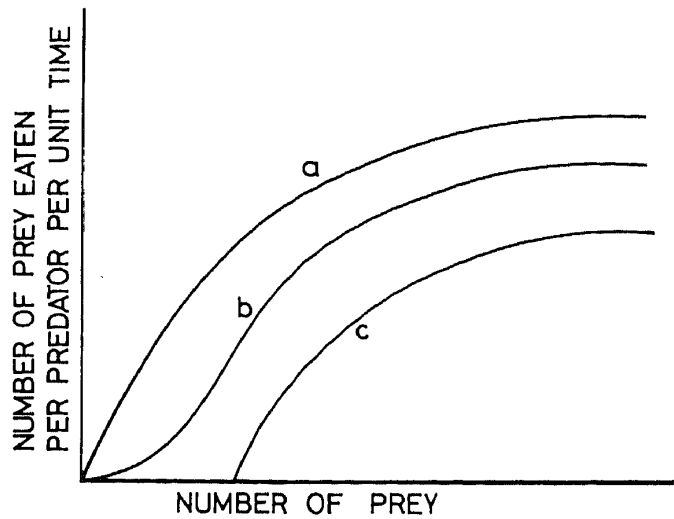
The predation term of equation (2) above pro-

FIG. 4. Example predator functional responses. Curve a is a Type II response, Curve b is a Type III response, and Curve c is a Type II response but with a nonzero intercept. All three types could in reality asymptote at the same level; they are drawn here with different asymptotes merely to illustrate the differences in forms.

duces the Type III functional response and has the two biologically relevant parameters indicated, B and P (C. S. Holling, personal communication). There are several ways to justify using the Type III instead of the Type II functional response. First, the predators of salmon fry are largely vertebrates (fish) which, according to Holling (1965), should show S-shaped functional responses because of their learning, forgetting, and switching characteristics. Second, an individual predator with a Type II (concave) functional response may actually have a zero attack rate at a nonzero prey density, thereby effectively creating a refugium for the prey (Curve c in Fig. 4). This turning-off point (the prey density below which there are no attacks) is probably not constant among all predators in a population; if it is assumed to be normally distributed among the predators, then the aggregate functional response of the total predator population will be an S-shaped (Type III) curve (C. J. Walters, University of British Columbia, personal communication). Finally, any tendency for predators to aggregate (a quick numerical response) will also result in a Type III functional response (Hassell and May 1974). Murdoch and Oaten (1975) show how an S-shaped predation function gives rise to the type of "depensatory recruitment curve" illustrated graphically by Ricker (1954, 1962).

However, an S-shaped functional response of individual or a population of predators is not necessary to create a recruitment curve with more than one stable equilibrium; predators

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having a Type II functional response with a non-zero intercept on the prey axis would suffice (Curve c in Fig. 4). Below that intercept, net gains in the prey population would become possible, compared with net losses at some higher prey densities.

The present model implicity assumes the predator population size is relatively constant through time and independent of the prey population, a reasonable assumption for pink and chum salmon (*O. keta*) prey, since the salmon fry are a food source for only a short period of time during downstream migration in any year.

The few studies that exist show that the percent predation mortality on young salmon is highest at relatively low prey densities (Foerster 1968; Hunter 1959; Neave 1953; 'Ricker 1962) and therefore the "dip" in the net recruitment curve occurs at these low levels. To illustrate more clearly the graphical effects of depensatory mortality, the recruitment curves in Fig. 1, 3, and 6 have been drawn with the "dip" slightly exaggerated.

Methods of Analysis

The model used here cannot be solved analytically for S (nor can the Ricker model), so to determine the location of the boundary between the two domains of stability for any sustained exploitation rate, it is necessary to solve for the sustainable harvest rate corresponding to any given boundary population size. For a given S, the net number of recruits (N) is calculated, giving a slope of N/S for the line connecting that point on the recruitment curve with the origin. Ricker (1958a) notes that the relation between this slope (M) and its corresponding sustainable exploitation rate (H) is:

(3) $H = 1 - (1/M)$

Therefore, each boundary population size X_0' can be associated with a particular sustainable exploitation rate. Finally, the maximum sustainable yield (MSY) harvest rate is determined by iteratively searching along the net recruitment curve for the point where it is the greatest vertical distance from the replacement line (Ricker 1973b).

Unless otherwise noted, the parameter values for all examples in this paper are as follows: $A = 1.6$; $E = 500,000$; $B = 150,000$; $P = 90,000$. These parameter values create a lower, stable equilibrium at about 20,000 spawners, or 4% of the upper equilibrium, perhaps a conservative estimate compared to the Atnarko River pink salmon or other situations. The resulting model was analyzed for deterministic and stochastic cases.

Results and Discussion

Single Stock, Deterministic Case

Figure 5 shows that the population size corresponding to the boundary between the two
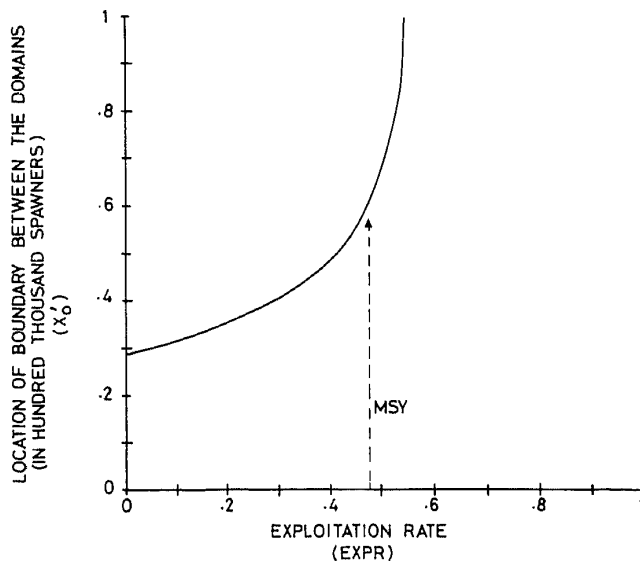

Fig. 5. Relation between X_0', the boundary between the two domains of stability, and exploitation rate. The dotted line designates the MSY exploitation rate for that stock (biological parameters given in text).

domains of stability increases sharply as high harvest rates are approached. Because the size of the lower domain increases as the exploitation rate increases, the proportion of spawning population sizes that will be in the lower domain increases dramatically. However, the most significant point for management is that the MSY exploitation rate comes dangerously close to the steeply rising portion of the curve (Fig. 5). Ricker (1973a) states that during the course of the development of fisheries, populations often are temporarily overexploited as the managers "zero in" on MSY (putting the system temporarily farther out on the ascending limb of the curve in Fig. 5). In such cases, an incremental change in natural mortality or in exploitation rate (possibly caused by increased gear efficiency) can cause greater alteration in the proportion of fish population sizes that are in the lower domain than the same unit change at lower exploitation rates. Ricker (1963) noted a similar nonlinear effect dealing with changes in population age structure.

These discussions assume a fixed exploitation rate that results in a population remaining forever in the lower stability region once it gets below the boundary associated with that harvest rate. However, in order to get the population back in the upper domain, the location of the boundary can be changed by altering the exploitation rate. But the exploitation rate must be dropped quickly enough to "catch" the population before it goes below the depensation level for the no-harvest case (X_0). The shape of the curve in Fig. 5 implies that at high harvest rates only a small reduction in harvest rate may be necessary to
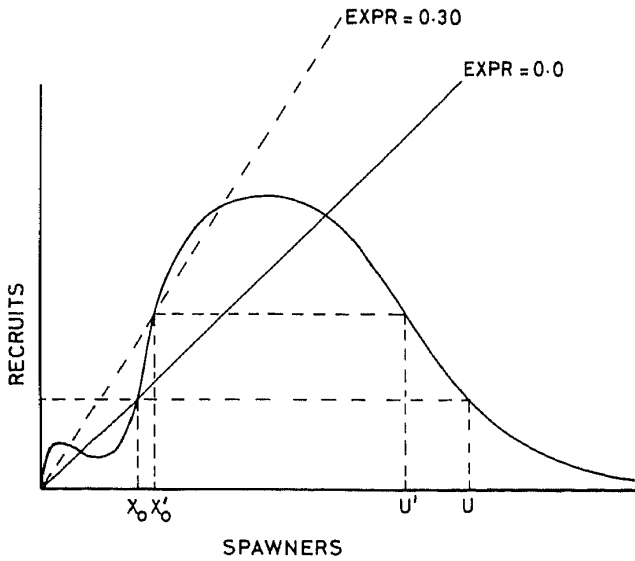
FIG. 6. Where there is strong density dependence in a stock, spawning populations greater than U will, on average, produce X_0 or fewer recruits, putting the population into the lower domain of stability in the next generation. When exploitation of recruits is increased above 0.0, the lower and upper bounds of the "desired" region change to X_0' and U', respectively, shrinking the size of that region.

achieve a given reduction in the boundary limit. Just how quickly harvest rates can be reduced in actual practice depends upon social and economic pressures as well as changes in gear efficiency. However, the significant management conclusion is that the process of changing sizes of stability domains is a highly nonlinear one. A discussion of how the foregoing applies to stocks having fluctuating survival rates will be held until a later section of this paper.

This simple case only considers the dynamics of low populations in the region where depensatory processes are important. However, we also need to examine the results of having large spawning populations if there are strong density-dependent (compensatory) processes operating at any life stage of the fish. In these cases, there may be very few recruits resulting from large spawning populations, causing the population to drop into the lower domain of stability, even in the absence of any exploitation (Fig. 6). This "reflection" of the lower region of stability on the right end of the recruitment curve has similar properties to the lower region; as the exploitation rate is increased, the boundary of this upper "reflected" region, U, is reduced to U' (see Fig. 6). The existence of the effect of this "reflection" of the lower domain of stability is consistent with, though it does not necessarily always explain, the commonly observed large recruitment just prior to collapse of fish populations such as in Peruvian anchovetas (Parrish 1973; Anon. 1974).

The region that management desires the popu-

lation to occupy thus becomes bounded on both ends by spawner levels that lead the population to the lower domain of stability within the next generation. Increasing exploitation rates increase the lower bound and decrease the upper bound, thereby shrinking the size of this range of desired population sizes. Figure 7 shows, for a reproduction curve with the parameter values given earlier, how the size of this region changes as a function of the exploitation rate. When the system is at MSY exploitation rate, the size of the domain is $<65\%$ of the size of the domain at an exploitation rate of zero. Furthermore, at the maximum possible sustainable exploitation rate (which is greater than MSY harvest rate but with low yield), the region's size is $<45\%$ of the size in the unexploited case. The spawning populations at which this phenomenon becomes important are, for the case illustrated in Fig. 7, much higher than the unfished equilibrium, but this is not true for all parameter combinations. Thus, the general characteristic of shrinking domains is probably of significance to managers. Again note that the MSY harvest rate falls very near the point at which the region's size collapses rapidly. Conclusions from this analysis are the same as before; fisheries operating near MSY harvest rates have much higher probabilities of dropping into lower domains of stability than might be intuitively expected, especially when uncertainties in exploitation and reproductive rates are taken into account (next section).

The conclusion resulting from the reflection of the depensatory effect onto the right limb of the recruitment curve does not, of course, apply to
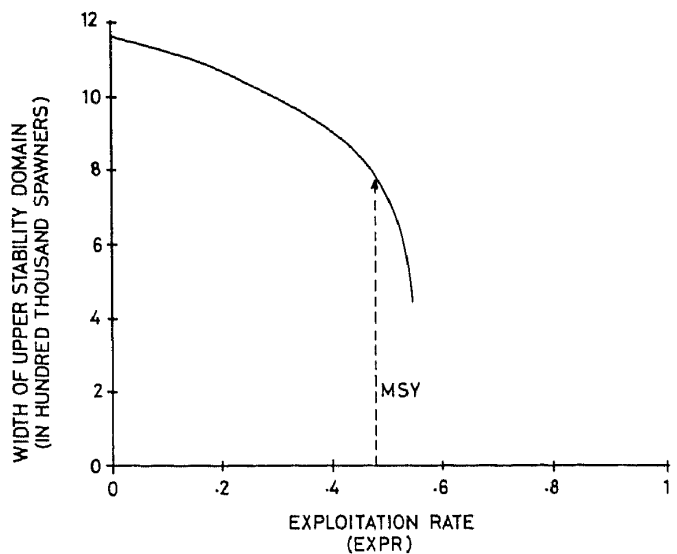

FIG. 7. The size of the domain of stability (delineated by X_0' and U' in Fig. 6) as a function of exploitation rate. Domain width is in number of fish, $U' - X_0'$. Arrow indicates MSY exploitation rate for this stock.

the case where a saturating model such as the Beverton–Holt describes the production of offspring, because in such a model there is no decrease in production at high numbers of spawners.

The catch curves for several single-stock, deterministic cases represent the above information in a different form. Figure 8 shows the relation between sustainable catch and exploitation rate for a family of depensatory recruitment curves with different A values. Because the effect of depensation has been included in the model, these catch curves break off at a certain exploitation rate. Above this exploitation rate, the stock becomes overexploited and there is either zero sustainable catch or a very small catch (if the population persists in the lower domain).

SINGLE STOCK, STOCHASTIC CASE

The deterministic recruitment curve above only calculates recruits resulting from a given number of spawners under average environmental conditions. Variation in environmental factors affecting reproductive output or survival is introduced into the model using the log-normal, multiplicative form argued for by Allen (1973) and Walters (1975),

$$V = \exp(G)$$

where G is a number drawn randomly from a normal distribution having a mean of 0.0 and a SD of 0.6. The distribution of the resulting environmental factor is similar to that of "Level A variability" of Ricker (1958b) and Larkin and Ricker (1964).
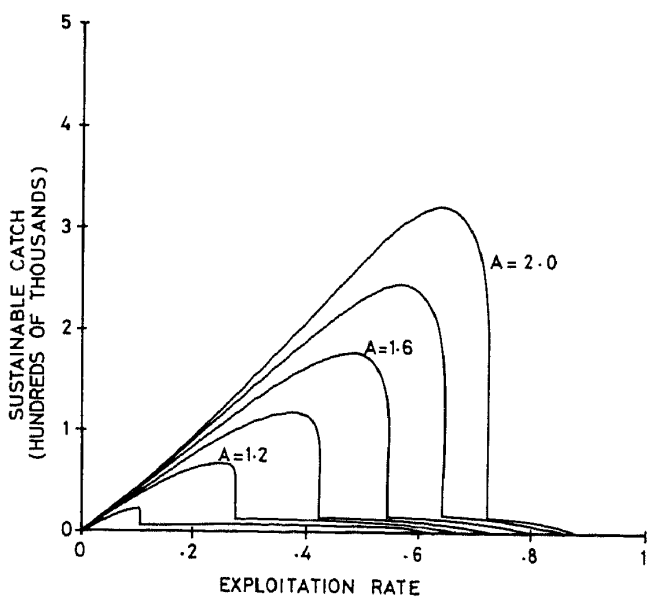
Equation (2) thus becomes

(4) $N = V \cdot \{R - [(B \cdot R^2)/(P^2 + R^2)]\}$

This survival factor shifts the net recruitment curve up or down, which causes a change in the location of the boundary between the upper and lower domains of attraction (Fig. 9). As V increases (environment becomes more suitable), the boundary population size decreases and the lower domain shrinks (Inset, Fig. 9). If the distribution of environmental factors is known, the statistical distribution of boundaries can be determined for any given exploitation rate and confidence bands can be calculated for the curves which describe where we expect to find the boundary (Fig. 10). Note that the boundary between the two domains never gets below 20,000 because the upper and lower domains merge into one domain when the environmental factor and exploitation rate get above certain levels, i.e. only the lower equilibrium exists.

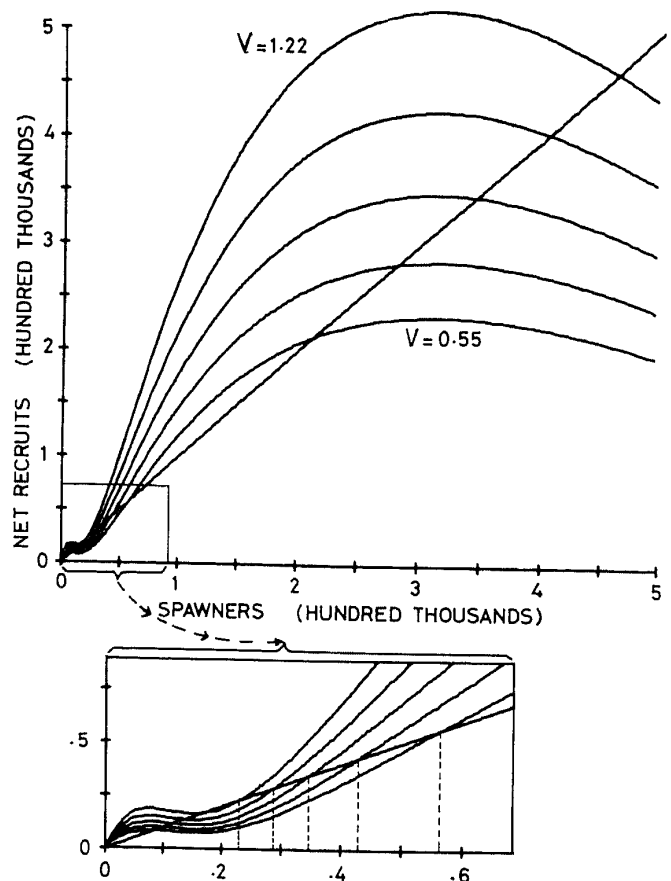This information on shifts in boundaries due

FIG. 9. Changes in the multiplicative environmental factor that affects recruits, as applied in this model, shift the whole recruitment curve and also its replacement line crossover points (dotted lines in the inset). Different values of V ranging from 0.55 to 1.22 were chosen to demonstrate some of the range of changes in the curve.

FIG. 8. The sustainable catch of stocks with A values ranging from 1.0 to 2.0 at intervals of 0.2 as a function of exploitation rate.
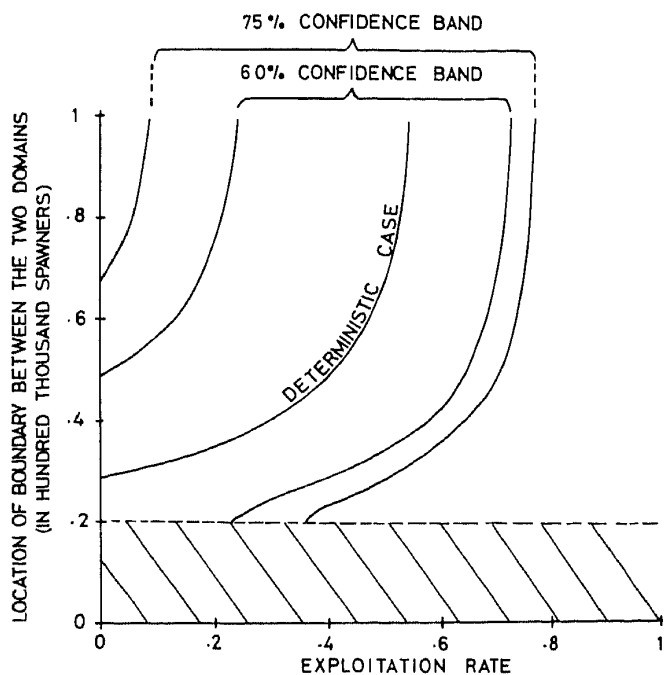
FIG. 10. The 60 and 75% confidence bands around the deterministic location of the lower bound using the distribution of survival factors described in text. In the hatched region, there exists only a single domain of attraction, in this case the lower domain.
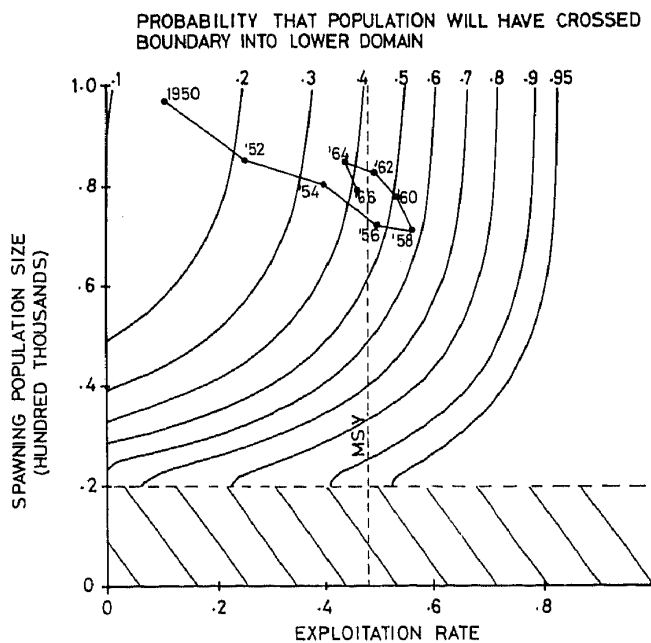

FIG. 11. The contours give the probability that a spawning population will cross into the lower domain if a given exploitation rate is applied to its offspring. Superimposed on these contours is the time course of a hypothetical developing fishery, similar to the events observed by Ricker (1973a) and Schaaf (1975). Note that as the MSY exploitation rate (vertical dotted line) is temporarily exceeded, the probabilities of the population being below its lower bound are relatively high. In hatched area, there exists only a single domain of attraction, in this case, the lower domain.

to changing environmental conditions can be presented in another form (Fig. 11), an isopleth diagram which shows the probability of any given spawning population causing the next generation to be in the lower domain, given the exploitation rate to be imposed on the offspring (this rate permits calculation of the replacement line's slope). This isopleth diagram can be useful to managers if the temporal sequence of environmental factors affecting offspring survival is unknown but their historical distributions are known, because it clearly illustrates the maximum exploitation rate that should be allowed to keep the fish population above the boundary with a given risk (a risk which can vary between different managers or situations).

The historical development of a hypothetical fishery can be traced on this isopleth diagram and population collapses can be interpreted in terms of domains of stability (Fig. 11). The classical course of events which has been observed in developing commercial fisheries (Ricker 1973a; Schaaf 1975) traces a spiral on this graph, where initial overshooting of the MSY exploitation rate is accompanied by high probabilities of the population crossing into the lower domain of stability. These high probabilities are dangerous if the exploitation rate is not reduced rapidly enough. For the case shown, the population succeeded in staying in the upper domain.

The nonlinear effect of environmental changes

on the location of the boundary between the upper and lower domains of attraction is related to the slope of the recruitment curve near the intersections with the replacement line. The flatter the curve at these points relative to the replacement line, the greater is the change in the lower bound for a given change in the environmental factor (refer back to Fig. 9). Since higher values of parameter A of equation (1) result in steeper recruitment curves, enhanced salmon stocks, which may have higher A values, will have less uncertainty in the boundary locations than less productive stocks.

Because of this phenomenon, it might seem logical to desire all stock productivities to be boosted as high as possible within existing management constraints. However, this may not be the best option, as will be discussed in the next section, which deals with multiple-stock fisheries.

MULTIPLE STOCKS, DETERMINISTIC CASE

The approaches to the single-stock case are equally applicable to multiple-stock systems for investigating effects of different relative stock productivities on probability of stock collapse

(meaning a drastic drop to a much lower level, though not necessarily to extinction). It is assumed in the following analyses that there is no interaction between stocks and that exploitation rates are applied equally over all stocks.

Salmon fisheries where more than one stock is harvested simultaneously create special problems. If the stocks have very different productivities (A values in equation [1]) exploitation rates designed to optimally harvest the more productive stocks will increase the likelihood of overexploiting the less productive stocks (Ricker 1958a). One possible cause of this commonly recognized problem could be the dropping of the less productive stocks into their lower domains of stability. On the other hand, if stocks fished simultaneously have similar A values, then there is a lower chance of overharvesting the less productive stock.

What are the characteristics of multiple-stock salmon fisheries, and how similar should the A values ideally be? If depensatory mortality is at all common and significant in these fish, then we can use pairs of equations of the present model to investigate the relationships between similarities of stock productivities, their different MSY exploitation rates, and the amount of drop in sustainable catch if and when any stocks become overexploited. When enhancement is successfully carried out, the exploitation rates will presumably begin to increase, but to some unspecified level. It is this increasing exploitation rate which is the source of potential overexploitation problems.

Figure 12 shows the relationships between sustainable catch and exploitation rate for each of six pairs of stocks having different relative productivities. All stocks have parameter values as defined before in the Methods of Analysis section, except the most productive stock in all cases has $A = 2.0$ and the less productive stocks have A values ranging from 1.0 to 2.0 at intervals of 0.2. Several characteristics of these catch curves are important:

D = difference in exploitation rates causing the collapse of, first, the less productive stock (OEX_1) and then, the more productive stock (OEX_2).

R_p = ratio of productivities of the two stocks involved in the fishery, where $A_2 = 2.0$ and

$$R_p = A_1/A_2$$

CC_1 = cost of the collapse of the less productive stock of the pair, measured here strictly in terms of the decrease in sustainable catch below what it was just before overexploitation occurred.

CC_2 = same as CC_1, but for the more productive stock of the pair.

The curves in Fig. 12 illustrate several points. First, as is intuitively obvious, the greater the
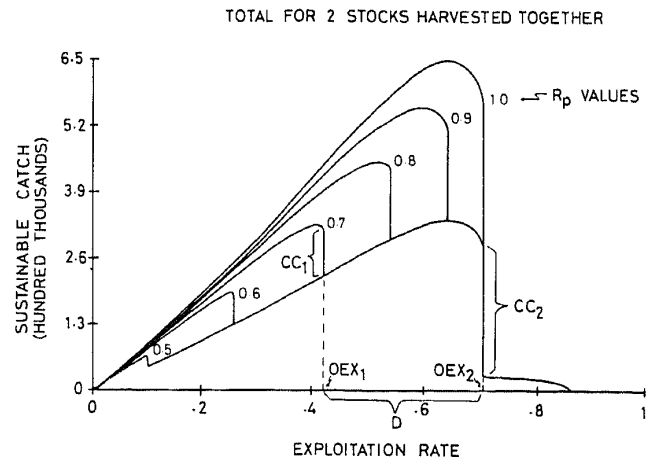

FIG. 12. The relation between exploitation rate and total sustainable catch from both stocks of different two-stock systems, each having different ratios of A values for their constituent stocks. See text for explanation of symbols.

similarity in productivities, the smaller is the difference between the exploitation rates that will cause each respective stock to drop into its lower domain of stability. On the other hand, if stock productivities are dissimilar, there might be more time to take corrective action on increasing exploitation rates before the most productive stock also becomes overexploited.

Second, the drop in sustainable catch owing to the collapse of the less productive stock (CC_1) increases as R_p approaches 1.0. When two stocks have similar productivities, the relatively large CC_1 acts as a strong warning signal, perhaps strong enough to stimulate the imposition of constraints on the developing fishery and to prevent the collapse of the second stock. But large feedback signals only occur when D is small. Thus, there is a trade-off. If the resolution of the monitoring system is such that practically all sizes of CC_1 are perceived as noise, then pairs of stocks with different R_p values will likely have little difference in the probability of overharvesting both stocks. Conversely, if good monitoring can detect a relatively small CC_1 as loss of a stock, then there will be great differences in chances of overexploiting both stocks between systems with different R_p values. The importance of generating and monitoring such feedback information is discussed by Holling (1969) and Walters and Hilborn (1976).

Finally the ratio CC_1/CC_2 increases with R_p, meaning that the loss of the less productive stock becomes more significant in terms of decreased sustainable catch when stocks have more similar A values. However, even if the probability of causing overexploitation of the second stock is low (D large), the cost of such a mistake is

nevertheless relatively large (i.e. the system may be more fail-safe, but the cost in the event of failure is high; Holling and Clark 1975). "Costs" as construed above imply "amount of disruption in the fishing industry" as well as lost profits or catch.

These results have interesting implications for one widely discussed plan for salmon enhancement in British Columbia, which is to bring many of the stocks fished simultaneously to about the same level of productivity, i.e. $R_p \simeq 1.0$ (Ricker 1975). This would certainly simplify management of these stocks, because then these stocks could sustain about the same maximum harvest rates. However, the situation is not simple. Increasing similarity in maximum harvest rates could increase the probability of causing a collapse of all stocks (by having decreased D), through a mistake in estimation of MSY or through variance in survival rates. The cost of such overexploitation (in terms of loss in catch) also increases with more similar A values. However, an attempt to retreat to the case of very dissimilar stock productivities will result in little feedback information being generated by loss of less productive stocks. Thus, the "best" mixture of stock productivities may be intermediate between the extremes of having all A values the same or having them quite diverse. Such an intermediate strategy would deliberately use the overexploitation of the less productive stock and the resulting drop in catch as a warning signal to control the developing fishery, and as feedback information to help determine boundaries of more productive stocks subject to the same predation. This approach perhaps seems inefficient because the less productive stock is made expendable to provide information about the total fishery complex. But this should be better than the situation where several stock productivities are identical and thus provide little feedback information until all stocks are overexploited more or less simultaneously. This point is particularly critical in salmon fisheries where, owing to their unusual nature, there is no precollapse shift in the age structure as there is in many long-lived species. One could even suggest that some salmon enhancement funds be set aside specifically for rehabilitation of these less productive stocks after they have generated feedback information.

The situation described above brings to mind the "Titanic Effect" (Watt 1974), which refers to the fact that the more improbable a disaster is, the more costly it will be when it inevitably happens because people will not have taken steps to minimize its impact. This attitude matches that of people who claim that enhanced salmon stocks

having similar reproductive parameter values will not be overharvested simultaneously (because we have learned much from our past mistakes), and who therefore will help guarantee large costs of such inevitable mistakes. While the probability of such a catastrophic event occurring may be very small, it cannot be exactly zero; therefore, given enough time the event is by definition inevitable.

Application of the Concepts of Catastrophe Theory

We can view in another way how changes in catch, population sizes, and stability domains occur with changing exploitation rates by using the approach of catastrophe theory, which looks at rapid qualitative jumps from one set of equilibria to another (Thom 1975; Zeeman 1976). This theory has been only recently applied to ecological systems (Jones 1977; Jones and Walters 1976), but it has already proven its value in conceptualizing interactions among variables and controls in complex systems.

For the present examples of fish systems having depensatory mortality, we can calculate the equilibria of population size and catch that would result from a given exploitation rate. It is explicitly recognized that exploitation rates would never be held constant over several fish generations; however, the equilibrium calculated for each harvest rate would be the level toward which the population would tend to move in that generation. Figure 13 shows equilibrium population
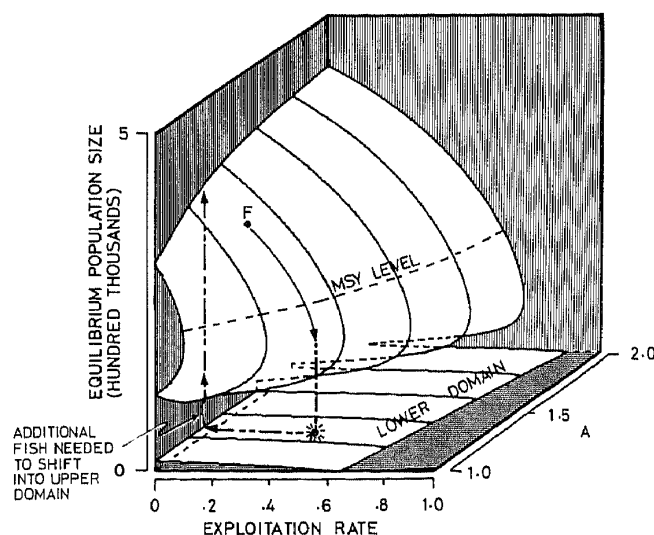

FIG. 13. Equilibrium population size for single stocks with A parameter values ranging from 1 to 2. For a given exploitation rate, there may be up to three equilibria, one stable in each of the upper and lower domains and one unstable (on the underside of the fold). These equilibria are the points A, B, and C of Fig. 1 (see text).
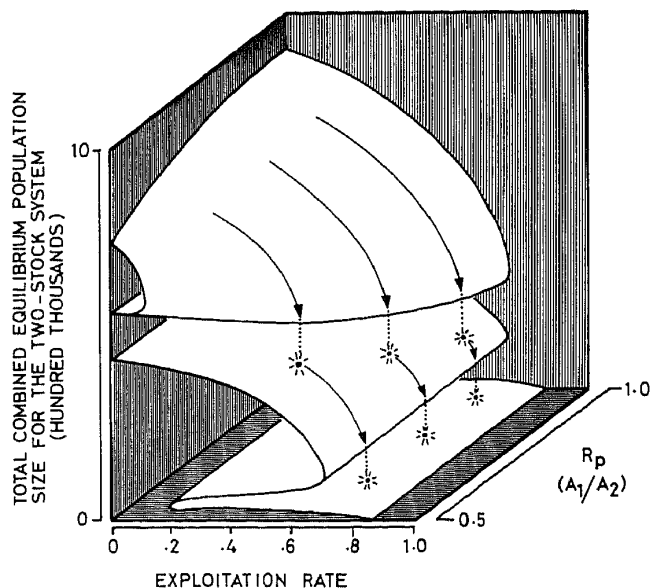
FIG. 14. Equilibria for different two-stock systems harvested simultaneously (see text). When the less productive stock of a given pair is overexploited, the system tends to drop toward the next stable equilibrium down on the surface below. Similarly, when the most productive stock is overharvested, the system drops into the lower domain.

sizes for several single stocks, each with an A value between 1.0 and 2.0. The total set of equilibrium points creates a surface called a manifold. The undersides of the folds are the unstable equilibria, so a population at any given A value and

harvest rate will tend to move toward one of the stable equilibrium surfaces (see Jones 1977). For example, a fishery following a course described by the arrows on Fig. 13 would start at point F, and move along the manifold to near the MSY level of exploitation, at which point a slight increase in harvest rate might result in the population dropping to the lower domain. The exploitation could be relaxed on the stock and the population would slowly increase, but it would still be trapped in the lower domain. For a stock with this A value, it can be seen that even a zero harvest rate would not be sufficient for the stock to get pushed into the upper domain (whereas a 10% harvest rate would be sufficient for a stock with $A = 2.0$, because below that exploitation only the upper equilibria exist). Thus, the upper domain for the low A value stock could only be reached if environmental noise were great enough to move the population above the boundary between the two domains or if fish productivity were increased sufficiently, say, through enhancement.

Figure 14 shows the manifold of population size for pairs of stocks in a multistock fishery, with the same range of A values as shown in Fig. 12. The equilibria on the surfaces are total combined population sizes for the two-stock complex. When stocks have similar A values (R_p close to 1.0), there is a greater chance of overharvesting both simultaneously as discussed

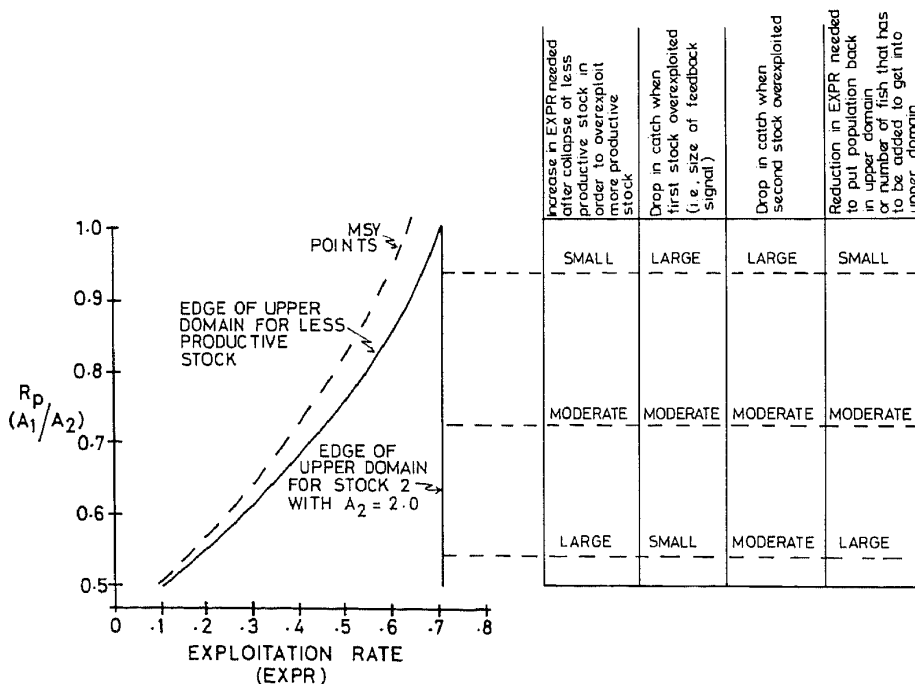|	Increase in EXPR needed after collapse of less productive stock in order to overexploit more productive stock	Drop in catch when first stock overexploited (i.e. size of feedback signal)	Drop in catch when second stock overexploited	Reduction in EXPR needed to put population back in upper domain or number of fish that has to be added to get into upper domain
	SMALL	LARGE	LARGE	SMALL
	MODERATE	MODERATE	MODERATE	MODERATE
	LARGE	SMALL	MODERATE	LARGE

FIG. 15. When the drop-off points from the two upper folds in Fig. 14 are projected on to the R_p–EXPR plane, they trace these critical lines. As indicated, there would be different costs and benefits resulting from different values of R_p, which are taken here to represent different mixes of enhanced salmon stocks.

earlier. The edges of the manifold representing overexploitation points can be projected onto the R_p–EXPR plane as shown in Fig. 15. This figure summarizes the advantages and disadvantages of having R_p values close to 1.0, as discussed earlier. The similarity in stock productivity which is deemed best will depend on the relative importance of these various measures.

Conclusions

Since fish populations exposed to strong depensatory mortality processes may have two or more potential equilibria and associated domains of attraction, it is not reasonable to assume that populations can easily recover after being forced to low levels. However, this is the assumption of the Ricker stock–recruitment model which is used in management of many fisheries. Furthermore, sizes of domains of attraction change with exploitation rate and further problems are created by uncertain environmental conditions. The realization that more than one stability domain can exist should ideally result in more cautious management at high exploitation rates.

It may be possible to plot data for past stock collapses and rapid stock increases on an "A value vs. exploitation rate" plane to determine where the edges of the manifolds occur. Alternatively, one could try to measure the depensatory mortality processes such as predation to deduce an underlying model. In either case, this approach should help to define ways of boosting a population back into its upper domain. For example, one could determine how much the exploitation rate would need to be dropped, how many predators should be removed, how much to increase A, or how many fish should be added.

Finally, the general conclusions described here do not depend on the particular parameter values chosen for illustration. In fact, any population that has a significant depensatory mortality agent may potentially have the characteristics discussed above, which result from shrinking domains of stability as exploitation rate increases.

Acknowledgments

ALLEN, K. R. 1973. The influence of random fluctuations in the stock-recruitment relationship on the economic return from salmon fisheries, p. 350–359. In B. B. Parrish [ed.] Fish stocks and recruitment. Rapp. P.-V. Reun. Cons. Int. Explor. Mer. 164.

ANON. 1974. Report of the fourth session of the panel of experts on stock assessment on Peruvian anchoveta. Bol. Inst. Mar. Peru-Callao 2: 685–723.

BEETON, A. D. 1969. Changes in the environment and biota of the Great Lakes. In Eutrophication: Causes, consequences, correctives. Nat. Acad. Sci., Washington, D.C.

BEVERTON, R. J. H., AND S. J. HOLT. 1957. On the dynamics of exploited fish populations. U.K. Min. Agric. Fish., Fish. Invest. (Ser. 2) 19: 533 p.

FOERSTER, R. E. 1968. The sockeye salmon, Oncorhynchus nerka. Bull. Fish. Res. Board Can. 162: 422 p.

HASSELL, M. P., AND R. M. MAY. 1974. Aggregation of predators and insect parasites and its effects on stability. J. Anim. Ecol. 43: 567–594.

HOLLING, C. S. 1965. The functional response of predators to prey density and its role in mimicry and population regulation. Mem. Entomol. Soc. Can. 45: 1–60.
        1969. Stability in ecological and social systems, p. 128–141. In Diversity and stability in ecological systems. Brookhaven Symp. Biol. 22.
        1973. Resilience and stability of ecological systems. Ann. Rev. Ecol. Syst. 4: 1–23.

HOLLING, C. S., AND W. C. CLARK. 1975. Notes towards a science of ecological management, p. 247–251. In W. H. Van Dobben and R. H. Lowe-McConnell. [ed.] Unifying concepts in Ecology. Dr. W. Junk B. V. Publishers, The Hague.

HUNTER, J. G. 1959. Survival and production of pink and chum salmon in a coastal stream. J. Fish. Res. Board Can. 16: 835–886.

JONES, D. D. 1977. The application of catastrophe theory to ecological systems. Simulation. (In press)

JONES, D. D., AND C. J. WALTERS. 1976. Catastrophe theory and fisheries regulation. J. Fish. Res. Board Can. 33: 2829–2833.

LARKIN, P. A., AND W. E. RICKER. 1964. Further information on sustained yields from fluctuating environments. J. Fish. Res. Board Can. 21: 1–7.

LeCREN, E. D., C. KIPLING, AND J. C. McCORMACK. 1972. Windermere: effects of exploitation and eutrophication on the salmonid community. J. Fish. Res. Board Can. 29: 819–832.

MURDOCH, W. W., AND A. OATEN. 1975. Predation and population stability. Adv. Ecol. Res. 9: 1–132.

NEAVE, F. 1953. Principles affecting the size of pink and chum salmon populations in British Columbia. J. Fish. Res. Board Can. 9: 450–491.

PARRISH, B. B. [ed.] 1973. Fish stocks and recruitment. Rapp. P.-V. Reun. Cons. Int. Explor. Mer. 164.

PAULIK, G. J. 1973. Studies of the possible form of the stock and recruitment curve, p. 302–315. In B. B. Parrish [ed.] Fish Stocks and Recruitment, Rapp. P.-V. Reun. Cons. Int. Explor. Mer. 164: 302–315.

RICKER, W. E. 1954. Stock and recruitment. J. Fish. Res. Board Can. 11: 559–623.
        1958a. Handbook of computations for biological statistics of fish populations. Bull. Fish. Res. Board Can. 119: 300 p.
        1958b. Maximum sustained yields from fluctuating environments and mixed stocks. J. Fish. Res. Board Can. 15: 991–1006.
        1962. Regulation of the abundance of pink salmon

populations, p. 155–211. *In* N. J. Wilimovsky [ed.] Symp. on pink salmon. Inst. of Fish., Univ. of British Columbia, Vancouver, B.C.

    1963. Big effects from small causes: two examples from fish population dynamics. J. Fish. Res. Board Can. 20: 257–264.

    1973a. Two mechanisms that make it impossible to maintain peak-period yields from stocks of Pacific salmon and other fishes. J. Fish. Res. Board Can. 30: 1275–1286.

    1973b. Critical statistics from two reproduction curves, p. 330–340. *In* B. B. Parrish [ed.] Fish stocks and recruitment. Rapp. P.-V. Reun. Cons. Int. Explor. Mer. 164.

    1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. 191: 382 p.

SCHAAF, W. E. 1975. Fish population models: potential and actual links to ecological models, p. 211–239. *In* C. S. Russell [ed.] Ecological modelling in a resource management framework. Johns Hopkins University Press, Baltimore, Md.

SKUD, B. E. 1973. Factors regulating the production of pink salmon, p. 108–112. *In* B. B. Parrish [ed.] Fish stocks and recruitments. Rapp. P.-V. Reun. Cons. Int. Explor. Mer. 164.

THOM, R. 1975. Structural stability and morphogenesis. W. A. Benjamin, Inc., Reading, Mass. 348 p. (Transl. from French by D. H. Fowler)

WALTERS, C. J. 1975. Optimal harvest strategies in relation to environmental variability and uncertainty about production parameters. J. Fish. Res. Board Can. 32: 1777–1784.

WALTERS, C. J. AND R. HILBORN. 1976. Adaptive control of fishing systems. J. Fish. Res. Board Can. 33: 145–159.

WATT, K. E. F. 1974. The Titanic effect. Planning for the unthinkable. Sinauer Assoc., Stamford, Conn. 268 p.

ZEEMAN, E. C. 1976. Catastrophe theory. Sci. Am. 234: 65–83.