

**EFFECT OF FISH MOVEMENT  
AND FLEET SPATIAL BEHAVIOR  
ON MANAGEMENT OF FISH SUBSTOCKS**

LENORE FAHRIG  
Ottawa-Carleton Institute of Biology  
Carleton University  
Ottawa, Canada K1S 5B6

**ABSTRACT.** I investigated the questions (i) how much movement of fish between areas within a stock is required before the areas can be managed jointly instead of separately and (ii) how is the trade-off between separate and joint management affected by the spatial behavior of the fishing fleet? I addressed these questions using a simulation model of a fishery on a stock that is divided into two areas (substocks) between which fish can move. Under joint management, fleet spatial behavior is characterized by its "switching level," or the biomass level in the currently fished area at or below which the fleet will switch to the other area. Catch levels were calculated under both separate and joint management for a range of movement rates and switching levels. I also studied the effect of differences in natural mortality rates between the two areas. When the natural mortality rates were the same for the two areas, (i) separate management resulted in higher catch than joint management, (ii) joint management only approached the catch of separate management when movement rate of fish between the two areas was very high, (iii) the difference between separate and joint management was greatest when (a) the switching level of the joint fleet was low (i.e., inertia was high) and (b) the joint fleet had a preference for one area. When natural mortality rate was different in the two areas, and (i) the joint fleet did not prefer one area, (a) separate management produced higher catches at low fish movement rates while joint management produced higher catches at high movement rates and (b) switching level had no effect on catch, and (ii) when the fleet had a preference for the area with the higher natural mortality rate, separate management resulted in higher catches than joint management, and the difference increased with increasing fish movement rate. These simulations suggest that the relative merits of separate and joint management of two areas depends on the assumptions one makes about the spatial behavior of the fishing fleet. This behavior is as important as movement of fish between the areas, which is normally assumed to be the overriding determinant of the relative merits of separate and joint management.

**KEY WORDS:** Fish management, fish movement, fleet

behavior, simulation model, spatial model, substock, areal quotas.

**1. Introduction.** A fish "stock" is a management unit, or a portion of a fish species that is delineated for the purposes of management. It is normally assumed that the boundaries of a fish stock should coincide with the boundaries of a fish "population," or a group of conspecific organisms that exhibit reproductive continuity from generation to generation (Futuyma [1979]). For example, Ihssen et al. [1981] define a stock as "an intraspecific group of randomly mating individuals with temporal or spatial integrity." The important notion in this definition is that of mating within (but not between) stocks of fish. This is also implied in other definitions of stock such as a "production unit" (e.g., Marshall et al. [1987]) and "a population of fish maintaining and sustaining Castle-Hardy-Weinberg equilibrium" (Booke [1981]).

Much of applied fisheries research is directed towards the delineation of fish stocks (e.g., Nakamura [1987], Almeida [1987], papers in Kumpf [1987]). This is because it is well recognized that problems may arise from managing two or more fish stocks in combination (Hilborn [1985a]). The problems fall into two categories. First, if the stocks differ substantially in population parameters such as fecundity or growth rate, then the calculated optimal catch levels will be incorrect. Second, different spatial and temporal distributions of fishing can lead to very different long-term population dynamics, even for the same overall harvesting level (Selgeby [1982], Fahrig and Atkinson [1991]). In the extreme, if all the fishing is concentrated on a subset of the stocks, and some stocks are fished to extinction, it may take many generations for these stocks to be replaced if the rate of movement of fish between stocks is low.

Although the ideal is to manage separate, self-sustaining populations, the distribution and subdivision of species does not usually fit neatly into this ideal. Movement of fish between management units defined as stocks can be substantial (e.g., Hourston [1982], Hansen and Lea [1982], Brunch [1985], Mulligan and Chapman [1986], Gharrett et al. [1988], Templeman [1989]). Furthermore, the ideal of the randomly mating unit is normally only strictly valid on very small spatial scales. It is common to find that the distribution of a fish species may cover a large geographic area without obvious distributional breaks; movement rates

between neighboring portions within the region are high and separate populations are not obvious. However, mating within the entire area is clearly not random; fish in neighboring areas are much more likely to mate than those separated by large distances. For example, Thurow [1985] describes three "stocks" of Baltic cod, where the central stock "is recruited by young fish of both neighboring stocks." Smith and Francis [1982] describe southern and northern stocks of New Zealand ling "with an area of stock mixing" between them. Division of the fish into "stocks" in such cases is still required because again, as described above, different spatial distributions of fishing can lead to very different population responses. However, these stocks do not correspond to the ideal randomly mating fish populations; their boundaries may be quite arbitrary and they are delineated for management purposes only.

The fact that movement between management units of fish does occur therefore begs the question: how much movement of fish between two areas is required before the areas can be managed jointly instead of separately? Stated in another way: how little movement between two areas within a stock (substocks) requires separate management of the two areas? This apparently simple question, which was the motivation behind the study reported here, is complicated by the fact that the overall consequences of fishing a spatially heterogeneous population depend on the spatial behavior of the fishing fleet.

Although the joint effects of fish movement and fleet spatial behavior have been largely ignored in fisheries management (Hilborn and Walters [1987], Hilborn [1989]), there is some evidence that these factors can have important consequences. For example, Polachek [1990] examined the effect of a closed area, using a two-area model with fish movement. He showed that limiting fishing to one area can increase spawning stock biomass from a cohort, and in some cases can increase the overall yield per recruit. The outcome is in large part determined by the movement rate of the fish between the two areas. However, he did not model variations in spatial behavior of the fishing fleet; fishing was either absent from the closed area, or the whole stock was fished homogeneously. Hilborn [1985b] studied the effect of fish movement across international boundaries. He showed that if the two countries manage their portions of the stock using different management objectives, the overall impact on the fish stock and the fisheries depends on the movement rate of the fish across the boundary. In Hilborn's model

the two areas were fished by two separate fleets (two countries or one country and an international fleet).

While the studies by Polachek [1990] and Hilborn [1985b] primarily examined the effects of fish movement, a highly disaggregated simulation study by Allen and McGlade [1986, 1987] examined the effect of fleet spatial behavior on catches. They describe two kinds of fishers characterized by their search behaviors: "Stochasts" are risk takers who will readily leave their current fishing locations in search of areas of greater stock densities; "Cartesians," on the other hand, are risk averse and are unlikely to take the risk of looking for an area of greater stock density if they are finding any fish at all in their present location. The simulations show that the spatial behavior of the fleet can have important effects on long-term catches, but they do not include the effects of fish movement.

In the present work I explicitly examine the joint effects of fish movement and fleet spatial behavior. The purpose of this work was to investigate the questions (i) how much movement of fish between two areas is required before the areas can be managed jointly and (ii) how is the trade-off between separate and joint management of two areas affected by the spatial behavior of the fishing fleet?

## 2. Methods.

*2.1. The model.* The model is a simulation model of a fish stock, divided into two areas (substocks), with a one-year time step. Each year there is fish movement between the areas, natural mortality, recruitment, and fishing, in that order. Each year's quota is set based on the previous year's final population (i.e., before this year's fish movement, natural mortality and recruitment occur). Fish are removed from the areas according to the specified type of fishing behavior (see section "Fishery Dynamics"). If the two areas are to be managed jointly, a total quota is set for both areas combined. If they are to be managed separately, separate quotas are set for the two areas. The model is

$$p_{t,i} = s_i[p_{t-1,i}(1 - m_{ij}) + p_{t-1,j}m_{ji}] + r_{t,i} - c_{t,i}$$

where  $p_{t,i}$  is the population size (or biomass) of fish at the end of year  $t$  in area  $i$ ,  $s$  is the annual survival rate,  $m_{ij}$  is the movement rate of fish from area  $i$  to area  $j$  and  $c$  is the catch.

Recruitment is calculated from the previous year's stock according to the equation of Beverton and Holt [1957]:

$$r_{t,i} = \frac{\alpha p_{t-1,i}}{1 + \beta p_{t-1,i}}$$

where  $\alpha$  and  $\beta$  are parameters determining the shape of the curve. In the present simulations they were arbitrarily set at 10 and 0.001, respectively.

*2.1.1. Fishery dynamics.* Fishing quotas are set according to one of two policies: escapement policy that maximizes sustainable harvest, or fishing mortality rate that maximizes sustainable harvest. I refer to these as the "e policy" and the "f policy," respectively.

I considered two management options, separate and joint management. Within joint management I considered two fishing patterns, "inertia," and "preference." The separate management option refers to separate management of the two areas. In this case the quota for each area is set using the areal biomasses. If the stock in an area drops below the amount set for the quota, in the separate option the remaining quota is not taken from the other area because the fish in the two areas are separate management units. In the joint management option the two areas combined are a single management unit. The total yearly quota is set using the total (both areas combined) biomass. The inertia and preference fishing patterns determine the portions of the quota taken from each area. The steps and equations for the implementation of the fishing (each year) are given in the Appendix.

The inertia fishing pattern represents a much simplified version of the complex fishing behavior modelled by Allen and McGlade [1986, 1987] in their spatially disaggregated model. Fleet spatial behavior is characterized by a level of inertia in fishing location. If the fleet has a high level of inertia, it remains where it is fishing and does not explore the other area unless the fish biomass in the first area becomes very low; this is similar to the cartesian fisher in Allen and McGlade. If the fleet has a low level of inertia it will move between the areas much more readily; this is similar to the stochast in Allen and McGlade. The parameter in the model that determines where on the gradient between stochast and cartesian the fleet behavior lies is the "switching level," and is the biomass level in the currently fished area at which the fleet

will switch to the other area. If both areas are fished down to the switching level, the fleet is assumed to fish both areas evenly. If the biomass in both areas is below the switching level, the fleet fishes in the area of highest biomass until the two areas have equal biomasses and then they are fished at equal rates. Each year the fleet is assumed to begin by going back to the area in which it was last fishing in the previous year (unless that area's biomass is below the switching level). If it was fishing in both areas in the previous year it chooses a starting area at random.

The preference pattern is similar to the inertia pattern except that the fleet is assumed to have a built-in preference for one particular area. This occurs when one area is closer to port and therefore preferable for economic reasons (Fahrig [1991a]). In this case the fleet begins each year in its preferred area, but again switches to the other area if the biomass in the preferred area goes below the switching level. The fleet behavior within a year is the same as in the inertia case, but each year the fleet first "tries" to fish in its preferred area before switching.

*2.2. Simulations.* The goal of the simulation experiment was to examine the effect of fish movement between the two areas on the relative effectiveness of separate vs. joint (inertia or preference) management, and to determine to what extent this effect is influenced by the spatial switching behavior of the fleet under the joint management option. A factorial simulation experiment (Fahrig [1991b]) was performed in which a separate run was conducted for each combination of several levels of the two parameters, movement rate between the areas and fleet switching level (for the inertia and preference patterns). The values used for the movement rate were 0, 0.001, 0.005, 0.025, 0.125, 0.25 and 0.5 of the biomasses in each area moving into the other area each year. The values used for the switching level were 0, 0.01, 0.05, 0.1, 0.15 and 0.3, expressed as a fraction of the unexploited biomass per area. Each combination was also run for each of two natural mortality conditions: (i)  $s_1 = s_2 = 0.8$ , and (ii)  $s_1 = 0.2$  and  $s_2 = 0.8$ .

To find the  $f$  policy that maximizes sustainable harvest, each combination (above) was run for each of five fishing rates, 0.1, 0.2, ..., 0.5. The maximum sustainable catch was obtained under the  $f$  policy with fishing rate at about 0.3 per year. To find the  $e$  policy that maximizes sustainable harvest, I first had to find the unexploited biomasses. This

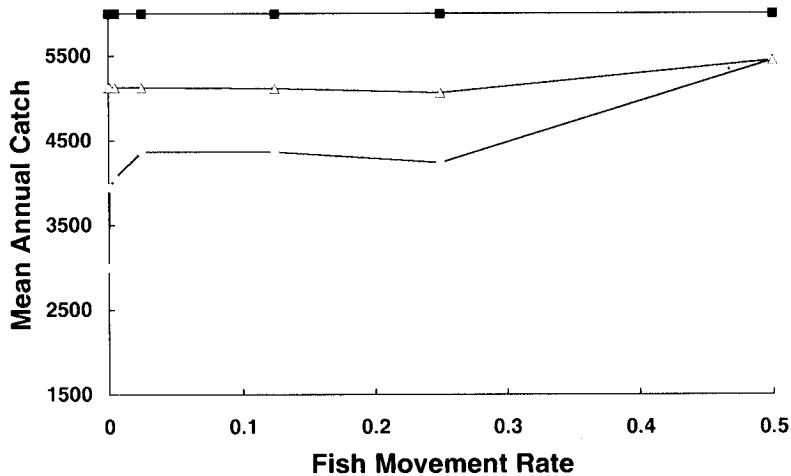


FIGURE 1A. Mean Annual catch (total for both areas) vs. rate of movement between the two areas. Natural survival rate in both areas is 0.8. See text for definitions.  $f$  policy, inertia fishing pattern. Closed squares: separate management, and inertia pattern with switching level = 0.3. Open triangles: inertia pattern with switching level = 0.01. Open circles: inertia pattern with switching level = 0.

was done by conducting simulations with no fishing. Note that when survival in the two areas is asymmetric (natural mortality condition (ii) above), the unexploited biomass depends on the movement rate of fish between the two areas. Simulations were conducted for each of the combinations (above) using the appropriate unexploited biomasses, and each of five escapement fishing rates, 10%, 20%, ..., 50% of the unexploited biomass. The maximum sustainable catch was obtained under the  $e$  policy with escapement level at approximately 30% of the unexploited biomass. The results reported below are those for which the  $f$  policy was 0.3 and the  $e$  policy was 30% of unexploited biomass.

The complete experiment therefore involved 196 runs: separate management option for 7 movement rates plus inertia and preference fishing patterns for 7 movement rates by 6 switching levels, for each of 2 management policies and 2 natural mortality conditions. Each simulation ran for 100 years. The mean annual catch (total for both areas) was

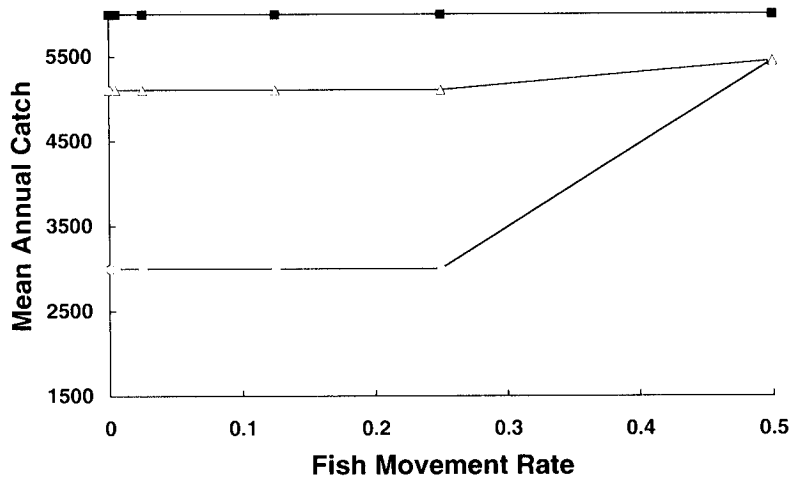


FIGURE 1B.  $f$  policy, preference fishing pattern. Closed squares: separate management, and preference pattern with switching level = 0.3. Open triangles: preference pattern with switching level = 0.01. Open circles: preference pattern with switching level = 0.

calculated over the final 30 years.

**3. Results.** The results of the simulations are shown in Figures 1 and 2. Figure 1 is the results for the condition of equal natural mortality in the two areas. Note that in each case the curve for joint management with high switching level (0.3) is identical to the curve for separate management. The results indicate that the behavior of the joint fleet has a large effect on the relative merits of joint and separate management. When the switching level is low (i.e., high inertia in the joint fleet), catch levels obtained by joint management are much lower than those for separate management. As expected the difference between separate and joint management decreases with increasing between-area movement rate of the fish, but even at very high movement rates separate management results in higher catch than joint management. The lower the switching level, the greater the proportion of the catch that is removed from one area. This depresses



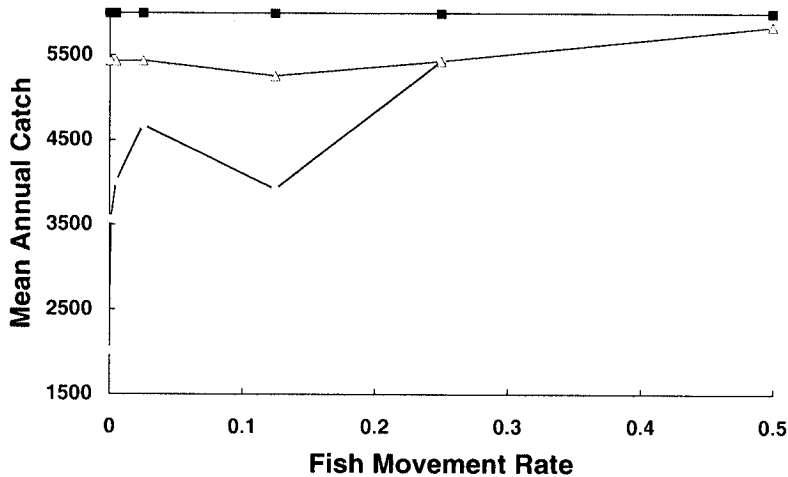


FIGURE 1C.  $e$  policy, inertia fishing pattern. Closed squares: separate management, and inertia pattern with switching level = 0.3. Open triangles: inertia pattern with switching level = 0.01. Open circles: inertia pattern with switching level = 0.

the recruitment level in that area. High movement rate between the areas corrects this to some extent. If the switching level is high, the catch is taken equally from both areas (as for separate management), leaving a large stock in both areas and resulting in a high overall recruitment level.

Figure 1 also indicates that the difference between separate and joint management is greater if the joint fleet has a preference for one area (compare Figures 1A and 1C with Figures 1B and 1D). This preference exacerbates the problem associated with high inertia because it means that the preferred area never has a chance for stock recovery. Also, under the escapement policy, at higher movement rates, catch levels of the joint fleet are closer to those obtained by separate management than under the constant fishing mortality policy (compare Figures 1A and 1B with Figures 1C and 1D). It has been shown that escapement policies in general result in lower likelihood of stock collapse than constant fishing mortality policies, because the stock is not permitted to reach critical

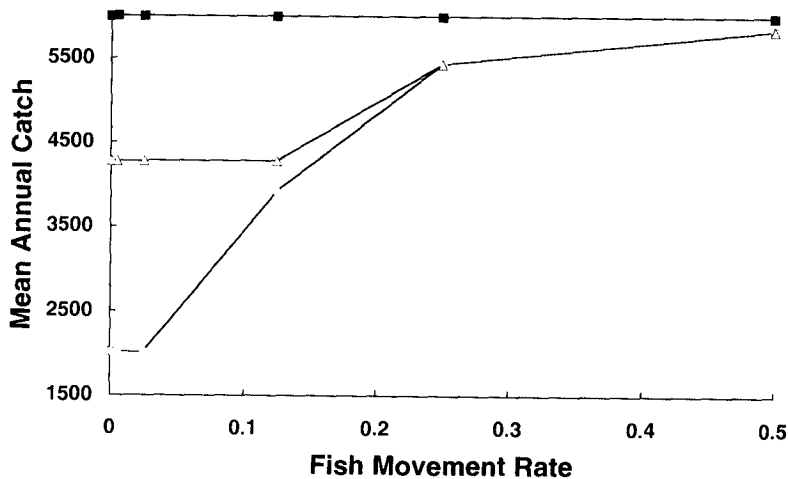


FIGURE 1D. e policy, preference. Closed squares: separate management, and preference pattern with switching level = 0.3. Open triangles: preference pattern with switching level = 0.01. Open circles: preference pattern with switching level = 0.

levels for recruitment (Getz et al. [1977], Koslow [1989]). The present result suggests that when fish movement rate is high, the escapement policy can buffer the effects of low switching levels to some extent.

Figure 2 shows the results for the condition that area 1 has much lower natural survival rate than area 2 (0.2 vs. 0.8). Note that this difference is an attribute of the areas themselves, not an intrinsic characteristic of the substocks; factors that cause fish mortality (e.g., lack of food, high predation rate) are assumed greater in area 1 than area 2. In all cases, catch level decreases with increasing between-area movement rate of fish. This is to be expected because the higher the fish movement rate, the greater the amount of fish (not the rate) transferred from the high survival area to the low survival area. This results in a larger overall natural mortality on the population, which results in smaller overall catch.

When the joint fleet has no area preference, switching level has no effect on catch (Figures 2A and 2C). This is because the fleet will tend

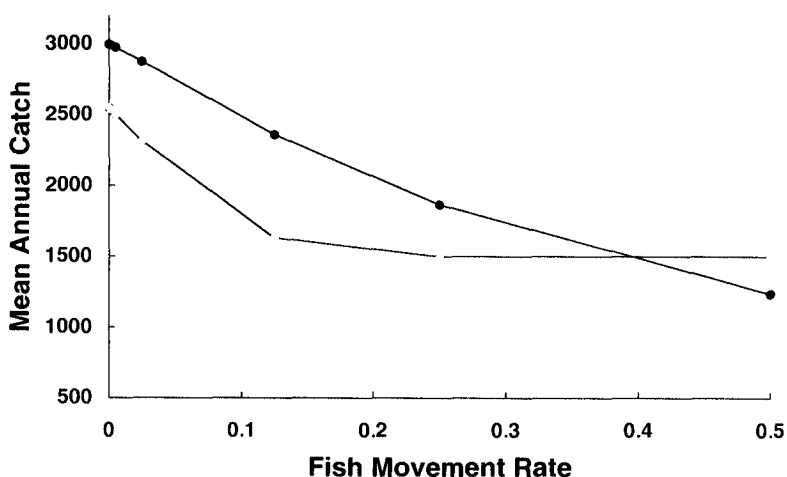


FIGURE 2A. Mean annual catch (total for both areas) vs. rate of movement between the two areas. Natural survival rate in area 1 is 0.2 and in area 2 is 0.8. See text for definitions.  $f$  policy, inertia fishing pattern. Closed circles: separate management. Open circles: inertia pattern with switching level = 0, 0.001, and 0.3.

to stay in area 2 where the biomass is always largest, so switching does not occur. Also, when there is no areal preference the relative catches of separate and joint management depend on the movement rate; separate catch is higher at low movement rates while joint catch is higher at high movement rates. At high movement rates under joint management, the biomass in area 1 (low natural survival rate) has a chance to recuperate to a level resulting in higher recruitment rate, through immigration and absence of fishing. The movement rate permitting recovery in area 1 will depend on the parameter values used in the stock-recruitment curve. If the curve is steep (recovery occurs for small stock biomasses), relatively small movement rates will allow recovery in area 1.

Finally, when the fleet has an areal preference for the area with the higher natural mortality rate (Figures 2B and 2D), separate management results in higher catches than joint management, and (unlike the case for equal natural mortality), the difference between separate and

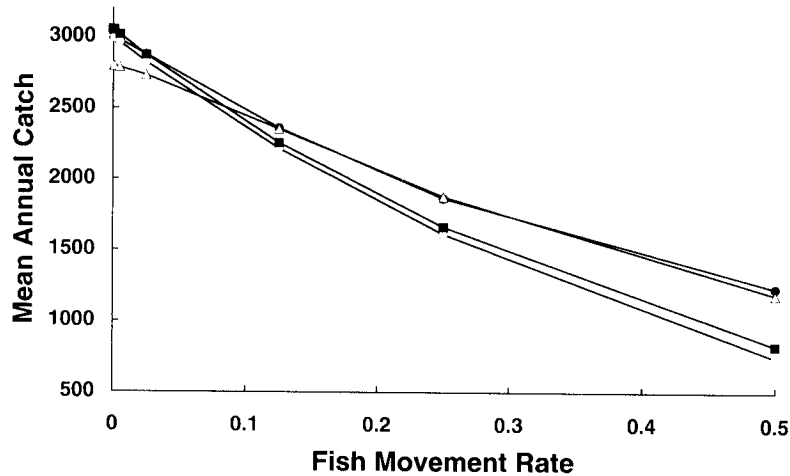


FIGURE 2B.  $f$  policy, preference fishing pattern. Closed circles: separate management. Closed squares: preference pattern with switching level = 0.3. Open triangles: preference pattern with switching level = 0.01. Open circles: preference pattern with switching level = 0.

joint management increases with increasing movement rate. When the fish movement rate is high, the stock in area 1 (the preferred area) remains above the switching level, so the fleet does not move out of this area. Overall recruitment is lower the longer the fleet stays in the area having the lower natural survival rate (area 1). Again, the point at which the fleet moves to area 2 will depend on the shape of the stock-recruitment relationship. If the curve is steep, the fleet will tend to stay in area 1, thus reducing the overall population size and the overall catch.

**4. Discussion.** The simulations demonstrate that the relative merits of separate and joint management of two areas depends to a large degree on the spatial behavior of fishing in the joint management case. It is therefore not meaningful to ask the question, "how much movement of fish between two areas is required before the areas can be managed jointly instead of separately?," unless one knows the spatial

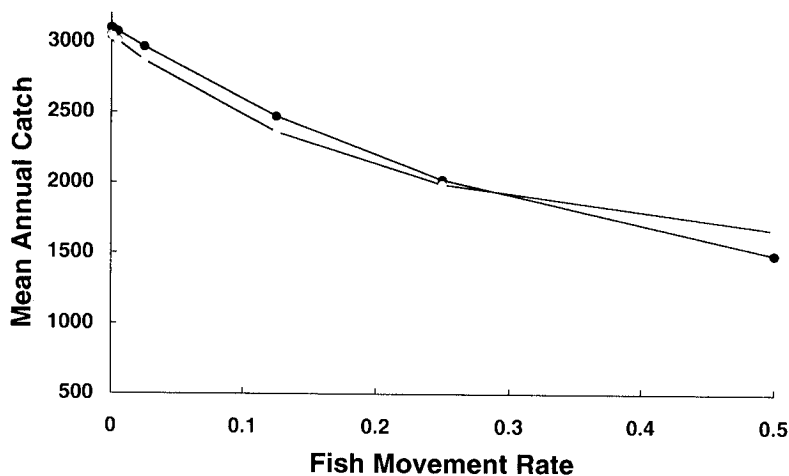


FIGURE 2C.  $e$  policy, inertia fishing pattern. Closed circles: separate management. Open circles: inertia pattern with switching level (see text) = 0, 0.001, and 0.3.

behavior of the fleet under the joint management option.

In the present simulations I have simplified this behavior by assuming that the fleet acts in concert and that its behavior can be described using a single parameter, the switching level. The degree to which the assumptions match a particular situation will vary depending on factors such as the areal extent of the stock and the ownership of the fleet. If the stock area is very large and the fleet is under single ownership, the assumptions here may hold approximately. At the other extreme, if the fleet is maximally spread over both areas and all ships act independently, the actions of the various ships will tend to cancel each other out, and the overall catch will be close to the separate management scenario, even if the switching levels for the individual ships are low.

It is important to note that the model is deterministic. In any real system there will be stochastic fluctuations in recruitment, survival and movement, as well as inaccuracies in the assessment of biomass at both the quota-setting point and the point at which the fleet decides

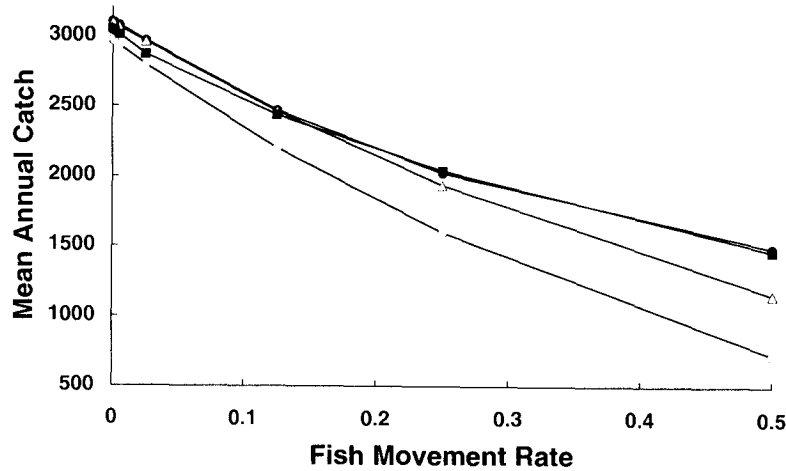


FIGURE 2D.  $e$  policy, preference fishing pattern. Closed circles: separate management. Closed squares: preference pattern with switching level = 0.3. Open triangles: preference pattern with switching level = 0.01. Open circles: preference pattern with switching level = 0.

to switch areas. These factors will have at least two qualitative effects on the results. First, whenever the population is low, there will be some chance of extinction due to stochastic variability. Second, the inaccuracies in stock assessment combined with variability in movement rates will result in a decrease in catch rate with increasing movement rate for the separate management option. The stock will be harvested suboptimally because (i) the stock assessment is in error and (ii) asymmetry in movement rates between the two areas due to variability will result in a further difference between the assessed and actual biomasses. This effect will be more important for separate management than for joint management, because in separate management the fleet cannot move between the areas to correct for these effects of variability. This will change the results of the simulations as follows: if different areas have similar natural survival rates, with increasing stochastic variability there will be a reduction in the movement rate required for joint management to equal the effectiveness of separate management.

As in any modelling study, certain simplifying assumptions were made in order to address the specific question at hand. For example, other assumptions could have been made about the stock-recruitment relationship, survival rates and the relationship between movement rate and stock density. Furthermore, the model is not age-structured, all fish were assumed to be biologically identical, and the choice of two areas only was taken for the sake of simplicity. The only economic considerations included in the model are implicit in the switching level and the preference scenario. The particular quantitative results of the simulations reported here are therefore not applicable to a particular fishery. They nevertheless serve to demonstrate the important point that the relative merits of separate and joint management of two areas depend heavily on the assumptions one makes about the spatial behavior of the fishing fleet under the joint management scenario. This behavior may in fact be more important than movement between the areas, which is normally assumed to be the most important determinant of the relative merits of separate and joint management.

**Acknowledgments.** I would like to thank the editor, R. Hilborn, for his helpful suggestions. Other useful comments were provided by W. Nuttle, P. Shelton, and two anonymous reviewers. Noel Cadigan provided programming assistance. Partial support for this work was provided under the Government of Canada's Atlantic Fisheries Adjustment Program (Northern Cod Science Program), and a Natural Sciences and Engineering Research Council of Canada Grant to L. Fahrig.

#### APPENDIX

The steps and equations for implementation of the fishing strategies (each year) are as follows. First, the quotas are set, where  $q_{t,i}$  = quota for year  $t$  in area  $i$ . The quotas depend on which of the four possible combinations of management policy and fishing option is being simulated:

- (1)  $f$  policy, separate option :  $q_{t,i} = fp_{t-1,i}$
- (2)  $e$  policy, separate option :  $q_{t,i} = en_i$ ,

where  $n_i$  is the natural (i.e., unexploited) equilibrium population in area  $i$ , and  $e$  is the escapement fraction.

(3)  $f$  policy, joint (inertia or preference) option:  $q_{t,i+j} = f(p_{t-1,i} + p_{t-1,j})$

(4)  $e$  policy, joint (inertia or preference) option:  $q_{t,i+j} = e(n_i + n_j)$ .

The actual catch taken from each area ( $c_{t,i}$ ) then depends on a combination of the quota, the current population size, and the fishing option:

I. Separate option:

if  $q_{t,i} \leq p_{t,i}$  then  $c_{t,i} = q_{t,i}$     if  $q_{t,i} > p_{t,i}$  then  $c_{t,i} = p_{t,i}$

II. Joint (inertia or preference) option: Note that the only difference between the inertia and preference patterns is that for the preference pattern  $i = 1$  always. For the inertia pattern,  $i$  is either the area that was last fished in the previous year, or if, at the end of the previous year both areas were fished equally, then  $i$  is selected at random between the two areas.

There are nine possible starting conditions for the two areas (where  $x$  is the switching level):

$$(1) \quad p_{t-1,i} > x + q_{t,i+j} \quad \text{and} \quad p_{t-1,j} > x + q_{t,i+j}$$

$$(2) \quad p_{t-1,i} > x + q_{t,i+j} \quad \text{and} \quad x + q_{t,i+j} > p_{t-1,j} > x$$

$$(3) \quad p_{t-1,i} > x + q_{t,i+j} \quad \text{and} \quad p_{t-1,j} \leq x$$

$$(4) \quad x + q_{t,i+j} > p_{t-1,i} > x \quad \text{and} \quad p_{t-1,j} > x + q_{t,i+j}$$

$$(5) \quad x + q_{t,i+j} > p_{t-1,i} > x \quad \text{and} \quad x + q_{t,i+j} > p_{t-1,j} > x$$

$$(6) \quad x + q_{t,i+j} > p_{t-1,i} > x \quad \text{and} \quad p_{t-1,j} \leq x$$



$$(7) \quad p_{t-1,i} \leq x \quad \text{and} \quad p_{t-1,j} > x + q_{t,i+j}$$

$$(8) \quad p_{t-1,i} \leq x \quad \text{and} \quad x + q_{t,i+j} > p_{t-1,j} > x$$

$$(9) \quad p_{t-1,i} \leq x \quad \text{and} \quad p_{t-1,j} \leq x.$$

For starting conditions 1, 2, and 3:

$$c_{t,i} = q_{t,i+j} \quad \text{and} \quad c_{t,j} = 0.$$

For starting condition 4:

$$\text{if } p_{t,i} - x \geq q_{t,i+j} \quad \text{then } c_{t,i} = q_{t,i+j} \quad \text{and} \quad c_{t,j} = 0$$

$$\text{if } p_{t,i} - x < q_{t,i+j} \quad \text{then } c_{t,i} = p_{t,i} - x \quad \text{and} \quad c_{t,j} = q_{t,i+j} - (p_{t,i} - x)$$

For starting condition 5:

$$\text{if } p_{t,i} - x \geq q_{t,i+j} \quad \text{then } c_{t,i} = q_{t,i+j} \quad \text{and} \quad c_{t,j} = 0$$

$$\text{if } p_{t,i} - x < q_{t,i+j} \quad \text{and} \quad (p_{t,i} - x) + (p_{t,j} - x) \geq q_{t,i+j}$$

$$\text{then } c_{t,i} = p_{t,i} - x \quad \text{and} \quad c_{t,j} = q_{t,i+j} - (p_{t,i} - x)$$

$$\text{if } p_{t,i} - x < q_{t,i+j} \quad \text{and} \quad (p_{t,i} - x) + (p_{t,j} - x) < q_{t,i+j} \quad \text{then}$$

$$c_{t,i} = (p_{t,i} - x) + \frac{1}{2}(q_{t,i+j} - ((p_{t,i} - x) + (p_{t,j} - x))) \quad \text{and}$$

$$c_{t,j} = (p_{t,j} - x) + \frac{1}{2}(q_{t,i+j} - ((p_{t,i} - x) + (p_{t,j} - x)))$$

For starting condition 6:

$$\text{if } p_{t,i} - p_{t,j} \geq q_{t,i+j} \quad \text{then } c_{t,i} = q_{t,i+j} \quad \text{and} \quad c_{t,j} = 0$$

$$\text{if } p_{t,i} - p_{t,j} < q_{t,i+j} \quad \text{then}$$

$$c_{t,i} = (p_{t,i} - x) + (x - p_{t,j}) + \frac{1}{2}(q_{t,i+j} - ((p_{t,i} - x) + (x - p_{t,j}))) \quad \text{and}$$

$$c_{t,j} = \frac{1}{2}(q_{t,i+j} - ((p_{t,i} - x) + (x - p_{t,j})))$$

For starting condition 7:

$$c_{t,i} = 0 \quad \text{and} \quad c_{t,j} = q_{t,i+j}$$

For starting condition 8:

$$\text{if } p_{t,j} - p_{t,i} \geq q_{t,i+j} \quad \text{then } c_{t,i} = 0 \text{ and } c_{t,j} = q_{t,i+j}$$

$$\text{if } p_{t,j} - p_{t,i} < q_{t,i+j}$$

$$\text{then } c_{t,i} = \frac{1}{2}(q_{t,i+j} - (p_{t,j} - p_{t,i})) \text{ and } c_{t,j} = p_{t,j} - p_{t,i} + \frac{1}{2}(q_{t,i+j} - (p_{t,j} - p_{t,i}))$$

For starting condition 9:

$$\text{if } p_{t,i} \geq p_{t,j} \text{ and } p_{t,i} - p_{t,j} \geq q_{t,i+j} \quad \text{then } c_{t,i} = q_{t,i+j} \text{ and } c_{t,j} = 0$$

$$\text{if } p_{t,i} \geq p_{t,j} \text{ and } p_{t,i} - p_{t,j} < q_{t,i+j} \quad \text{then}$$

$$c_{t,i} = p_{t,i} - p_{t,j} + \frac{1}{2}(q_{t,i+j} - (p_{t,i} - p_{t,j})) \text{ and } c_{t,j} = \frac{1}{2}(q_{t,i+j} - (p_{t,i} - p_{t,j}))$$

$$\text{if } p_{t,j} > p_{t,i} \text{ and } p_{t,j} - p_{t,i} \geq q_{t,i+j} \quad \text{then } c_{t,i} = 0 \text{ and } c_{t,j} = q_{t,i+j}$$

$$\text{if } p_{t,j} > p_{t,i} \text{ and } p_{t,j} - p_{t,i} < q_{t,i+j} \quad \text{then}$$

$$c_{t,i} = \frac{1}{2}(q_{t,i+j} - (p_{t,j} - p_{t,i})) \text{ and } c_{t,j} = p_{t,j} - p_{t,i} + \frac{1}{2}(q_{t,i+j} - (p_{t,j} - p_{t,i}))$$

## REFERENCES

- P.M. Allen and J.M. McGlade [1986], *Dynamics of discovery and exploitation: The case of the Scotian Shelf groundfish fisheries*, *Canad. J. Fish. Aquat. Sci.* **43**, 1187-1200.
- P.M. Allen and J.M. McGlade [1987], *Modelling complex human systems: A fisheries example*, *European J. Operational Research* **30**, 147-167.
- F.P. Almeida [1987], *Stock definition of silver hake in the New England-Middle Atlantic area*, *N. Am. J. Fisheries Management* **7**, 169-186.
- R.J.H. Beverton and S.J. Holt [1957], *On the dynamics of exploited fish populations*, U.K. Minist. Agric. Fish. Food (Lond.) Fish. Invest. **19**, 533 pp.
- H.E. Booke [1981], *The conundrum of the stock concept—are nature and nurture definable in fishery science?* *Canad. J. Fish. Aquat. Sci.* **38**, 1479-1480.
- R.M. Brunch [1985], *Characteristics of the yellow perch population in southwestern Lake Michigan*, Programs and Abstracts of the 28th Conference on Great Lakes Research, University of Wisconsin-Milwaukee, June 3-5, 1985, p. 31.

- L. Fahrig [1991a], *Evaluation of stock protection strategies based on areal quotas*, International Council for the Exploration of the Sea C.M. 1991/D:36.
- L. Fahrig [1991b], *Simulation methods for developing general landscape-level hypotheses of single-species dynamics*, in *Quantitative methods in landscape ecology* (M.G. Turner and R.H. Gardner, eds.), Springer-Verlag, New York, 417-442.
- L. Fahrig and D.B. Atkinson [1991], *Uncertainty in a mixed stock fishery: A redfish simulation study*, NAFO Studies **16**, 25-37.
- D.J. Futuyma [1979], *Evolutionary biology*, Sinauer, Sunderland, MA.
- W.M. Getz, R.C. Francis and G.L. Swartzman [1977], *On managing variable marine fisheries*, Canad. J. Fish. Aquat. Sci. **44**, 1370-1375.
- A.J. Gharett, C. Smooth, A.J. McGregor and P.B. Holmes [1988], *Genetic relationships of even-year northwestern Alaskan pink salmon*, Trans. Am. Fish. Soc. **117**, 536-545.
- L.P. Hansen and T.B. Lea [1982], *Tagging and release of Atlantic salmon smolts (Salmo salar L.) in the River Rana, northern Norway*, Rep. Inst. Freshwat. Res., Drottningholm **60**, 31-38.
- R. Hilborn [1985a], *Apparent stock recruitment relationships in mixed stock fisheries*, Canad. J. Fish. Aquat. Sci. **42**, 718-723.
- R. Hilborn [1985b], *Spatial models of tuna dynamics in the western Pacific: Is international management necessary? in Modeling and management of resources under uncertainty* (T.L. Vincent, Y. Cohen, W.J. Grantham, G.P. Kirkwood and J.M. Skowronski, eds.), Lecture Notes in Biomathematics **72**, Springer-Verlag, New York, 276-286.
- R. Hilborn [1989], *Beyond the unit stock: Adding spatial representation to fisheries models*, in *Natural resource modelling and analysis* (A.T. Charles and G.N. White, eds.), Proceedings of the First Interdisciplinary Conference on Natural Resource Modelling and Analysis, Centre for Resource Systems Analysis, Halifax, NS, Canada, 19-22.
- R. Hilborn and C.J. Walters [1987], *A general model for simulation of stock and fleet dynamics in spatially heterogeneous fisheries*, Can. J. Fish. Aquat. Sci. **44**, 1366-1369.
- A.S. Hourston [1982], *Effects of the number of years tagged fish were at large on homing to British Columbia herring management units*, Canad. Tech. Rep. Fish. Aquat. Sci. No. **1056**.
- P.E. Ihssen, H.E. Booke, J.M. Casselman, J.M. McGlade, N.R. Payne and F.M. Utter [1981], *Stock identification: Materials and methods*, Canad. J. Fish. Aquat. Sci. **38**, 1838-1855.
- J.A. Koslow [1989], *Managing nonrandomly varying fisheries*, Canad. J. Fish. Aquat. Sci. **46**, 1302-1308.
- H.E. Kumpf (ed.) [1987], *Proceedings of the stock identification workshop*, November 5-7, 1985, Panama City Beach, Florida, NOAA Tech. Memo.: NOAA-TM-NMFS-SEFC199.
- S. Marshall, D. Bernard, R. Conrad, B. Cross, D. McBride, A. McGregor, S. McPherson, G. Oliver, S. Sharr and B. Van Alen [1987], *Application of scale patterns analysis to the management of Alaska's sockeye salmon (Oncorhynchus nerka) fisheries*, Canad. Spec. Pub. Fish. Aquat. Sci. **96**, 307-326.

T.J. Mulligan and R.W. Chapman [1986], *Stock identification on white perch, Morone americana, based on mitochondrial DNA analysis*, ICES Council Meeting 1986 (Collected papers): ICES-CM-1986/M:20.

E.L. Nakamura [1987], *MEXUS-Gulf coastal pelagic fish research 1977-84*, Mar. Fish. Rev. **49**, 36-38.

T. Polachek [1990], *Year around closed areas as a management tool*, Natural Resource Modeling **4**, 327.

J.H. Selgeby [1982], *Decline of lake herring (Coregonus artedii) in Lake Superior: An analysis of the Wisconsin herring fishery, 1936-78*, Canad. J. Fish. Aquat. Sci. **39**, 554-563.

P.J. Smith and R.I.C.C. Francis [1982], *A glucosephosphate isomerase polymorphism in New Zealand ling (Genypterus blacodes)*, Comp. Biochem. Physiol. B **73B**, 451-455.

W. Templeman [1989], *Variation of vertebral numbers with fish length in Atlantic cod (Gadus morhua) of the eastern Newfoundland area, 1947-71*, J. Northwest Atlan. Fish. Sci. **9**, 45-52.

F. Thurow [1985], *Wohin wandern die Ostseedorsche?* Inf. Fischwirtsch **32**, 9-14.