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Scale Misperceptions And The Spatial Dynamics Of A Social-Ecological System

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Introduction

The interactions between an ecosystem and the human rules for the use of that system can be very complex. This complexity means that it is hard to design foolproof and sensible rules. Here we explore a particular set of difficult questions: What are the consequences of not understanding or misperceiving, the structure of populations we wish to exploit? What if the "scale" of natural populations and their interactions do not match the scale of our decisions? For example, what if we think we are managing a single large population, when in fact there are multiple, small, spatially discrete populations?

These are important and relevant questions. In the 1950's and 60's many of environmental programs were initiated at the national or international level. As a consequence, both the theory and practice of environmental and resource management have focused on a scale

of authority appropriate to national and international regulatory bodies. In fisheries, for example, the first serious attempts at management began with the international organizations for the northwest and northeast Atlantic and the whale and the tuna commissions. With the advent of extended fisheries jurisdiction (i.e., the 200 mile limit), national organizations took over much of the authority of the international bodies, but often retained intact the same scale of regulation (generally over large areas involving thousands of square kilometers). Of necessity, regulatory bodies operating at this scale are forced to ignore the fine-scale aspects of the systems they regulate.

The poor performance of regulated ocean fisheries provides ample reason to question the scale of regulatory attention. A number of recent papers (Meyers and Hutchins, Ames, Wilson, et al., Sinclair) have focused attention on the existence of populations at a smaller scale than that usually managed by national or international regulatory authorities. The usual thrust of these arguments is that regulatory regimes that ignore smaller scale events and phenomenon such as habitat and local stocks may lead, inadvertently, to the erosion of the spatial structure of a population and the depletion of the resource. Put differently, scale misperceptions might lead to a different form of overfishing than that usually hypothesized. In particular, rather than overfishing simply by harvesting too many fish, it may be possible to overfish by inadvertently destroying the spatial structure of a population.

The existence of localized spawning groups of a number of important species has been known for a long time (Sinclair). But are these local-scale spawning groups relatively distinct populations, together forming the 'structure' of the larger fishery of which they are a part? If so, they may need to be managed separately. Or, are these groups simply the spatial expression of a larger population, in which case it may be appropriate to ignore the local particulars? The principal question is really: At what scale (or scales) should fishery management operate?

Many marine biologists have argued that localized populations (and thus issues of scale) are irrelevant to management because of the high rates of larval mixing among marine populations (Hilborn, Forgarty and Gunderson). If a local population is extinguished, it is likely that its population 'space' will be quickly recolonized by members of other populations. In this view, because the population is panmictic, there is no need to manage local populations separately. From the management perspective, only the aggregate population is relevant for the

application of restraints, or rules. If this view of population behavior is correct, then the scale misperceptions with which we're concerned would appear to have no practical impact.

An alternative view, the metapopulation perspective, is more common among terrestrial ecologists (Gilpin, etc.). In metapopulation theory, a local population is relatively discrete and reproductively separated to some degree from other local populations. The reasons for the separation might be genetic, imprinted or learned behavior that brings members of the local population back to the same spawning site. However, fidelity to spawning grounds is imperfect and a few members of any population may well stray to other populations. If local populations are extinguished due to natural or man-made causes, strays from other proximate populations can wander to the spawning site and recolonize the population "space," although more slowly than in panmictic situations. If local extinction is rare, recolonization can restore the spatial structure of the metapopulation and maintain its resiliency in the face of local extinctions. However, if the extinction rate of local populations exceeds the recolonization rate, the resilience of the metapopulation is eroded.

From a management perspective, a metapopulation differs from a panmictic population principally in terms of: 1) the causes, or patterns, by which fishing might bring about the collapse of a large population; 2) the speed of recolonization; and 3), the mechanisms by which local and large populations can, or are likely to, rebuild on their own or through human intervention.

All of these difference are critical to appropriate strategies for the management of fisheries. A panmictic population, for example, is reduced simply by taking too many fish from the entire (aggregate) population; only the total take, not its spatial distribution, matters. Rebuilding a panmictic population should depend principally upon the normal spawning and recruitment processes of the population and, as a result, can occur quite rapidly so long as fishing leaves an adequate spawning biomass. The pattern of collapse of a metapopulation through fishing can be best summarized as "piece by piece" disappearance, until the overall population structure is reduced to fragmented remnant local populations. A metapopulation may take a long time to recover from overfishing and local population extinction, depending upon the factors governing recolonization (especially how potential in-migrant members of the population acquire the behavior that leads to spawning site fidelity). Management strategies for

rebuilding metapopulations may depend upon knowledge of behavioral and other aspects of a species' life history, factors about which we now have little firm knowledge.

While answers to these questions are critical to the design of appropriate management regimes, it is almost impossible to get sufficient empirical data to test these hypotheses. One can, however, build models of panmictic and metapopulations to explore these questions. Consequently, here we explore a series of illustrative models in which local populations - modeled as either panmictic or metapopulation structures - are managed as if they comprised a single large population. These models are a dynamic version of the generic bioeconomic model of a single stock (Clark, Anderson) and are used to investigate the circumstances under which common regulatory procedures might lead to depletion of the fishery.

The Model

The basic model used here is an extension of "Beijer World I" (Low et al, this volume); the principle difference between this and our earlier model is that this one incorporates three 'local,'¹ connected populations. Different versions of the model are employed to examine diverse ways these populations might interact - i.e., as a panmictic or as a meta-population - and several rules managers might use in the fishery - open access, constant percent quota and sole ownership.

In each version of the model the three "local" populations are given identical carrying capacities. The populations are arranged in an implicit "triangular" spatial structure that allows fish from any of the three populations to move directly to either adjacent population¹. As is common in fisheries management (Sinclair), the regulatory authority perceives or treats the three local populations as if they were a single unified population and manages accordingly. Typically, this management approach is based (1) on the assumption that populations in the ocean have a high level of mixing and consequently act as if they were single

¹ In Beijer World I (this issue), most analyses focus on single-unit (isolated) fisheries; the only multi-unit model involved populations arranged in a linear fashion which may reflect a few coastal fisheries, but is not representative of most fisheries, where fish can move to more than one possible neighboring *local* population.

populations, and/or (2) on the often high costs and difficulty of monitoring and assessing separate populations (Hilborn, Forgarty and Gunderson).

The model implements the three management rules in ways that tend to dampen feedback from their (self) implementation, i.e., the rules are implemented so that they do not, by themselves, tend to destabilize the system.

The open access rule is constructed so that when average profits per harvester are positive entry takes place; when average profits per harvester are negative exit takes place; obviously, when profits are zero no entry or exit takes place. Furthermore, the entry (or exit) response to non-zero profits increases non-linearly as profits diverge more from zero. This tends to prevent overshoot and oscillations due to too many or too few boats relative to zero profits. This formulation implicitly assumes boats and operators entering and exiting the fishery have no problems finding alternative employment and that there are no regulatory barriers that impede inward mobility. Additionally, it is assumed there are no lags that might cause entry and exit to continually over or undershoot the appropriate target. We considered, but rejected, a rule that based entry and exit upon a trend in average profits rather than just current average profits; this would have led to greater stability in the model but it violates the basic strategy behind open access entry and exit (i.e., move before your competitor).

The constant percentage quota rule is implemented as a simple translation of the number of fish to be caught (constant percent times stock size) into the right number of boats to catch that number. Here also there are assumed to be no barriers or lags that might impede the implementation of this rule or contribute to a problem of overshoot or undershoot. In particular, it is assumed that measurements about the current size of the stock(s) are without error and are analyzed correctly with the resulting quotas implemented in a timely fashion.

The profit maximizing sole owner rule is implemented as a search process that compares 'the owner's' past actions (adding vs. subtracting boats) with the subsequent results (more or less profit). The rule uses a five year trend to allow the impact of more or fewer boats to work its way through all the fisheries so that the sole owner can sort out signal from noise in circumstances when populations are variable. This way of implementing the profit maximizing rule tends to slow the rate at which maximum profits are achieved, but has the advantage of

being much more robust (in the sense of finding the true maximum rather than some local maximum) and stable in circumstances of high population variability.

All three of these rules could have been designed with alternative formulations that might be argued to be more realistic, e.g., 'sticky' entry and exit, errors and delays in measurement, and so on. However, our objective here is to isolate problems that arise because of a misperception of scale. Consequently, we have tried to minimize the kinds of dynamic problems that might arise if these management rules were more 'realistic' so that we might better recognize any scale related problems.

The two population types are differentiated from one another in a very simple way: For panmictic populations no critical minimum population size is specified. For the metapopulation versions a critical minimum size was specified for each of the local populations. This was always set at .05 of carrying capacity, K . This assumes that below the critical minimum, there are too few individuals in the local population either to attract conspecifics or to spawn successfully. When that critical minimum size is reached, both recruitment and in-migration cease (cf. Ray, Gilpin and Smith) and the local population is eventually extinguished. The model does not contain a mechanism for recolonization after extinction occurs. This treatment thus mimics shorter term metapopulation dynamics, in which extirpated local populations are rarely recolonized, and illustrates nicely the effect of local extinctions.

The long run dynamic of each local population is characterized by a Schaefer stock/recruitment relationship:

$$S_{t+1} = rS_t(1-S_t/K) \quad [1]$$

where S_t is the population numbers at time t , r is the intrinsic growth rate of the population and K is the carrying capacity stated in terms of the maximum number of individuals in the population (see Figure 1). Taken by itself the equation states that the population in the current period is a function of the size of the population in the previous period such that at low population levels the rate of increase in the population is high but decreases until at a high population corresponding with the carrying capacity the rate of increase is zero. At its carrying capacity, K , there is no tendency to change and the population is in a stable equilibrium. As

mentioned above, in the metapopulation version the recruitment relationship is modified with a requirement for a critical minimum population size.

In addition to recruitment, each local population is affected by movements of fish to and from adjacent populations and by withdrawals due to harvesting. The basis for movement between populations is defined as:

$$\text{Trans}_{a,b} = \text{transrate} * (S_a/K_a - S_b/K_b) \quad [2]$$

where the amount of transfer or migration between populations a and b is given by a transfer rate, "transrate", which is a function of the difference in the density (relative to carrying capacity) of the two populations. At a value for "transrate" of 0.5, fish achieve a free distribution within one period; at a value of 0.0, fish cannot move between populations. (At values above 0.5 the movement of fish tends to overcompensate for density differences among the populations and leads to large cyclical swings. We limit tests of the model to values at or below 0.5.)

The harvest rate for each local population is determined by the effort allocated to that population. In each period of the simulation, changes in the total level of harvesting effort (i.e., for all three populations) are determined by the centralized management authority using one of the three harvest rules described above. Total effort is then allocated to each population by a mechanism that allocates the sum of (1) changes in total fishing effort and (2) a specified portion of existing effort - given by 'switchrate', so that profits per boat are equalized in each of the three local fisheries. In other words, the management rule determines the overall level of effort for all three fisheries taken together, but the allocation of effort to each of the three fisheries is driven by the relative profits earned by boats fishing each local population. When the value of the variable "switchrate" is equal to 0.5, fishermen achieve a free distribution quickly; basically, fishermen are free to move boats and equipment and rapidly equalize profits in the three local fisheries. When "switchrate" equals zero, boats are confined to the fishery to which they were initially assigned and profits are not equalized except by chance. This formulation of the model assumes that fishermen are able to perceive the small scale population structure that managers either fail to perceive or choose to ignore.

The third factor determining harvest rates is the efficiency of harvest, where efficiency is measured in terms of percent of the population harvested annually by a single boat. Efficiency is assumed to be partly due to the number of other boats in the fishery (the more boats the less efficient each boat) and the behavioral characteristics of the fish in the populations which alters search costs, especially as populations decline. Finally, harvest rates for each of the three local populations are also partly determined by the differences in the costs of harvesting each local population - i.e., differences in costs lead to differences in profits and eventually to differences in the allocation of effort to each local population.

Given this description of the model we return now to the broad question we wish to ask: "Does management misperception of the appropriate population scale make a difference? And, if so, under what circumstances? Our originating premise was that the underlying population structure - whether of panmictic or metapopulation type - is likely to be an important differentiating circumstance. Also, given the way we have articulated the problem, our intuition leads us to expect scale misperception problems when circumstances drive one or all local populations towards the critical minimum. Broadly, these circumstances might be expected to occur when (1) 'deterministic' aspects of the model (e.g., an open access rule) would lead to low population levels and (2) when external or internal sources of variability also contributed to low population levels. Following are several hypotheses about when those circumstances might arise:

1. An open access rule is known from analytical models to lead to depleted populations (given sufficient market demand). It would seem reasonable, therefore, that an open access rule would frequently drive populations into a range near the critical minimum and that metapopulation structures would be especially vulnerable to this management rule. On the other hand, analytical models indicate that both the constant percent quota rule and the sole owner rule maintain populations at relatively high levels well removed from the critical minimum level. Consequently, **one would not** expect these **two** rules to lead to scale misperception problems.
2. The ability of fishermen to switch easily between populations should reduce the profit differentials between populations and the tendency of a local population **to** be depleted. In other

words, as a local population approached depletion or extinction, profits should fall and cause effort to move to healthier local populations, providing thereby some measure of protection.

3. The extent of migration or transfer of fish from one population to another should affect the viability of local populations; in particular, we expect that high levels of movements of fish between populations would tend to make the three local populations act like a single large population. At low rates of interpopulation movement one might expect individual populations to be more vulnerable to depletion or extinction.

4. Differences in the cost of exploiting one local population relative to another might create an economic preference that puts strong pressures on, and might possibly deplete or extinguish, the least costly-to-exploit population.

5. Finally, we would expect variability, whether generated as part of the internal dynamics of the model or from external sources, to increase the possibility of populations reaching critical minimum levels.

To test these expectations we initiated an extensive series of sensitivity runs that covered a reasonable sub-set of the values of the relevant variables. The general method behind our explorations was to start with a set of parameter values - or circumstances that generate a dynamic solution that mirrors or approximates the results expected from steady state analytical models (Clark). Due to the complexity of the model, a steady state 'base' of this sort helps greatly in the identification and analysis of more complex dynamic behaviors.

Our first test was to compare our three population, panmictic model with a 'true' single population model. Our purpose was to see whether the migration of fish and fishermen in our panmictic model led to different results than might be found with a 'true' single population. We set the maximum migration rates for fish and fishermen to 0.25 (i.e., up to 25% of each population could conceivably move each year). Both models produce similar time paths for each of the three management rules (see figure 1); however, there the numerical results differ significantly.

Figure 1. Baseline case - sum of all populations for three management rules

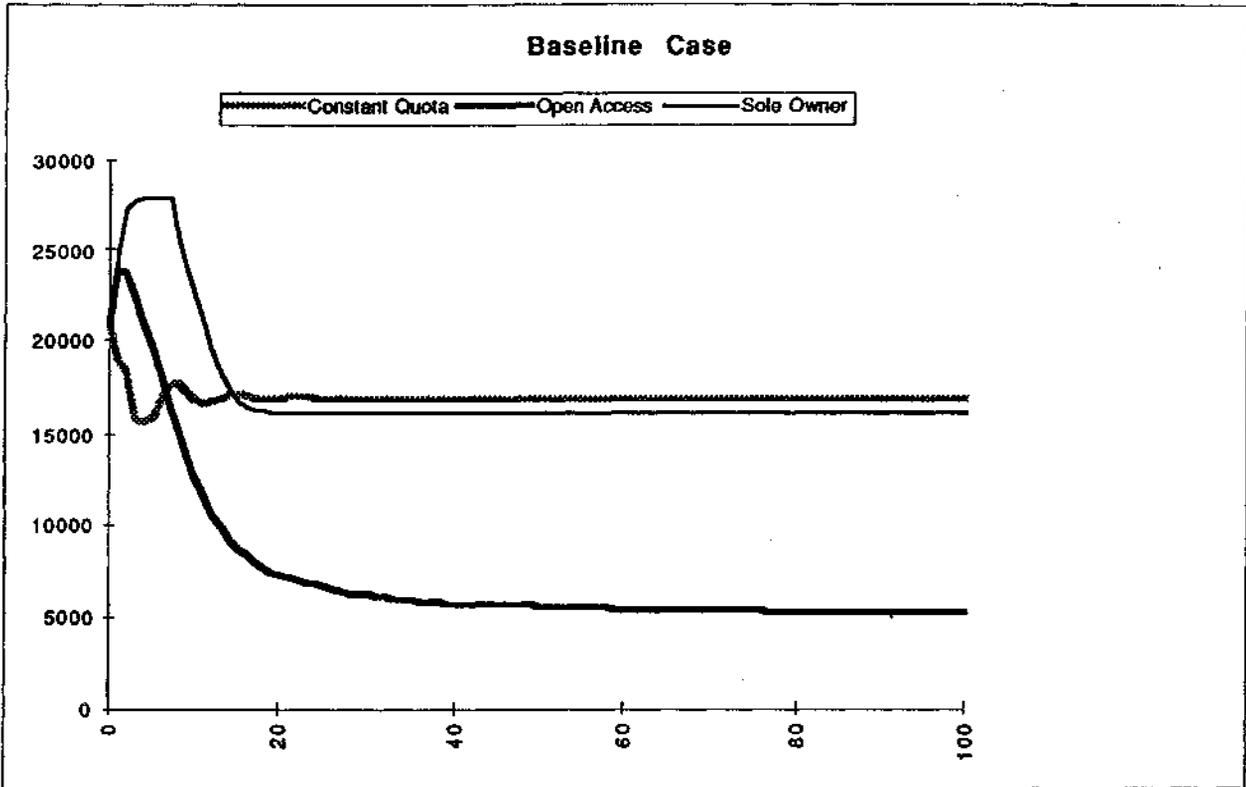


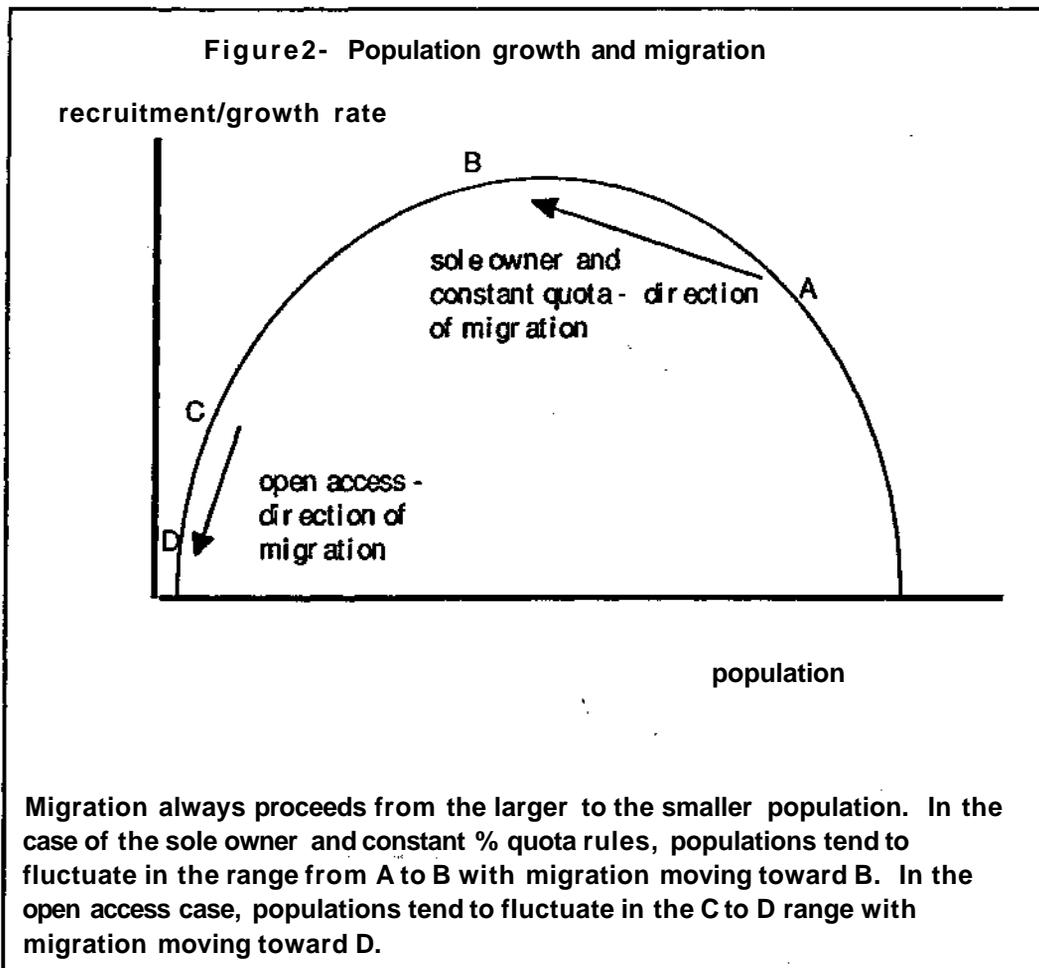
Table 1 Single population model

decision.... rule....	open access	constant % quota	sole owner
avg. harvest as % of carrying capacity	11	23	22
avg. pop size as % of carrying capacity	18	61	59

Table 2 Panmictic population with three local populations

results	decision rule	open access	constant % quota	sole owner
avg. harvest as % of carrying capacity		08	15	14
avg. pop size as % of carrying capacity		08	57	54

Comparing Tables 1 and 2 it is readily apparent that all three rules tend to result in lower stock sizes when applied as aggregate rules to the three population case. The reason for this is that the migration of fish and fishermen from population to population tends to mask the true state of the overall population. The migration of fish is always towards the smaller population. In the case of healthy populations - such as under the sole owner and constant quota rules - the smaller populations generally tend to be the populations with a higher growth rate. Consequently, migration tends to raise the average growth rate of the system leading to higher sustained harvests but at lower sustained population levels. This effect is interesting but is totally dependent upon the assumed parabolic shape of the recruitment curve and so might be legitimately argued to be simply an artifact of the model - there are few if any marine fish populations for which a recruitment curve has been validated over the full range of population size, much less one with a parabolic shape. (Hall) The movement of fishermen from population to population, on the other hand, leads to the preponderance of harvests coming from the largest or healthiest sub-populations. That is, as the component populations vary in size fishermen always move to the largest populations; this increases their profits but also contributes to higher sustained average catches at lower average sustained population levels. (compare tables 1 and 2)

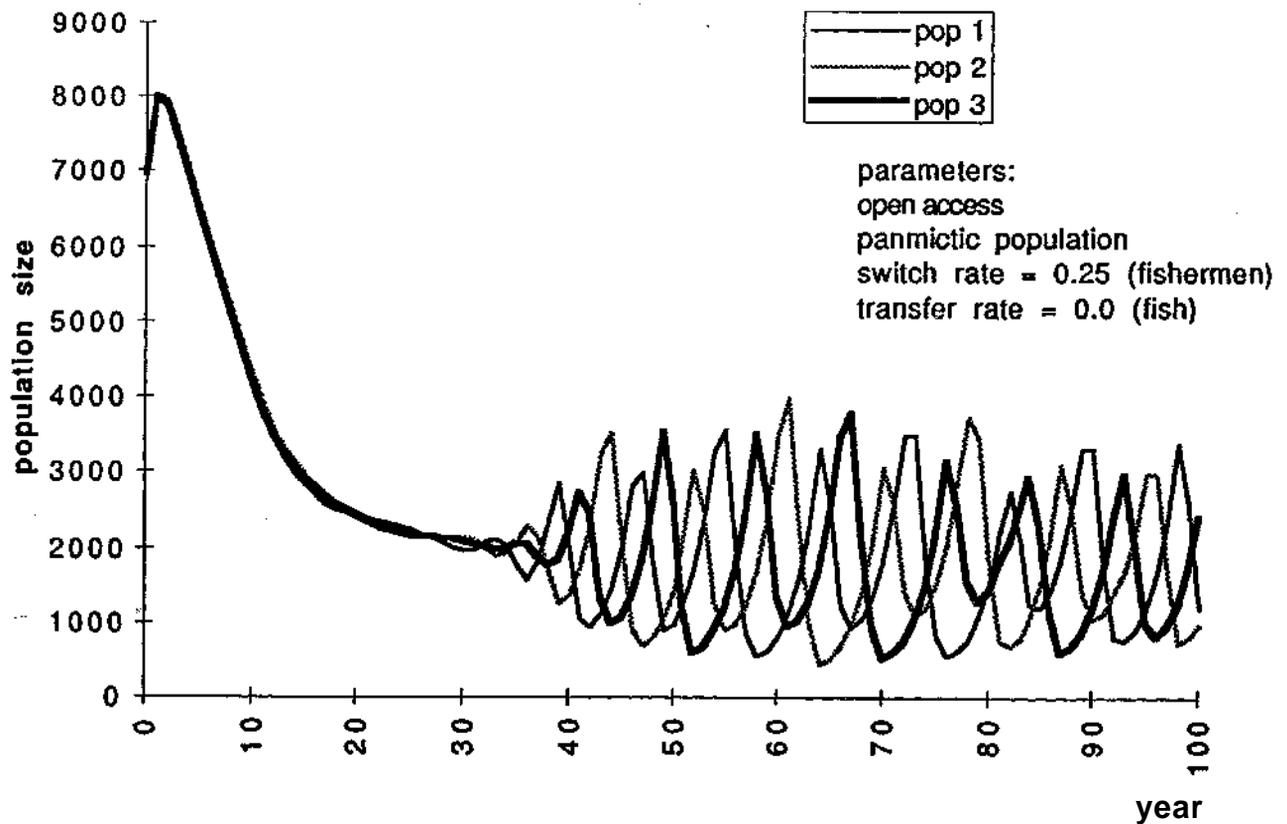


In the case of the open access rule, however, the growth effects of migration work in the opposite direction (see Figure 2). Here migration tends to move towards stocks with lower growth leading to significantly lower sustained harvests than might be expected to occur in a true panmictic population. In this instance, more significance might be attached to the result since it does appear that at very low population levels some sort of recruitment relationship exists (Hutchins and Meyers). In other words, given the assumed migration of fish from stronger to weaker stocks and of fishermen from weaker to stronger stocks, management's misperception of a single large stock might lead to an understatement of the severity of the overfishing problem.

From this baseline we began to explore the model for sources of internal dynamic variability. Two variables unique to the three population structure, i.e., the rate at which fish migrate

between populations - 'transrate'- and the rate at which fishermen switch between populations - 'switchrate' - are important sources of internal variability. Sensitivity analyses for all combinations of values of 'transrate'¹ and 'switchrate'¹ of 0.0, 0.1,...0.5, were run. These runs point up an interesting internal dynamic in the model - namely, as fish and fishermen attempt to adjust at varying rates towards a 'free distribution' or 'equal profits' there tends to be some overshoot since movement from two populations towards one is uncoordinated. Figure three shows how this internal dynamic affects the three populations. In this instance, the results were for an open access rule in which fish were restricted to their originating population but up to 25% of fishermen were free to move between populations each year. Similar results arise when fish are free to move between populations. Clearly, this aspect of the model points to a mechanism that might contribute to populations approaching the critical minimum.

Figure 3. Periodicity in populations arising from migration of fishermen



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Other sources of internal dynamic variability (not illustrated here) include:

1. The intrinsic growth rate of the population, r . In the steady state version r is set at 1.0 for all three local populations. At a value for r in the vicinity of 2.00 large periodic fluctuations in the local populations begin to occur. At values around 4.0 chaotic fluctuations start (the exact value at which periodic and chaotic fluctuations occur depends upon the amount of harvesting). (May, 1974) In all the examples that follow a value of $r=1$ was used for all three local populations.

2. The reaction time and rates of response of decision makers are normally set so they will yield a steady state solution. However, when delays in the receipt of information, or analysis, or errors of measurement or a host of other factors are incorporated in the model all three decision (or management) rules consistently tend to overshoot or undershoot their effort targets leading to circumstances of high variability. Again, in all the examples that follow model formulations consistent with a steady state solution were used in order to exclude these sources of variability.

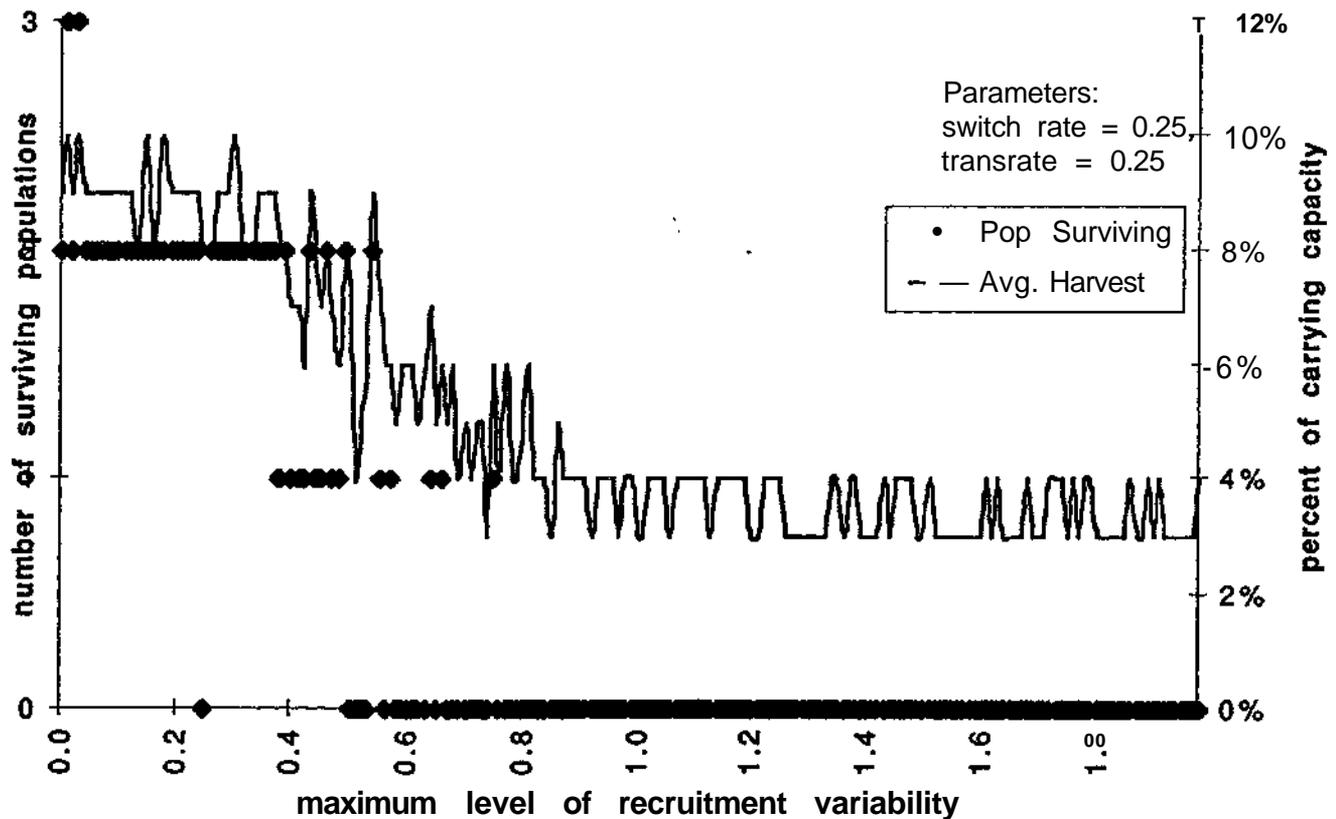
Additionally, one would expect a fishery of this sort to be subject to a variety of external sources of variability - weather, human intervention, etc. If all external and internal sources of variability were included in the model it would yield results that are almost immune to analysis. Consequently, in the descriptions of the model from this point out, we restrict the variability in the model to two sources: variability due to interpopulation movements by fish and fishermen and external variability that affects only recruitment to the population.

Testing hypotheses

1. Does the management rule make a difference? The answer to this question is clearly yes but only if the system is subject to some (internal or external source of) variability. To illustrate the importance of variability we re-ran the baseline model with levels of externally induced recruitment variability ranging from 0 to 200%. (This is not as high as it might seem. In a typical run 200% recruitment variability results in average population variability from year to year in the range of 20 to 25%. The figure is greater for the open access case, in which the fishery is heavily dependent upon recruitment, and less in the sole owner and constant quota cases where high standing populations provide more of a buffer.) In the panmictic case with the open access rule (not shown) local populations frequently fall to very low levels and then

rebuild only very slowly. In the metapopulation case with the open access rule, extinction of populations begins to occur with recruitment variability as low as 10% (see figure 3a). Here the model leads us to conclude that results of open access are likely to be worse than expected when the panmictic case is compared with a single population case and far worse in the metapopulation case.

Figure 3a
Population Extinction and Harvest:
Open Access with Metapopulations



The other two management rules tend to be more robust in the face of recruitment variability, but they also begin to yield extinctions in the metapopulation case when recruitment variability reaches 60-100% (see figures 3b and 3c). Since these are rather low levels of variation for marine systems, the model strongly suggests that rules that are optimal for single

Figure 3b
Population Extinction and Harvest:
Constant Quota with Metapopulations

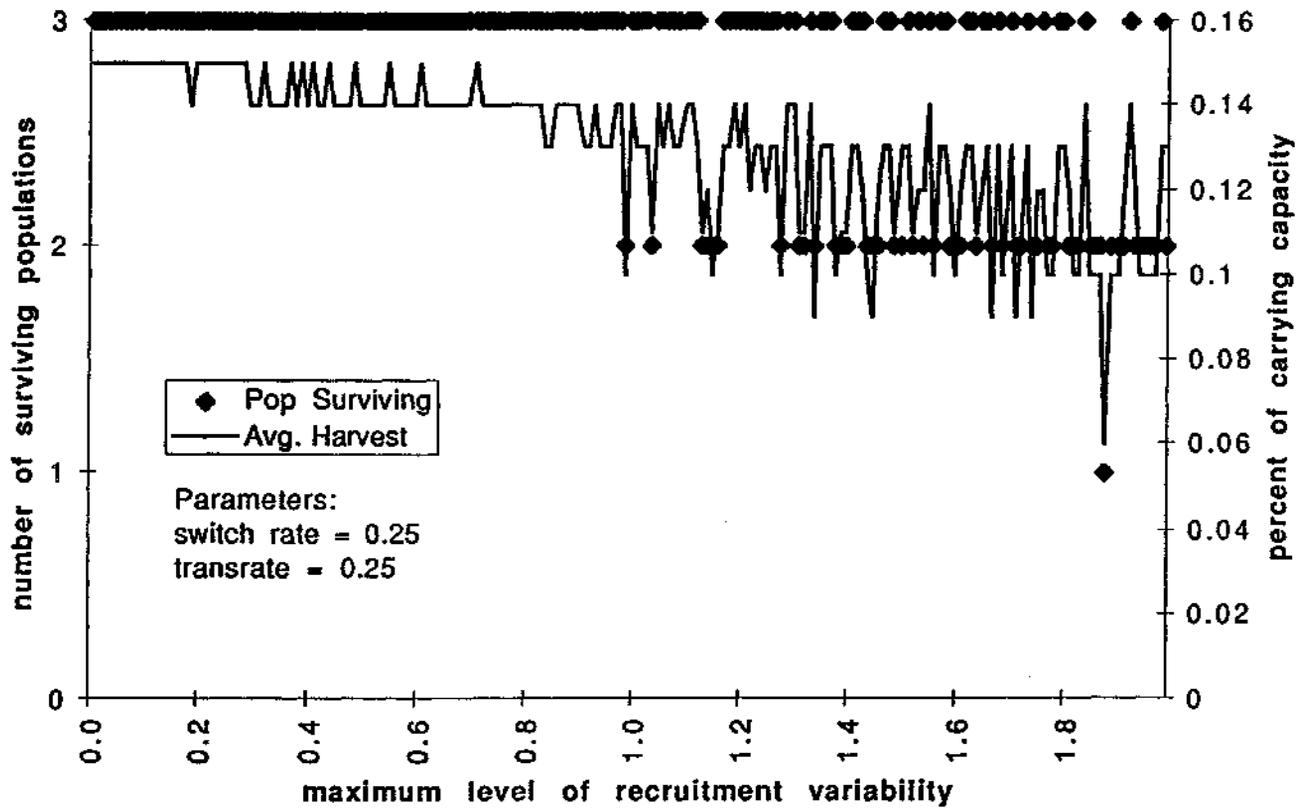
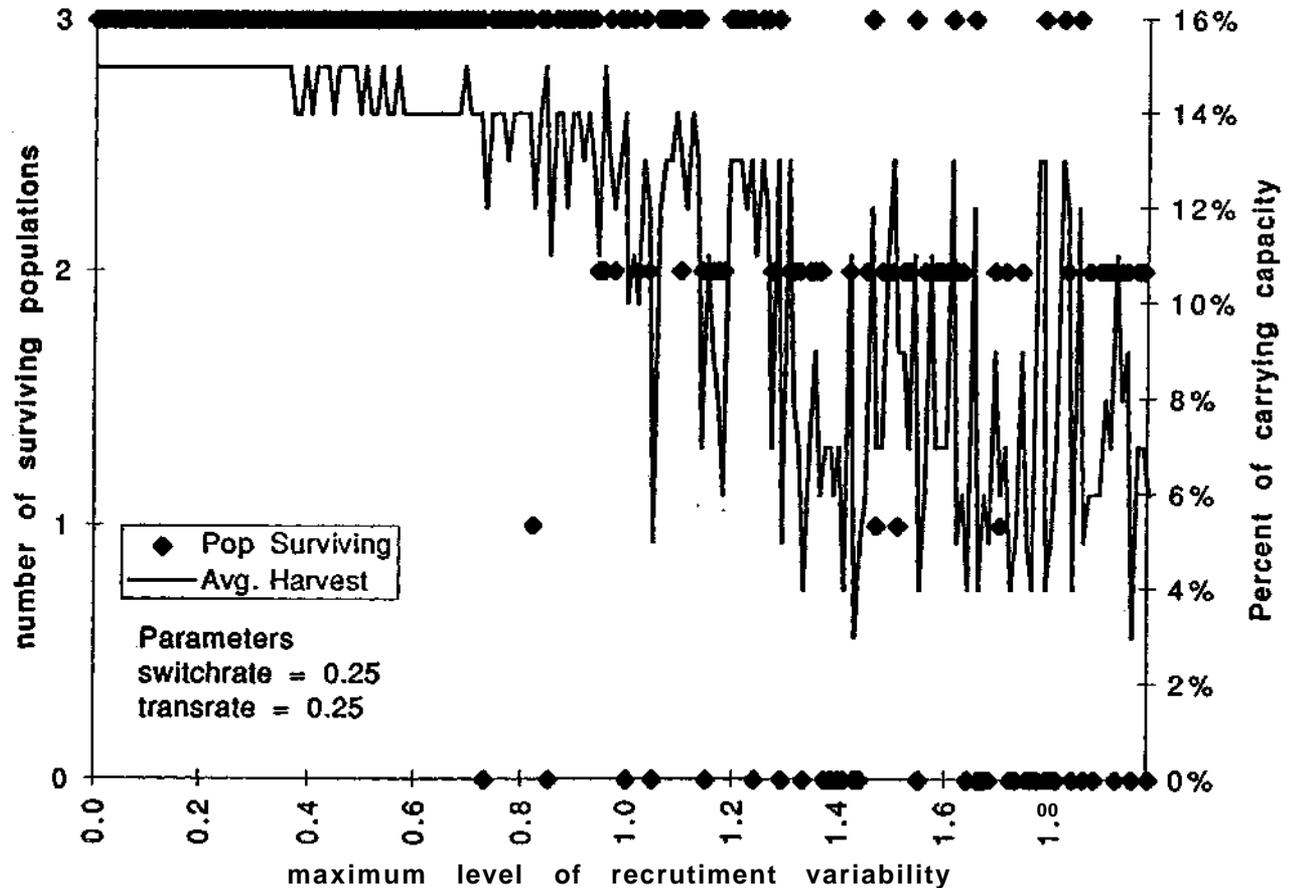


Figure 3b
Population Extinction and Harvest:
Sole Owner Rule with Metapopulations



populations may lead to extinctions of local populations (that may be interpreted as the depletion of a single large population) when there is a scale misperception problem.

2. and 3. Does the migration of either fish or fishermen tend to protect local populations against depletion? In both instances the answer is yes, up to a point. If, by chance, one of the local populations declines migration of fish will tend to reinforce that population and at the same time fishermen - attempting to equalize profits - will desert the population and move to others where densities and profits are higher. Consequently, the migration of both fish and fishermen

tends to stabilize, or protect, local populations. The extent to which this is true depends upon the rate at which migration can take place. At very low permitted rates the protection effect is very weak. So long as there is little or no variability in the local populations this is not a problem; however, with almost any level of variability present, local populations tend to be more vulnerable to extinction than they are with moderate permitted migration of either fish or fishermen. At high permitted rates the migration of either fish or fishermen can have a strongly destabilizing effect. Consider a situation in which fish are perfectly mobile and differences in the density of fish occur between local populations. Say two populations, a and b, are of equal density and the third, c, is of lower density. Populations a and b respond independently to this difference; if the 'permitted' migration rate ('transrate') is high enough both populations will each tend to send enough migrants to c to erase the density differential. The result is twice as many fish moving to c as would be necessary to actually equalize densities and, consequently, large periodic swings in all three populations would set up. The same is true for fishermen migrating in response to unequal profits. From the human perspective this kind of destabilizing behavior is a watery equivalent of the hog cycle; it is not hard imagining fishermen outsmarting themselves by collectively overreacting. Whether fish are this smart or not is hard to say. Whatever the case, the model does suggest that there are circumstances where this kind of behavior could destabilize a fishery that management incorrectly perceived to be a single large population.

Table 3a.

Metapopulation, Open Access, Sum of pops as % of K
recruitment variability = 0.0

*s indicate the number of populations extinguished

Transrate (fish)	Switchrate(boats)					
	0.0	0.1	0.2	0.3	0.4	0.5
0.0	0.18	0.17	0.18	0.12*	0.09**	0.00***
0.1	0.18	0.18	0.17	0.17	0.05**	0.00***
0.2	0.18	0.18	0.17	0.17	0.12*	0.00***
0.3	0.18	0.18	0.11*	0.13*	0.00***	0.00***
0.4	0.18	0.18	0.17	0.13*	0.12*	0.00***
0.5	0.18	0.17	0.17	0.11*	0.08**	0.00***

Table 3b

Metapopulation, Open Access, Sum of pops as % of K
recruitment variability = 0.25

*s indicate the number of populations extinguished

Transrate (fish)	Switchrate(boats)					
	0	0.1	0.2	0.3	0.4	0.5
0	0.18	0.17	0.18	0.12*	0.09**	0.00***
0.1	0.16	0.12*	0.10*	0.09**	0.00***	0.00***
0.2	0.14*	0.11*	0.09**	0.18	0.00***	0.00***
0.3	0.14*	0.08**	0.18	0.00***	0.00***	0.00***
0.4	0.13*	0.15*	0.08**	0.13*	0.00***	0.00***
0.5	0.14*	0.04**	0.13*	0.00***	0.00***	0.00***

4. Do differences in the cost of exploiting one local population relative to another make a difference? The behavior of the model indicates that this is likely to be much less of a problem than we had anticipated. The reason, very simply, is that the migratory behavior of both fish and fishermen (at moderate levels - 'transrate' and 'switchrate' <0.10-0.25) tends to protect populations that might otherwise be subject to heavy pressures. For example, if a population is fished heavily relative to others, its density and numbers fall, then fish from other populations tend to be attracted via migration and fishermen tend to be repelled by falling profits. Of course, as pointed out above, migration of both fish and fishermen can overcompensate, destabilize the fishery and lead to a greater chance of extinction.

Conclusions

Our interest in scale misperceptions arises from the historical events that have led to the large scale management of fisheries when, at the same time, there appears to be strong evidence that spawning for many fishery populations is relatively localized. This misperception of the appropriate ecological scale, on its face, could possibly lead to serious management problems. Consequently, we reformulated the basic model we have been using so that it was capable of investigating the implications of scale misperceptions. Our intention was to use the model to put a little more logical 'meat' on our intuition that these misperceptions might lead to management problems.

What we found was that the extent of the problem depends greatly upon the kind of population structure assumed for the observed localized spawning groups. When local populations are modeled as if they were a panmictic population, that is, one that mixes freely and uses local spawning areas in some proportion to its overall state, scale misperceptions tend to lead to few

management problems. The model suggests that there might be a tendency for standard management approaches to understate the extent of overfishing at low population levels but this conclusion is, at best, weak.

On the other hand, when local populations were modeled as a metapopulation, that is, one in which local spawning groups are relatively independent of one another, our results suggest management misperceptions of appropriate scale might be a serious cause of overfishing. In particular, under conditions of high variability which are very common in marine populations, all three management rules tended to lead to the "piece by piece" reduction of the overall metapopulation. The open access rule, which we used as a worst case comparison, leads to the quick extirpation of localized stocks. The constant percent of stock quota and the sole owner rules, which are generally considered to be 'optimal', proved to be much more robust than the open access rule, but also led to the "piece by piece" reduction of the overall metapopulation even with moderate levels of fishing effort and population variability.

These conclusions direct our attention to another way that overfishing can occur. Conventional wisdom and the standard scientific view of overfishing involves catching so many fish that a population cannot sustain itself. Our model suggests that overfishing can occur when we misperceive the appropriate scale at which populations operate. Under these circumstances, what might be thought to be optimal rules can lead to the destruction of local substocks even though only moderate levels of fishing effort are employed. The further implication is that the avoidance of overfishing may involve much more than simply catching only the 'right number'¹ of fish. We may need to pay attention to the structure of local populations and the habitat and other biotic and abiotic factors necessary for their continued existence. This implies an emphasis on where, when and how fishing takes place rather than simply an emphasis on the 'right number' to catch. From a social perspective, the model strongly suggests a need to move away from our current emphasis on centralized management organizations and to cultivate the growth of complementary local management organizations that can deal effectively with **local** ecological phenomenon.

Table 4 The principle variables for each version of the model, their default or normal values and the range of values for which sensitivity runs were conducted.

Variables**	Steady state	Panmictic Population		Metapopulation	
	values	Normal Value	Sensitivity Range	Normal Value	Sensitivity Range
transfer rate	0.00	0.25	0-0.5	0.25	0-0.5
switch rate	0.00	0.25	0-0.5	0.25	0-0.5
cost differences	0.00	0.00	0-100	0.00	0-100
critical minimum	0.00	0.00	n.a.	0.05	n.a.
recruitment variability	0.00	0.00	0-200	0.00	0-200

**Transfer rate - 'transrate'¹ - gives the maximum proportion of fish that can migrate from one population to another. Switch rate - 'switchrate' - gives the maximum proportion of boats that can switch from one to another population. Cost differences - 'cost diff' - gives the percent differences in the costs of fishing each of the three local populations. Recruitment variability - 'Vary' - gives the maximum percent random variation around the calculated level of recruitment.

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