

ANALYSIS

# Scale misperceptions and the spatial dynamics of a social–ecological system

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## 1. 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 misunderstanding or misperceiving the spatial 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 1950s and 1960s many 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 regula-

tory 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 theory and 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 (Sinclair, 1988; Hutchins and Meyers, 1995; Ames, 1996; Wroblewski et al., 1996; Wilson et al., 1998) 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

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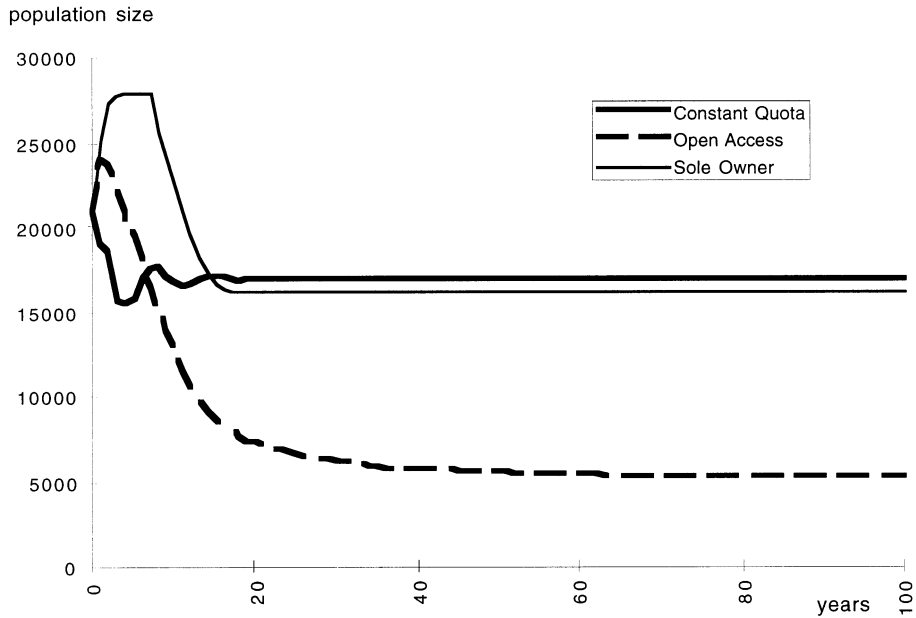


Fig. 1. Baseline case — single population model, three management rules.

Table 1

The principal parameters for each version of the model, their default or normal values and the ranges over which sensitivity runs were conducted

| Variables <sup>a</sup>  | Steady state values | Panmictic population |                   | Metapopulation |                   |
|-------------------------|---------------------|----------------------|-------------------|----------------|-------------------|
|                         |                     | 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                 | NA                | 0.05           | NA                |
| Recruitment variability | 0.00                | 0.00                 | 0–200             | 0.00           | 0–200             |

<sup>a</sup> Transfer rate ('transrate') gives the maximum proportion of fish that can migrate from one population to another in a year. Switch rate ('switchrate') gives the maximum proportion of boats that can switch from one to another population in a year. 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 percentage of random annual variation around the calculated level of recruitment.

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, 1988). 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

Table 2

Single population model and panmictic population with three local populations

|  | Decision rule |                  |            |
|--|---------------|------------------|------------|
|  | Open access   | Constant % quota | Sole owner |
| <i>Single population model</i>                           |               |                  |            |
| Average harvest as % of carrying capacity                | 11            | 23               | 22         |
| Average population size as % of carrying capacity        | 18            | 61               | 59         |
| <i>Panmictic population with three local populations</i> |               |                  |            |
| Average harvest as % of carrying capacity                | 8             | 15               | 14         |
| Average population size as % of carrying capacity        | 8             | 57               | 54         |

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 migration and larval mixing among marine populations (Fogarty et al., 1997). 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 were correct, then the scale misperceptions with which we are concerned would appear to have no practical impact.

An alternative view, the metapopulation perspective, is more common among terrestrial ecologists (Gilpin, 1996). 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 spawn-

ing site and recolonize the population ‘space’. If local extinction is rare, recolonization can restore the spatial structure of the metapopulation and maintain its reproductive or spawning potential in the face of local extinctions. However, if the extinction rate of local populations exceeds the recolonization rate, the spawning potential of the metapopulation is eroded.<sup>1</sup>

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 ease or speed of repopulation of local areas, 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 differences are critical to appropriate strategies for the management of fisheries. A panmictic population, for example, is reduced

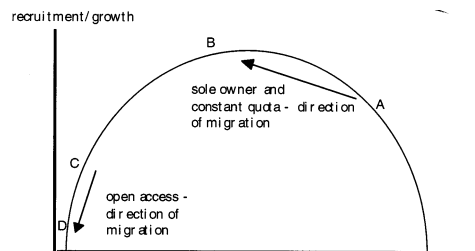


Fig. 2. Population growth and migration.

<sup>1</sup> Ames reports extinguished cod and haddock spawning areas on the Maine coast that have not been recolonized over a 50-year period.

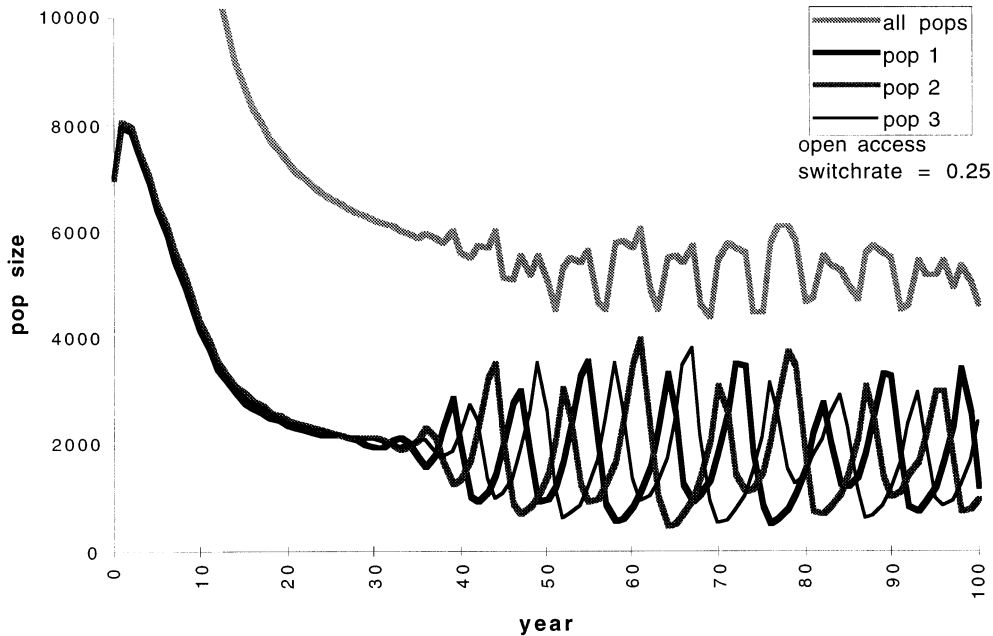


Fig. 3. Periodicity in populations due to fishermen switching.

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 the behavior 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 (Wilson et al., 1998). One can, however, build models of panmictic populations and metapopulations to explore these questions. Consequently, 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, 1976; Anderson, 1986) and are used to investigate the circumstances under which common regulatory procedures might lead to depletion of the fishery.

## 2. The Model

The basic model used here is an extension of the one used by Low et al. (this volume). There are three local, harvested populations. The populations are arranged in an implicit ‘triangular’ spatial structure that allows fish or fishers to move directly to either adjacent population area. Fish-

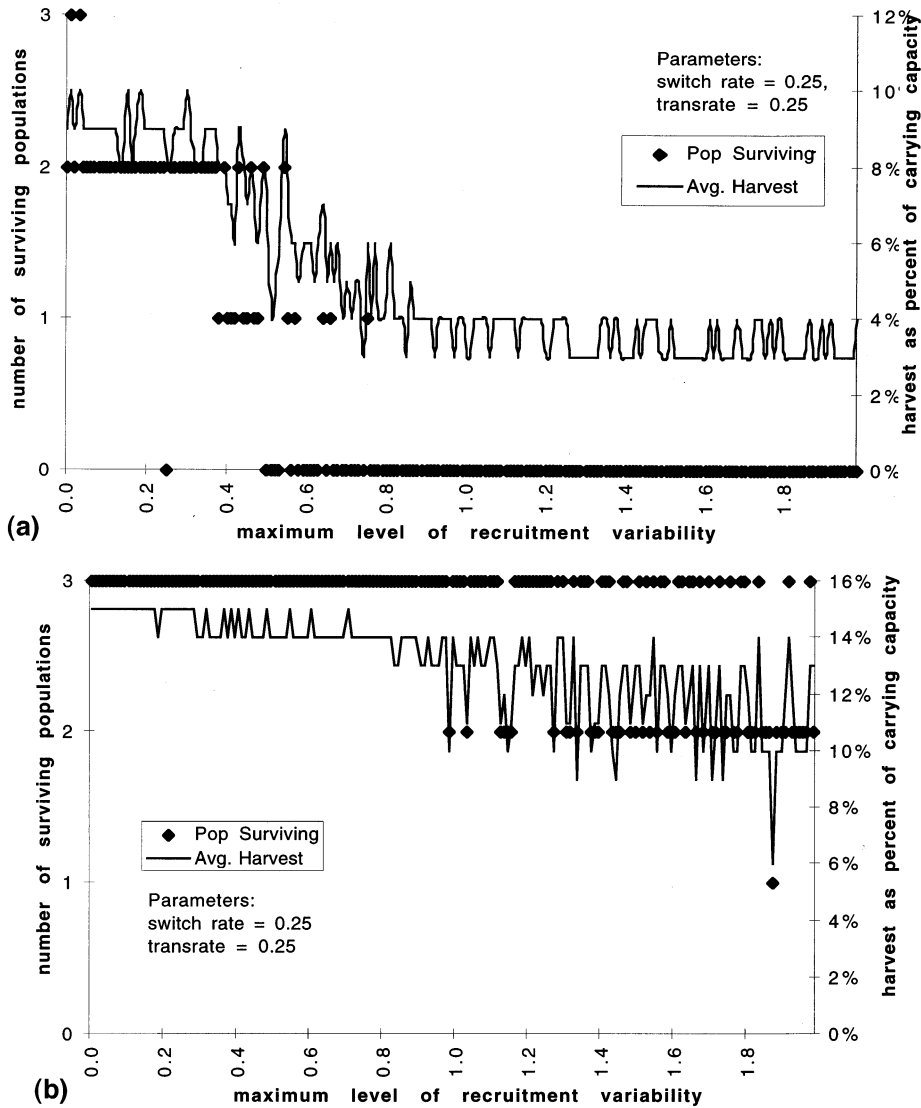


Fig. 4. (a) Population extinction and harvest open access with metapopulation. (b) Population extinction and harvest constant quota with metapopulation. (c) Population extinction and harvest sole-owner rule with metapopulation.

ery managers perceive the three local populations to be a single undifferentiated large population whose spatial characteristics are irrelevant to the management problem. We examine (1) different possible configurations of these populations, i.e. as a panmictic population or as a metapopulation, and (2) how those configurations might affect fishery outcomes under various rules managers might use — open access, constant percent harvest quota and sole ownership.

In each version of the model the three ‘local’ populations are given identical carrying capacities. As is common in fisheries management (Sinclair, 1988), 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 populations, and/or (2)

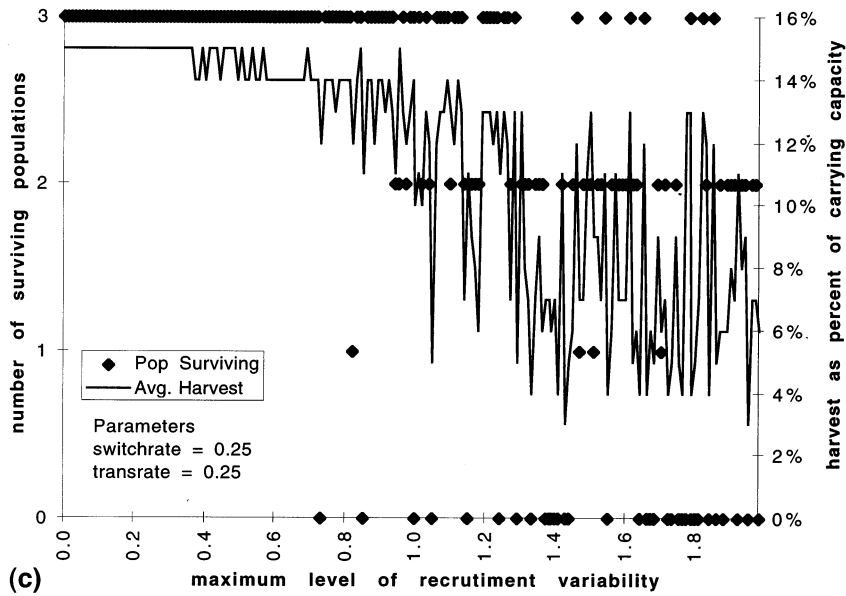


Fig. 4. (Continued)

Table 3

The effect of migration and switching on total average harvests (fraction of  $K$ ) and population extinction with no recruitment variability and with recruitment variability

| Transrate (fish)                     | Switchrate (boats) |                   |                   |                   |                   |                   |
|--------------------------------------|--------------------|-------------------|-------------------|-------------------|-------------------|-------------------|
|                                      | 0.0                | 0.1               | 0.2               | 0.3               | 0.4               | 0.5               |
| <i>Recruitment variability, 0.0</i>  |                    |                   |                   |                   |                   |                   |
| 0.0                                  | 0.18               | 0.17              | 0.18              | 0.12 <sup>a</sup> | 0.09 <sup>b</sup> | 0.00 <sup>c</sup> |
| 0.1                                  | 0.18               | 0.18              | 0.17              | 0.17              | 0.05 <sup>b</sup> | 0.00 <sup>c</sup> |
| 0.2                                  | 0.18               | 0.18              | 0.17              | 0.17              | 0.12 <sup>a</sup> | 0.00 <sup>c</sup> |
| 0.3                                  | 0.18               | 0.18              | 0.11 <sup>a</sup> | 0.13 <sup>a</sup> | 0.00 <sup>c</sup> | 0.00 <sup>c</sup> |
| 0.4                                  | 0.18               | 0.18              | 0.17              | 0.13 <sup>a</sup> | 0.12 <sup>a</sup> | 0.00 <sup>c</sup> |
| 0.5                                  | 0.18               | 0.17              | 0.17              | 0.11 <sup>a</sup> | 0.08 <sup>b</sup> | 0.00 <sup>c</sup> |
| <i>Recruitment variability, 0.25</i> |                    |                   |                   |                   |                   |                   |
| 0.0                                  | 0.18               | 0.17              | 0.18              | 0.12 <sup>a</sup> | 0.09 <sup>b</sup> | 0.00 <sup>c</sup> |
| 0.1                                  | 0.16               | 0.12 <sup>a</sup> | 0.10 <sup>a</sup> | 0.09 <sup>b</sup> | 0.00 <sup>c</sup> | 0.00 <sup>c</sup> |
| 0.2                                  | 0.14 <sup>a</sup>  | 0.11 <sup>a</sup> | 0.09 <sup>b</sup> | 0.18              | 0.00 <sup>c</sup> | 0.00 <sup>c</sup> |
| 0.3                                  | 0.14 <sup>a</sup>  | 0.08 <sup>b</sup> | 0.18              | 0.00 <sup>c</sup> | 0.00 <sup>c</sup> | 0.00 <sup>c</sup> |
| 0.4                                  | 0.13 <sup>a</sup>  | 0.15 <sup>a</sup> | 0.08 <sup>b</sup> | 0.13 <sup>a</sup> | 0.00 <sup>c</sup> | 0.00 <sup>c</sup> |
| 0.5                                  | 0.14 <sup>a</sup>  | 0.04 <sup>b</sup> | 0.13 <sup>a</sup> | 0.00 <sup>c</sup> | 0.00 <sup>c</sup> | 0.00 <sup>c</sup> |

<sup>a</sup> One extinguished population.

<sup>b</sup> Two extinguished populations.

<sup>c</sup> Three extinguished populations.

on the often high costs and difficulty of monitoring and assessing separate populations. 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 (rents) 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 harvest 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 of the current size of the stock(s) are without error and are analyzed correctly with the resulting quotas implemented in a timely fashion, that is, in the year immediately following receipt of the information. In all runs of the model the harvest percent used is 28% of current stock. This number approximates the steady state results for the sole owner rule and leads to higher long run profits (rents) than any other percentage rate.

The profit or rent 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 5-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 0.05 of carrying capacity,  $K$ . This assumes that below the critical minimum, there are too few adult 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 and the local population is eventually extinguished. The model does not contain a mechanism for recolonization after extinction occurs. This treatment thus mimics short-term metapopulation dynamics in which extirpated local populations are rarely recolonized, and illustrates well the effect of local extinctions.

The long-run dynamic of each local population is characterized by a discrete version of the logistic stock/recruitment relationship:

$$S_{t+1} - S_t = rS_t \left(1 - \frac{S_t}{K}\right) \quad (1)$$

where  $S_t$  is population numbers at time  $t$ ,  $r$  is a so-called lumped parameter that represents the net effect of population growth and mortality from all sources except those otherwise specified,

e.g. harvesting.  $K$  is the carrying capacity stated in terms of the maximum number of individuals in the population (see Fig. 1). Because fish spawn once each year, a time step of 1 was used in all the calculations presented here.<sup>2</sup> 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, in both the panmictic and metapopulation versions 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:

$$\text{Trans}_{a,b} = \text{transrate} \left( \frac{S_a}{K_a} - \frac{S_b}{K_b} \right) \quad (2)$$

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  $\pm 0.5$ , fish achieve equal densities in all three populations within one period; at a value of 0.0, fish cannot move between populations.<sup>3</sup>

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. These changes in total fishing effort and a specified portion of existing effort — given by ‘switchrate’, are then allocated among populations so that profits per boat tend towards equality 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 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 spatial structure of the overall population that managers either fail to perceive or choose to ignore.

The third factor determining harvest rates is the productivity of each harvester, where productivity is measured in terms of percent of the population harvested annually by a single boat. Productivity is assumed to be partly due to the number of other boats in the fishery (the more boats the less productive each boat) and from behavioral characteristics of the fish which alters catch rates, especially as populations decline — e.g. do fish maintain the same density over a smaller spatial extent or is density reduced as populations decline? In all runs of the model (except where explicitly mentioned) congestion effects are present but have a minimal effect upon harvesting efficiency. The effects of changes in fish population density are modeled so that harvesting efficiency falls off dramatically as fish density approaches zero. This tends to create strong feedback that protects (but not completely) local populations against extinction. 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, to differences in the allocation of effort to each local population, and eventually to differences in local population sizes.<sup>4</sup>

### 2.1. Exploring the model

Given this description of the model, we return now to the broad question we wish to ask: “Does

<sup>2</sup> The model was investigated at time steps down to 0.0625 with damped persistence of its basic behavior.

<sup>3</sup> At values above 10.51 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 10.51.

<sup>4</sup> STELLA equations for the critical population, decision rule and effort allocation aspects of the model are contained in Appendix A.



management misperception of the appropriate population scale make a difference? And, if so, under what circumstances?” Our original 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 are most likely to occur 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 the size of a local population declines, profits from that population should fall and cause effort to move to healthier local populations, providing thereby some measure of protection against depletion or, in the metapopulation case, extinction (i.e. falling below the critical minimum threshold.)
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, sooner or later, critical minimum levels (in the metapopulation case).

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 (see Table 1). The general method behind our explorations was to start with a set of parameter values that generate a dynamic solution that mirrors or approximates the results expected from the steady state analytical model (Clark, 1976). 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. The 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 Fig. 1); however, the numerical results differ significantly (see Table 2).

From comparison in Table 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 — as generally occurs with the sole owner and constant quota rules — the smaller local 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 (See Fig. 2). The resulting change in harvests causes a decline in the larger population and growth in the smaller, reinforcing the effect of fish migration. The movement of fishermen is towards the largest or healthiest sub-populations.

In the case of the open access rule, however, the growth effects of migration work in the opposite direction (see Fig. 2). Here migration tends to move towards stocks with lower growth, leading to 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, 1995). Also, if management relied upon the best productivity levels (catch per unit effort) or a major indicator of overall stock size, the assumed migration of fish from stronger to weaker stocks and, especially, of fishermen from weaker to stronger stocks, might lead to an understatement of the severity of the overfishing problem.<sup>5</sup>

## 2.2. Sources of variability

From this baseline we began to explore the model for sources of internal dynamic variability. Two variables unique to the three population structures, 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' and 'switchrate' 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 'equal density' or 'equal profits' there tends to be some overshoot; this occurs because there is a delay between the time profit or density differences occur and the migratory response of fish or fishermen. During that delay, of course, the size of the population (both donor and recipient) is altered by other density dependent responses, in this case recruitment. This effect is most pronounced at times or in circumstances where small differences in population size lead to large changes in recruitment (e.g. low populations such as points C and D in Fig. 2). As a consequence this source of internal variability only occurs in the sole owner and constant quota cases at those times when other factors drive populations to low levels. For open access, however, the effect is pronounced. Fig. 3 shows how this internal dynamic affects the three populations under open access. In this instance, fish were not able to migrate 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.

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

1. The intrinsic growth rate of the population,  $r$ . With a time step of 1 and a value for  $r$  around 1 the population is very stable; in the vicinity of  $r = 2.0$  large periodic fluctuations in the local populations begin to occur. At values around  $r = 4.0$  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 time step of 1 and 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 (measurement errors of 30–50% are common with fish popu-

<sup>5</sup> Hutchins and Meyers (1995) point out that at very low stock sizes exactly the opposite may occur — i.e. fish may tend to desert sub-populations or schools or patches that have too few fish. Under these circumstances productivity indication would understate the extent of overfishing even more.

lations) or a host of other factors are incorporated in the model all three decision 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 not captured by recruitment 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.

### 3. Testing hypotheses

Does the management rule make a difference if there is a misperception of appropriate population scale? The answer to this question is clearly yes but only if the system is subject to some (internal or external) 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%.<sup>6</sup> 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 Fig. 4a). 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.<sup>7</sup> (Fig. 4a–c are each the result of 200 separate runs of the model. For each run the range of random recruitment variability was incremented by 0.01 above the previous run.)

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% (Fig. 4b and c). Since these are rather low levels of variation for marine systems, the model strongly suggests that rules that are optimal for single 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.

Does the migration of either fish or fishermen tend to protect local populations against depletion when management has a scale misperception problem? In both instances the answer is yes, so long as the rate of migration or switching does not lead to overcompensation. 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 tend to leave 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 low migra-

<sup>6</sup> 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 20–25%. 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.

<sup>7</sup> We were interested in whether the choice of a time step of 1 significantly affected these results and so reran the model at lower time steps. The general effect of the time step is to set up the internal variability illustrated in the figure above. This source of variability diminishes with lower time steps with the result that population failure tends to occur at somewhat higher levels of external variability than otherwise. In other words, population failure at low levels of external variability tended to occur when a chance run of bad recruitment was combined with a downturn due to internal variability. With time steps lower than 1 downturns due to internal variability are weaker and it is not until stronger external variance enters that population failure begins to occur.

tion rates are 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 effect is reinforced by 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 3 summarizes the relationships between migration, switching, recruitment variability and local population failure.

Do differences in the cost of exploiting one local population relative to another make a difference when there is a scale misperception problem? 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. One persistent effect of harvesting cost differentials, *ceteris paribus*, is population size differences that are inversely related to the cost differentials. This tends to create circumstances in which the

populations with high harvesting costs become a ‘source’ for fish continuously migrating to low harvesting costs, ‘sink’, population. 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.

There is, however, one set of circumstances in which the model produces the behavior originally hypothesized (i.e. extinction of the population least costly to fish first and then extinction of other populations in order of least costly to most). Those circumstances arise when boat productivity does not decline with declines in fish abundance. This might occur, for example, when boats harvest spawning aggregations at known locations and times. Under these circumstances boats might experience high productivity right up to the last haul of the nets containing the last fish in the population. If managers of this kind of fishery rely upon measures such as ‘catch rate per boat’ to signal a decline or change in the population, that measure will fail to provide appropriate feedback until the populations are extinguished and it is much too late to respond adequately.

#### 4. 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 lead possibly 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.

We found 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 of abundance, 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’ 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, especially if local spawning groups mix together at other times of the year, e.g. when feeding. This implies an emphasis on where, when and how fishing takes place rather than simply an emphasis on the ‘right number’ to catch. Stated in terms of the precautionary principle, the existence of local stocks, or even uncertainty about their existence, suggests that scale misperceptions (or the deliberate aggregation, or ‘pooling’, of local stocks for management purposes) can lead to very risky management practices. Finally, 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.

## Appendix A

Equations for (1) effort allocation, (2) fish population and (3) decision rules

### A.1. Ecosystem 1

$$\begin{aligned} \text{Pop1}(t) = & \text{Pop1}(t - dt) \\ & + (\text{Growth1} + \text{trans} \\ & \text{\_13} - \text{Harvest1} - \text{Mortality1} \\ & - \text{Transfer\_12}) * dt \end{aligned}$$

$$\text{INIT Pop1} = 5000$$

INFLOWS:

$$\begin{aligned} \text{Growth1} = & \text{minpop\_1} * \text{External\_Influences} \\ & - 1 * (\text{Growthrate} * \text{Pop1} * (1 \\ & - (\text{Pop1} / \text{Carrying\_capacity}))) \\ & \text{trans\_13 (Not in a sector)} \end{aligned}$$

OUTFLOWS:

$$\text{Harvest1} = \text{harvesters\_1} * (\text{Harvest\_Efficiency} + \text{stock\_density}) * \text{Pop1}$$

$$\text{Mortality1} = \text{Pop1} * .02$$

$$\text{Carrying\_capacity} = 10000$$

Growthrate = 1  
 stock\_density = GRAPH(Pop1): (0.00, 0.00),  
 (1000, 0.00595), (2000, 0.0083), (3000, 0.009),  
 (4000, 0.00915), (5000, 0.0093), (6000, 0.00955),  
 (7000, 0.0096), (8000, 0.00965), (9000, 0.00965),  
 (10000, 0.00975)

DOCUMENT: Gives the relationship between the efficiency of harvesting and the size of the stock being harvested. A strictly linear positive relationship gives a harvest per unit effort that is proportional to stock size. A 'log' shaped relationship indicates harvest per unit effort that remains strong until the stock is very small. This may occur with many species that congregate — e.g. herring, perhaps groundfish such as cod.

### A.2. Profit based Decisions

harv\_unit\_trend\_all  
 = TREND(sum\_harv\_units,trendlength)  
 \*100

DOCUMENT: See note for profit trend.

profit\_trend\_all  
 = TREND(profits\_all,trendlength)\*100  
 DOCUMENT: A trend is used rather than the most recent profit level because feedback from the biological sector can cause the most recent profit level to produce a false signal. A 5-year trend generates a somewhat slower response but tends to search out the maximum much more reliably.

SOLE\_OWNER\_all = IF(profit\_trend\_all)  
 > 0  
 THEN(IF(harv\_unit\_trend\_all) > 0  
 THEN(effort\_rate\_all)  
 ELSE(– effort\_rate\_all))  
 ELSE(IF(harv\_unit\_trend\_all) > 0  
 THEN(– effort\_rate\_all)  
 ELSE(effort\_rate\_all))

DOCUMENT: Profit maximizing solution. Simple search that assumes the relationship between profits and harvest units is a smooth, single peaked function. However, when the model is far from equilibrium or subject to high

levels of variability this rule is insufficient and has to be supplemented with a second rule that takes into account more 'global' conditions.

trendlength = 5

effort\_rate\_all

= GRAPH(ABS(profit\_trend\_all)\*2):  
 (0.00, 0.00), (3.00, 0.05), (6.00, 0.25), (9.00,  
 0.55), (12.0, 1.05), (15.0, 1.65), (18.0, 2.50),  
 (21.0, 3.45), (24.0, 4.75), (27.0, 6.55), (30.0,  
 9.85)

DOCUMENT: Assumes the change in the rate of harvest effort reflects the magnitude of recent changes in the level of profits. If this response rate is set so that it is too sensitive effort changes will be consistently too large in both directions (but with one dominating) and lead to a cascading increase or decrease in harvesting.

OPEN\_ACCESS\_all = GRAPH(avg\_profit):  
 (– 1000, – 10.0), (– 800, – 5.90), (– 600, –  
 3.40), (– 400, – 2.00), (– 200, – 1), (0.00, –  
 1.11e – 16), (200, 0.9), (400, 2.10), (600, 3.50),  
 (800, 5.90), (1000, 10.0)

DOCUMENT: Entry continues until positive profits are driven to zero. Exit occurs until negative profits are driven to zero.

assessdelay = 1

DOCUMENT: Set to reflect the delays necessary to survey, measure and analyze data to determine stock size.

HARVEST\_%\_all = stock\_%

–all\*delay(sum\_NC, assessdelay)

DOCUMENT: LIMITS harvest to the fraction stipulated (in stock\_%) of the current stock of natural capital.

### A.3. Allocation sector

abs\_alloc

= ABS(alloc%\_1) + ABS(alloc%\_2)  
 + ABS(alloc%\_3)

alloc%\_1 = if prof\_harv < 0 then 0.001 else  
 prof\_harv

DOCUMENT: if statement avoids possible division by zero problem

alloc%\_2 = if prof\_harv\_2 < 0 then .0010 else prof\_harv\_2

alloc%\_3 = if prof\_harv\_3 < 0 then 0.001 else prof\_harv\_3

avg\_profit = (prof\_harv + prof\_harv\_2 + prof\_harv\_3)/3

harv\_units\_1 = if alloc%\_1 > 0 then (alloc%\_1/abs\_alloc)\*(har\_unit\_change + realloc) else -abs(((.01 + alloc%\_1 /abs\_alloc))\*(har\_unit\_change + realloc))

DOCUMENT: Assigns the appropriate change in harvesting units after finding, first, the proportion and then applying it to the sum of changes in the total number of harvesting units, har\_unit\_change, and the number of units available for switching or reallocation.

harv\_units\_2 = if alloc%\_2 > 0 then (ailoc%\_2/abs\_alloc)\*(har\_unit\_change + realloc) else -abs(((0.1 + alloc%\_2)/abs\_alloc)\*(har\_unit\_change + realloc))

harv\_units\_3 = if alloc%\_3 > 0 then (alloc%\_3/abs\_alloc)\*(har\_unit\_change + realloc) else -ABS(((.01 + alloc%\_3)/abs\_alloc)\*(har\_unit\_change + realloc))

prof\_harv = if profits\_1/harvesters\_1 < > 0 then if profits\_1/harvesters\_1 < 1000000 then profits\_1/harvesters\_1 else 0.01 else 0.01

prof\_harv\_2 = if profits\_2/harvesters\_2 < > 0 then if profits\_2/harvesters\_2 < 1000000 then

profits\_2/harvesters\_2 else 0.01 else 0.01

prof\_harv\_3 = if profits\_3/harvesters\_3 < > 0 then if profits\_3/harvesters\_3 < 1000000 then profits\_3/harvesters\_3 else 0.01 else 0.01

realloc = realloc\_1 + realloc\_2 + realloc\_3

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