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Abstract: Different age classes do not generally experience the same rates of fishing mortality. The processes resulting in age- (or length-) selection operate at several scales. At the broadest scale, population-selection measures the age-specific probability of capture, while at the finest scale contact-selection describes the vulnerability of fish that encounter the fishing gear. Population-selectivity is the process most relevant to fish population dynamics and stock assessment, but it has received far less attention than processes operating at gear-specific scales. Despite wide recognition of the diverse shapes possible for population-selectivity, the processes determining these shapes are poorly understood. This paper develops a reasonably simple model of population-selectivity from a set of survival equations, coupled to allow movement between subpopulations, and explores the conditions necessary to produce different shaped population-selection curves. Important factors influencing the population-selectivity model are the gear-specific selection characteristics of the fleets, their effort levels relative to one another, the spatial distribution of fishing mortality, and the movement of fish between subpopulations. The model can generate quite complicated curves and has surprising properties. For example, under a wide variety of conditions, even though the same asymptotic gear-selectivity applies in all subpopulations, the overall population-selectivity will be dome-shaped unless fishing mortality is uniform across all subpopulations.

Résumé : Les différentes classes d'âge ne subissent généralement pas les mêmes taux de mortalité due à la pêche. Les processus qui expliquent la sélection en fonction de l'âge (ou de la taille) agissent à plusieurs échelles. À l'échelle la plus large, la sélection de la population décrit la probabilité de capture spécifique à l'âge et, à l'échelle la plus fine, elle représente la vulnérabilité des poissons à la rencontre des engins de pêche. La sélectivité de la population est le processus le plus pertinent pour la dynamique de population et l'évaluation des stocks de poissons, mais elle a été beaucoup moins étudiée que les processus qui agissent aux échelles spécifiques aux engins de pêche. Bien que l'on reconnaisse qu'il existe diverses formes de courbes possibles de sélectivité de la population, les processus qui déterminent ces formes restent mal compris. Notre travail met au point un modèle relativement simple de sélectivité de la population à partir d'un ensemble d'équations de survie, couplées de manière à permettre des déplacements entre les sous-populations, et explore les conditions nécessaires pour la production des différentes formes de courbes de sélection de la population. Les facteurs importants qui influencent le modèle de sélectivité de la population sont les caractéristiques spécifiques de sélection des flottes de pêche en fonction des engins, les niveaux d'effort de pêche des flottes les unes par rapport aux autres, la répartition spatiale de la mortalité due à la pêche et les déplacements des poissons entre les sous-populations. Le modèle peut produire des courbes assez complexes et il possède des propriétés plutôt étonnantes. Par exemple, sous une large variété de conditions et bien que la même courbe asymptotique de sélectivité de l'engin de pêche s'applique à toutes les sous-populations, la sélectivité globale de la population aura une courbe en forme de dôme à moins que la mortalité due à la pêche ne soit uniforme dans toutes les sous-populations.

[Traduit par la Rédaction]

Introduction

A feature common to most types of fishing gear is that they are not uniformly effective at capturing the full spectrum of length classes of fish present in a population. Most fishing processes deliberately try to catch big fish that produce larger per-recruit yields and command higher prices. Small fish are under-represented in the catches either because these fish are able to escape from the gear or because the gear is deployed in areas where small fish are less prevalent. This phenomenon of fishing effectiveness varying with the size of the fish is generally described as selection or selectivity (Bever-

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ton and Holt 1957; Quinn and Deriso 1999). Because fish generally increase in length as they age, the processes that result in selection by size also produce selection by age. The term "selective fishing" is also used to describe the ability of fishing operations to target certain fish species and avoid the incidental bycatch of species that have special legal status (e.g., trawl-caught halibut in Alaska; Rose and Gauvin 2000) or that require protection from fishing because of low levels of abundance (e.g., Hannah et al. 2005; Madsen et al. 2006). The study here focuses on the first form of selectivity, namely for different ages (or sizes) from a single target species.

Millar and Fryer (1999) distinguish between three types of length-selection curves. The population-selection curve measures the probability that a fish of a given length in the population is captured; the available-selection curve measures the probability that a fish of a given length is captured when it is available to the gear (e.g., in the path of a trawl); and the contact-selection curve, which they also describe as the retention curve, measures the probability that a fish of a given length is captured when it comes in contact with the gear. The three types of curves differ with regard to the spatial scales over which they operate, with population-selection acting on the broadest scale and contact-selection acting at the finest scale. The population-selection process is the one most relevant to fish population dynamics and stock assessment (Nedreaas et al. 1996; Sun et al. 2002).

Most of the myriad of published studies on selectivity have focused on measuring contact-selection curves (e.g., Pope et al. 1975; Wileman et al. 1996) or understanding factors that influence this relationship (e.g., Dahm et al. 2002). There have been a few published studies that have attempted to measure and understand factors influencing available-selection curves (e.g., Engås and Godø 1986; Somerton et al. 1999). The focus of the current study is the population-selection curve, which measures the size- or age-dependent fishing mortality experienced by a fish population. Our analysis does not distinguish between available-selection and contact-selection. Instead we make a distinction between population-selection versus gear-selection, with the second form encompassing both available-selection and contact-selection. Fundamental to our model is the division of the fish population into subpopulations that occupy distinct spatial regions. Gear-selection operates at the level of these subpopulations. Also, our analysis focuses on age-based selection and ignores the added complexity that is required to account for variability in length at age (e.g., Quinn and Deriso 1999; Punt et al. 2002).

Materials and methods

In an age-structured model for fish population dynamics, when the instantaneous rate of fishing mortality (F) during a year (or other suitable time step) is not the same for all age classes, so that fishing mortality is age-dependent, the selection (or selectivity) coefficients measure the relationship between age a and F_a, after standardization to account for year-to-year changes in the overall rate of fishing. The set of points (a, F_a) is often represented by a smooth curve passing through all the points. If the F_a values are uniform across all age classes, then the selection curve is a horizontal line and we can state that there is no selectivity. If the selection coefficients increase with age to a plateau, we can describe the selection curve as being asymptotic. If the selection coefficients increase to a maximum and then decline, we can describe the selection curve as being domed or dome-shaped. Although this concept of a selection curve implies that selectivity is a continuous function of age, selection curves are commonly used with data that have been discretized into age or length classes.

The mathematical definition of selectivity differs across regions. On the Pacific side of North America the F_a values within a year are usually standardized into selection coefficients by dividing each F_a value by the maximum value observed for any age class in that year (e.g., Deriso et al. 1985). In Europe and on the Atlantic side of North America the F_a values are usually standardized by dividing by the average (called $\overline{F}$) of the F_a values observed over a defined range of age classes (e.g., Darby and Flatman 1994). In stock assessment and fishery population dynamics models, the individual F_a values for a given year (y) are recovered by multiplying the selection coefficient with that year's maximum F_a or $\overline{F}$ value, as in

$$F_{a,y} = \max(F_{a,y})S_a \quad \text{or} \quad F_{a,y} = \overline{F}_y S_a$$

If selectivity in the model varies from year to year, then the selection coefficients (S_a) would include an index for the year ($S_{a,y}$). These selection coefficients define the population-selection curve.

Simplified spatial model for population age structure

To explore the role of the population-selection curve in fish population dynamics, consider the population to be partitioned into distinct subpopulations occupying discrete spatial regions (indexed by r), with some limited exchange of fish between the regions. The fish within each region all suffer the same instantaneous rate of natural mortality (M for all ages), but they potentially experience different instantaneous rates of age-specific fishing mortality ($F_{a,r} = F_r s_a$). In this formulation the gear-selection curve (s_a) is the same across all regions, but the fish in each region suffer a (potentially) different absolute level of fishing mortality. We describe the s_a values, denoted by a lower case S, as the gear-selection curve to distinguish them from the age-specific relative F values that are derived by combining the fish in the separate regions. The population-selection values (S_a, denoted by an upper case S) are a composite, weighted average of the F_a values operating in each region. The population-selection curve will be the same as the gear-selection curve only under special circumstances (below).

If the population is exploited by several types of fishing gear that differ in their gear-selection characteristics, then each gear type would have its own selection curve ($s_{a,\text{gear}}$), and we would partition the age-specific, instantaneous rates of fishing mortality accordingly. For now we assume that all gear types have the same gear-selection curve.

To keep the notation and mathematics relatively simple, we use the standard exponential decay equation to represent the mortality processes operating within each region during a year (or other unit time step). At the end of each year, the fish mix instantaneously among the regions. Further, we consider only the equilibrium situation in which recruitment to each region and the rates of fishing mortality within each region are constant from year to year. The assumption of constant recruitment could be relaxed, but in this case the equations below apply to the age classes in a single year class, and the variable for abundance should have a subscript for year as well as age and region. The equilibrium assumption avoids this notational complication.

For each age class a, the number of living fish at the start of each year within region $r = i$ is given by

$$\begin{aligned}(1)\qquad N_{a,i} = {} & N_{a-1,i}\exp\left(-M - F_i s_{a-1}\right)\left(1 - \sum_{i \neq j} P_{j,i}\right) \\ & + \sum_{i \neq j} N_{a-1,j}\exp\left(-M - F_j s_{a-1}\right)P_{i,j}\end{aligned}$$

The coefficient $P_{j,i}$ denotes the proportion of fish that move into region j from region i. The first term in the right-hand side of eq. 1 represents the individuals in the focal region i at the start of the year that survive and remain in the region; the second term represents the individuals that move into the region from the other regions.

Mortality in this formulation is treated as a continuous process, but movement occurs abruptly (and unrealistically) at the end of each year. The equation can be viewed as an approximation to a differential equation system in which there is continuous movement of fish among regions. When the mixing rates are high and nondirectional, one can ignore the regional differences and treat the population as occupying a single region. Equations similar to eq. 1 have been used to represent spatial fish population dynamics in stock assessment models (Hampton and Fournier 2001), in models of no-take marine reserves (Apostolaki et al. 2002), and in the operating models for management strategy evaluations (e.g., Punt et al. 2002; Pelletier et al. 2009).

Equation for population-selectivity

At the population level, the number of age-a fish alive at the start of each year is given by the age-specific abundances summed over all the regions.

$$(2)\qquad N_a = \sum_r N_{a,r}$$

The population-selection coefficients are proportional to the age-specific fishing mortality coefficients for the population, which, because of the equilibrium condition, can be obtained from the ratios of successive N_a values.

$$\begin{aligned}(3)\qquad F_a &= -\ln\left(\frac{N_{a+1}}{N_a}\right) - M \\ S_a &= \frac{F_a}{\max(F_a)}\end{aligned}$$

The divisor in the equation for S_a is shown here as the maximum F_a value, but we could instead use the average F_a value ($\overline{F}$), with the average taken over some suitable age range.

By substituting the right-hand side of eq. 1 into eqs. 2 and 3, we can derive a messy equation that relates population-selectivity with gear-selectivity.

$$(4)\qquad S_a = \frac{-\ln\left\{\dfrac{\displaystyle\sum_i\Big[N_{a,i}\exp(-Z_{a,i})\Big(1 - \sum_{i\neq j}P_{j,i}\Big) + \sum_{i\neq j}N_{a,j}\exp(-Z_{a,i})P_{i,j}\Big]}{\displaystyle\sum_i\Big[N_{a-1,i}\exp(-Z_{a-1,i})\Big(1 - \sum_{i\neq j}P_{j,i}\Big) + \sum_{i\neq j}N_{a-1,j}\exp(-Z_{a-1,j})P_{i,j}\Big]}\right\} - M}{\max\left(F_a\right)}$$

Here the gear-selection coefficients (s_a) are embedded in the age- and region-specific total mortality coefficients, $Z_{a,r} = M + F_r s_a$.

The above model for population-selectivity has no provision for a plus-group, which is an accumulator class for all the ages greater than some reference age. Stock assessment models commonly use a plus-group to reduce the number of age categories that must be accounted for. This simplification assumes that the vital rates for these older age classes are sufficiently similar that they can be treated in the aggregate with inconsequential loss of accuracy. The underlying mathematical equation for plus-group abundance follows from

$$\begin{aligned}N_{a+} &= \sum_{i=a}^{\infty} N_i = N_a + N_a\theta + N_a\theta^2 + N_a\theta^3 + \ldots \\ &= \frac{N_a}{1-\theta}\end{aligned}$$

where θ is the annual survival fraction, assumed constant for all ages equal to a or greater. In the model for population-selectivity, one cannot apply a similar approach unless one assumes that there is no movement of fish among the different regions. When there is movement of fish among regions, the abundance for a given region at the start of an age class depends not only on the survivors from that region but also on the survivors from other regions.

The population-level fishing mortality and selection coefficients satisfy the catch equation for the population.

$$C_a = N_a\frac{FS_a}{Z_a}\left[1 - \exp(-Z_a)\right]$$

where $Z_a = M + FS_a$. Similarly, for each region the region-level fishing mortality and selection coefficients satisfy a region-level catch equation.

$$C_{a,r} = N_{a,r}\frac{F_r s_a}{Z_{a,r}}\left[1 - \exp(-Z_{a,r})\right]$$

where $Z_{a,r} = M + F_r s_a$. These equations are just extensions to the calculation of effective fishing mortality described in Beverton and Holt (1957).

From eq. 4 it is difficult to discern the behavior of the population-selection curve because each S_a value is the logarithm of the ratio of two sums of exponentials. However, for a certain special case this defining equation can be greatly simplified. Before considering this case, we first determine the general conditions required to produce a decreasing (or increasing or constant) sequence of population-selection coefficients.

Conditions for dome-shaped population-selection curves

The population-selection coefficients are just scaled F_a values and will decrease (or increase) with age if the F_a values for adjacent age classes are decreasing (or increasing). Population-selectivity is decreasing if and only if the following conditions are satisfied:

$$(5)\qquad F_{a+1} = -\ln\left(\frac{N_{a+2}}{N_{a+1}}\right) - M < F_a = -\ln\left(\frac{N_{a+1}}{N_a}\right) - M$$

$$N_{a+2}\,N_a > (N_{a+1})^2$$

Assuming that selectivity is smallest for the youngest age classes, if inequality condition 5 is satisfied for at least one age class, then the population-selection curve will be dome-shaped or will have a local maximum at an intermediate age. If condition 5 is not satisfied for any age class, then the population-selection curve will be strictly increasing, or increasing and then horizontal, or just horizontal. The population-selection coefficients will be the same for adjacent age classes (a, a+1) if and only if $N_{a+2}\,N_a = (N_{a+1})^2$.

Direct substitution of the general equations for N_a, N_{a+1}, and N_{a+2} into condition 5 produces a very untidy expression that appears intractable, but useful results can be obtained for the simpler problem in which there is no movement of fish between the regions ($P_{j,i} = 0$ for all regions j and i) and the gear-selection coefficients are the same for the three adjacent age classes ($s_a = s_{a+1} = s_{a+2} = s$). In this special case, it is shown in Appendix A that condition 5 reduces to the following:

$$(6)\qquad \sum_{i\neq j} N_{a,i}\,N_{a,j}\exp(-2M)[\exp(-F_i s) - \exp(-F_j s)]^2 > 0$$

Because M is always nonnegative, the initial exponential term in eq. 6 is positive for all combinations of regions, and the condition will be satisfied except when the final squared term is zero, which occurs if $F_i = F_j$ for all i and j, or in the limit as the F_i go to zero. That is, even though the gear-selection curve is flat for some set of age classes, the population-selection curve for those same age classes will also be flat only if the same rate of fishing mortality is applied in all regions or if the rates of fishing mortality are vanishingly small. Otherwise the population-selection curve for this set of age classes will be declining; the population-selection curve will be dome-shaped. Also, from condition 6 it is evident that the degree of difference among the regional F values controls how much the population-selection curve departs from flat selection. The greater the differences among the F values, the more pronounced the domed shape.

Composite gear-selectivity from multiple gear types operating in the same region

When different types of fishing gear, with differing selectivity characteristics, operate together in some region r, then the overall age-specific fishing mortality for the fish in that region will be the summation of the age-specific fishing mortality rates produced by each gear type.

$$(7)\qquad F_{a,r} = F_{r,\text{gear.1}}\cdot s_{a,\text{gear.1}} + F_{r,\text{gear.2}}\cdot s_{a,\text{gear.2}} + \ldots$$

These composite $F_{a,r}$ values substitute for the $F_r s_a$ terms in eq. 1. The composite gear-selection coefficients for region r are obtained from successive values of $N_{a,r}$.

$$(8)\qquad F_{a,r} = -\ln\left(\frac{N_{a+1,r}}{N_{a,r}}\right) - M$$

$$s_{a,r} = \frac{F_{a,r}}{\max(F_{a,r})}$$

The gear-selection curve for the region is a weighted average of the different individual gear-selection curves and is directly influenced by the relative amounts of fishing mortality produced by the different gear types.

Exploring the shape of population-selectivity curves

To explore the possible shapes of population-selection curves we developed a spreadsheet model[1] that implements eq. 4 for three regions, 15 age classes, M = 0.2 year^{-1}, 3000 recruits annually, and logistic curves for gear-selectivity. We considered a series of four scenarios in which all regions have the same gear-selection curve but have different conditions for fish movements, the rate of fishing mortality, and the number of recruits.

In scenario 1, the simplest case, there is no movement of fish between regions and the initial recruitment is uniform across the regions. This is an idealized situation that might be realistic for some sessile organisms, but probably it is unrealistic for most fish species. It corresponds to the circumstances that produced condition 6, which indicated that selectivity is domed unless the rates of fishing mortality in the regions are all equal or are vanishingly small. We used the spreadsheet model to generate population-selectivity curves for situations where the rate of fishing mortality in region 1 is twice the level in region 2, which is twice the level in region 3. In case A the F values are (0.4, 0.2, 0.1); in case B they are (0.08, 0.04, 0.02), smaller by a factor of five.

Scenario 2 is similar to scenario 1 in that recruitment is spread uniformly, but there is symmetric dispersion of fish between the regions at a rate of 5%·year^{-1}. We considered two cases that differ in the regional fishing rates. In case A the F values are (0.4, 0.2, 0.1), as in case A of scenario 1; in case B they are (0.4, 0.2, 0.0), to mimic the effect of a no-take reserve in region 3.

Scenario 3 uses the same set of parameters as case A of scenario 2, but the regional distribution of recruits is no longer uniform. Instead they are distributed to regions as (1500, 1000, 500). Again, we considered two cases that differ in the regional fishing rates. In case A the F values are (0.4, 0.2, 0.1), as in case A of scenarios 1 and 2; in case B they are reversed (0.1, 0.2, 0.4).

In scenario 4, which is the most complex one that we considered, all the recruits begin in region 1 and gradually disperse (5%·year^{-1}), first into region 2 and then into region 3.

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[1] Supplementary data are available with the article through the journal Web site (http://nrcresearchpress.com/cjfas).

This form of slow directional movement results in differences in the regional age distributions, with higher than average numbers of young fish in region 1 and higher than average numbers of old fish in region 3. It is a simple modeling trick for mimicking ontogenetic movement of the fish, for example from nearshore nursery areas to different grounds where adults are found. Again, we considered two cases that differed in the regional fishing rates. In case A the *F* values are (0.4, 0.2, 0.1), as in case A of scenarios 1, 2, and 3; in case B they are reversed (0.1, 0.2, 0.4).

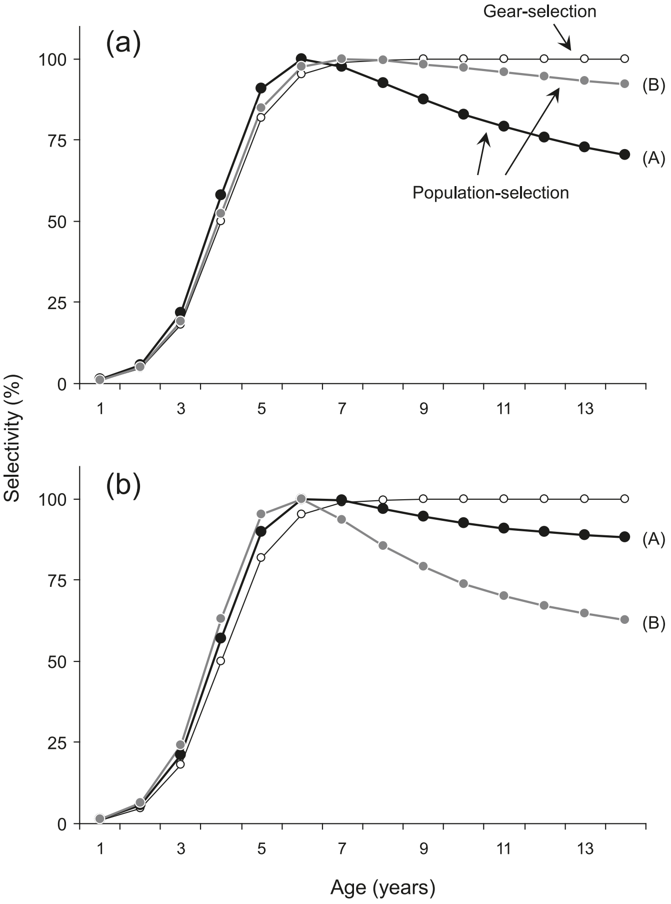
In addition to the four scenarios described above, in which there was a single asymptotic gear-selection curve, we also explored the possible shapes of population-selection when there are two distinct gear-selection curves. For scenario 5 the model was configured identically to case A of scenario 2 except that the gear-selection curves for regions 2 and 3 were shifted to the right by four age units. This mimics conditions in a fishery for which there is spatial segregation of two distinct gear types (e.g., small-mesh versus large-mesh trawls). Further, we adapted the spreadsheet model to explore composite gear-selection curves based on modifications to eq. 4 that incorporated eqs. 7 and 8. Scenario 6 was configured identically to scenario 5 except that region 2 had a composite gear-selection curve that was a 50:50 mixture of the two asymptotic gear-selection curves that were applied separately in regions 1 and 3, thus mimicking a situation where there is partial spatial segregation of two gear types.

Results

The model for population-selectivity has four main types of parameters: the set of regional fishing mortality coefficients, the set of spatial movement coefficients, the spatial distribution of the recruits, and the curve (or curves) for gear-selection. With the spreadsheet version of the model, we explored the influence of these parameters. Scenario 1 examined the effect of changing the scale of the fishing mortality coefficients (Fig. 1*a*). The fivefold reduction in the *F* values caused a considerable reduction in the magnitude of the domed shape. Further reductions in the *F* values (not shown in a figure) caused the population-selection curve to become increasingly similar to the underlying gear-selection curve. When the regional *F* values were all equal (to any positive value), then the population-selection curve was identical to the common asymptotic gear-selection curve, as predicted by condition 6.

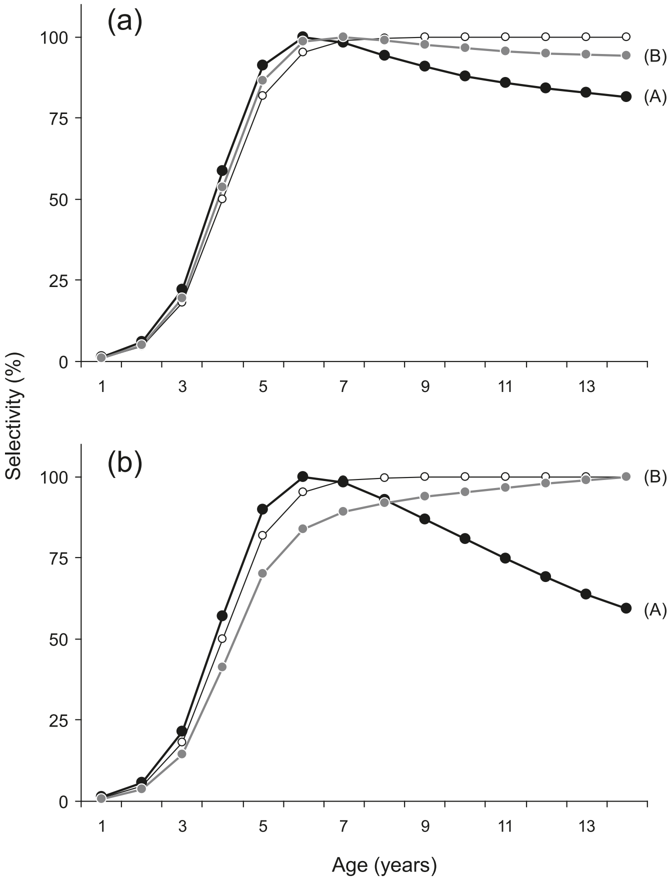
Scenario 2 explored the effect of eliminating fishing in a single region (Fig. 1*b*) and, when compared with case A of Fig. 1*a*, the effect of nondirectional spatial dispersion. When there was no fishing in region 3, the domed shape of the population-selection curve became more exaggerated (Fig. 1*b*, line B). If fishing was eliminated from either of the other regions (not shown in a figure), the population-selection curves had a similar shape but with a less pronounced dome. Regarding the effect of dispersion, the population-selection curve was less pronounced when there was dispersion (Fig. 1*b*, line A) than when there was no dispersion (Fig. 1*a*, line A). As with scenario 1, the population-selection curve was identical to the gear-selection curve if $F_1 = F_2 = F_3$. This result is consistent with condition 6 even though the derivation of that condition was based on the assumption of no fish movements between regions.

Fig. 1. Population-selection curves generated by a three-region spreadsheet model with differing instantaneous rates of fishing mortality in each region. All regions have the same asymptotic gear-selection curve, shown by the thin line with small open circles. In the upper panel (*a*), there is no movement of fish between regions and fish recruit equally to each region. In case A, shown by the thick, black line with larger solid circles, the regional rates of fishing mortality are (0.4, 0.2, 0.1); in case B, shown by the grey line with grey solid circles, they are (0.08, 0.04, 0.02), smaller than in case A by a factor of five. In the lower panel (*b*), there is symmetric dispersion of fish between regions at a rate of 5%·year^{-1}. In case A, shown by the thick, black line with larger solid circles, the regional rates of fishing mortality are (0.4, 0.2, 0.1), the same as in case A in the upper panel. In case B, shown by the grey line with grey solid circles, the *F* values are (0.4, 0.2, 0.0), to mimic the effect of a no-take reserve in region 3.



Scenario 3 explored the effect of the spatial distribution of fishing relative to the spatial distribution of the recruits (Fig. 2*a*). Population-selectivity had the strongest domed shape in case A in which the rates of fishing were almost proportional to the recruit values. Relative to case A of Fig. 1*b*, in which the recruits were evenly distributed, the population-selectivity curve had a more pronounced dome (Fig. 2*a*, line A). As with scenarios 1 and 2, the population-selection curve was identical to the gear-selection curve if $F_1 = F_2 = F_3$.

Fig. 2. Population-selection curves generated from nonuniform regional distribution of the recruits, but otherwise with similar conditions as in Fig. 1*b*, case A. Here in the upper panel (*a*), the recruits are distributed to regions as (1500, 1000, 500). In case A, shown by the thick, black line with larger solid circles, the *F* values are (0.4, 0.2, 0.1), as in the A cases in Figs. 1*a* and 1*b*. In case B, shown by the grey line with grey solid circles, the *F* values are reversed (0.1, 0.2, 0.4). In the lower panel (*b*), there is directional movement of fish with all the fish recruiting to region 1 and spreading to region 2 and then to region 3 at a rate of 5%·year^{-1}. In case A, shown by the thick, black line with larger solid circles, the *F* values are (0.4, 0.2, 0.1), as in the A cases in Figs. 1*a*, 1*b*, and 2*a*. In case B, shown by the grey line with grey solid circles, the *F* values are reversed (0.1, 0.2, 0.4).



In scenario 4 there was unidirectional dispersion of the fish from region 1 to region 2 to region 3. For case A, in which the rate of fishing mortality was highest in the region that received all the recruits, the population-selection was strongly dome-shaped (Fig. 2*b*, line A); more highly domed than observed in any of the other scenarios we examined. However, in the contrasting case B, in which *F* was lowest in the region receiving the recruits, the population-selection curve took on a form that was neither domed nor asymptotic. It was continuously increasing with peak selection at the oldest age considered in the model. Of all the situations we explored, this was the only case that generated a population-selection curve that was not dome-shaped.

The population-selection curves produced under scenarios 2, 3, and 4 differed in their sensitivity to the value chosen for the movement parameter. When movement was increased to 10%·year^{-1} (not shown in a figure), the curves in scenarios 2 and 3 became markedly less dome-shaped, whereas the domed curve in scenario 4 (case A) became more dome-shaped and the strictly increasing curve (case B) became less curved. To understand these phenomena, consider that nondirectional fish movements, as in scenarios 2 and 3, tend to break down differences in age structure among the spatial subpopulations, with the result that population-selectivity tends to revert to the underlying gear-selectivity. In contrast, directional fish movement, as in scenario 4, accentuates differences in the age structure among the subpopulations, which results in increased divergence between the population-selection and gear-selection curves.

At first glance it seems strange that the population-selection curve, under most circumstances, could be dome-shaped when the underlying gear-selection curves have a strictly asymptotic form. However, the mechanism producing this result becomes clearer if one considers the age-specific fishing mortality curves in the individual regions. For example, the asymptotic F_a curves for two regions with $F = 0.4$ in one region and $F = 0.1$ in the other region are shown (Fig. 3), similar to the configuration in case A of scenario 1. The F_a curve for the population is intermediate between the F_a curves for the two regions. The population-level F_a curve must lie between the regional F_a curves. The higher rate of fishing mortality in the one region results in higher catches of young fish, decreased abundance and catches of older fish in this region, and a reduced contribution to the population-level F_a curve. Thus the population F_a curve is dominated at young ages by the upper F_a curve, but gradually shifts with age to being dominated by the lower F_a curve; it therefore takes on a domed shape. Of course, if there is rapid diffusion of fish among the regions, then the spatial age structuring evaporates and the population-selection curve reverts to the underlying gear-selection curve.

Scenarios 5 and 6 explored the consequences of having more than one gear-selection curve. The simpler scenario (5), which maintained strict regional separation of the two gear types, produced a population-selection curve that had a complex form with three inflection points and an intermediate plateau (Fig. 4*a*). In the other scenario (6), there was mixing of the two gear-selection curves in region 2, so that the composite gear-selection curve for region 2 and the overall population-selection curve both had complex shapes with three inflection points (Fig. 4*b*). In both scenarios the population-selection coefficient for the last age class was less than the population-selection coefficient for the second to last age-class, suggesting that the curves would have been dome-shaped if more age classes had been included.

Discussion

In this study we developed a reasonably simple mathematical representation for population-selectivity, which measures the age-specific rates of fishing mortality experienced by an exploited fish population. The main ingredients of population-selectivity are one or more gear-selection curves, the spatial distribution of the fish, and the spatial distribution of the fishing. When there are multiple types of fishing gear with differing gear-selection curves, then the relative amounts

Fig. 3. Heuristic demonstration of why spatial averaging of asymptotic gear-selection curves results in a population-selection curve that is dome-shaped, indicated by the thick, black line with larger solid circles. Both regions have the same asymptotic gear-selection curve (not shown). The fishing mortality at age in region 1, shown by the thin solid line with open circles, is four times the fishing mortality at age in region 2, shown by the thin grey line with grey solid circles. Region 1, with its elevated rates of fishing mortality at age, contributes more young fish to the overall catch but fewer old fish because the higher F_{age} causes reduced abundance of older fish.

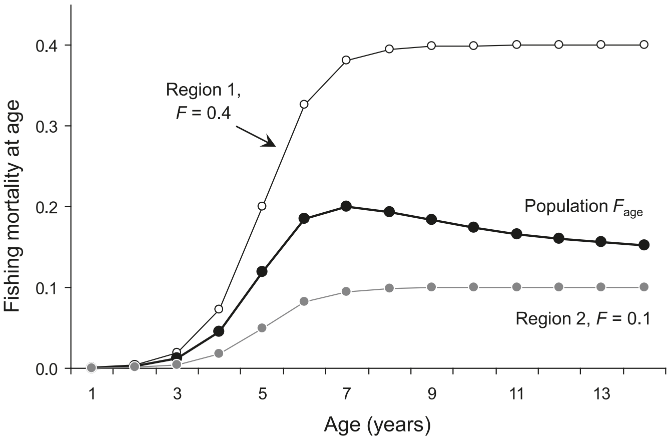
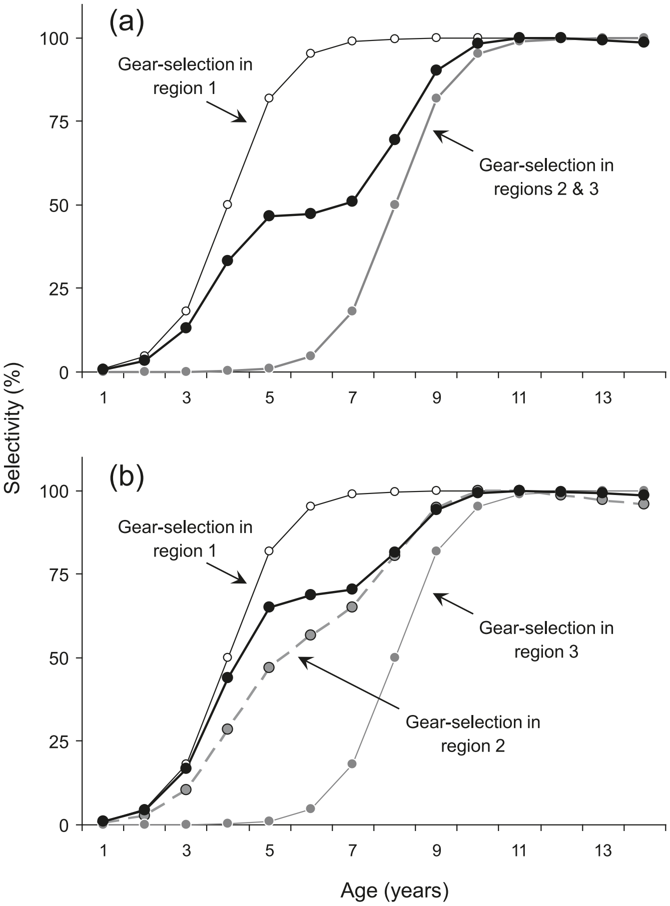


Fig. 4. Population-selection generated from composite gear-selection curves. In the upper panel (*a*) the population-selection curve, shown by the thick, black line with larger solid circles, was generated by a three-region spreadsheet model with two distinct gear-selection curves that were spatially segregated. The configuration was identical to case A in Fig. 1*b*, except that the gear-selection curves for regions 2 and 3 were shifted to the right by four age units. In the lower panel (*b*) the population-selection curve (shown by the thick, black line with larger solid circles) was generated from similar conditions as in panel (*a*), but in region 2 there was 50:50 mixing of the two asymptotic gear-selection curves.



of fishing by the different gear types are an additional influential factor. We demonstrated that this simple model for population-selectivity can generate curves with quite complicated shapes. One emergent property of the model, which we were very surprised to discover, was the capability for completely flat gear-selectivity to generate population-selectivity that decreases with age. We think it extraordinary that the simple mechanism of unevenly distributed fishing mortality will produce domed selectivity over a wide range of circumstances provided the fish population is spatially structured.

Although the population-selectivity model is an equilibrium model that does not directly describe the dynamics of selectivity, one can deduce that the population-selection curve will change with time as the distribution of fishing changes and the fish population consequently undergoes a transition from one steady state to another. As an extreme example, consider what happens in a fishery similar to the one modeled in scenario 4, where there is slow directional movement of the fish between regions. If the regional rates of fishing mortality are all equal, then the population-selection curve will have the same form as the asymptotic gear-selection curve. However, if there was an abrupt change in the distribution of fishing similar to what was modeled in case A, with a higher *F* value in the region that receives all the recruitment, then the population-selection curve would undergo a transition to a domed curve as it evolved towards its new equilibrium form. If there was an additional abrupt change in the regional *F* values so that the region receiving all the recruitment now had the lowest rate of fishing, then the population-selection curve would undergo an additional transition to a strictly increasing form. That population-selection curves are sensitive to the regional distribution of fishing mortality implies that any factors causing fishing effort to redistribute in space (e.g., changes in fish prices or fishing costs; Sampson 1991) will also cause temporal changes in population-selectivity. Given that most fish stocks exhibit spatial structure and given that the spatial distribution of fishing is variable in time, it seems that having a constant population-selection curve is more likely to be an exception rather than the rule.

The population-selectivity model has important implications regarding what stock assessment models assume about selection coefficients. Because these coefficients modulate the instantaneous rate of mortality experienced by a fish stock, they play a central role in the models of stock dynamics that underlie age-structured stock assessments. In developing our model of population-selectivity, we assumed values for the gear-selection coefficients and derived the resulting population-selection coefficients. An age-structured stock assessment turns this around and estimates parameter values (possibly including the selection coefficients) from observed values of catch-at-age (or catch proportions-at-age).

Assessments based on virtual population analysis (VPA) (Gulland 1965) and its modern successors directly provide scaled estimates (F_{age}) of the population-selection coefficients. In general the VPA methods impose few constraints on selectivity. However, it is common practice to configure a VPA so that the estimates of F_{age} each year are the same for the two oldest age classes. While it may be reasonable on theoretical grounds to assume that gear-selectivity is constant for the oldest age classes (e.g., if selection is size-based and there is little change in size with age), our population-selectivity model indicates that over a wide range of conditions, flat gear-selectivity will produce declining population-selectivity unless the fishing mortality has been applied uniformly across spatial regions, which seems an unlikely event. Hence, for a wide range of general conditions, population-selectivity is probably more likely to be domed than asymptotic. It would be instructive to explore the sensitivity of VPA results to underlying assumptions about selectivity.

In contrast with VPA, assessments based on statistical catch-at-age (SCAA) methods are often applied to catch-at-age data that have been partitioned into separate matrices for two or more distinct fleets, with each fleet having its own selection curve determined by a small set of unknown parameters (Quinn and Deriso 1999). When the data are partitioned by fleet, the SCAA methods estimate gear-selection coefficients for each fleet and no estimates of population-selectivity are required. Partitioning the catch-at-age data in this manner avoids the problem of changes in population-selectivity when there are changes in the relative rates of fishing by the different fleets. SCAA models therefore do not need to account for mixtures of gear-selection curves (e.g., scenarios 5 and 6), provided the catch-at-age data have been suitably partitioned. However, SCAA models do need sufficient flexibility to account for the distortions that arise when the spatial application of fishing mortality is uneven or variable through time. A major premise in many SCAA models is that fleet-level selectivity remains constant for extended periods, except possibly for a small number of abrupt changes between periods. The validity of this assumption often remains untested. If an SCAA model assumes that selectivity is time-invariant when in fact it is changing, the resulting suite of assessment estimates can be quite badly biased (Sampson 1993). Applications of SCAA models should explore the sensitivity of their results to assumptions regarding time-invariant selection curves.

The population-selectivity model also has important implications for conducting simulation-based management strategy evaluations (MSEs), which in recent years increasingly have been used as a tool for risk evaluation and decision analysis in fisheries management (Butterworth and Punt 1999; DeOliveira et al. 2008). The MSE process uses simulation testing to investigate the expected performance of a specified management strategy given a range of plausible alternative scenarios that describe the potential dynamics of the real fishery system. The representation of the underlying fishery system is termed the operating model, and the success (or otherwise) of the MSE framework depends on the extent to which the true range of uncertainty can be identified and represented in the suite of operating models investigated. Variability in selectivity is not always explicitly considered in MSEs. Where it has been included, it has often been implemented as a randomly varying quantity based on historic observations. The possibility for temporal shifts in population-selectivity is rarely, if ever, considered. The behavior of our population-selectivity model indicates that variability in gear-specific effort levels and geographic distribution will cause changes in population-selectivity. When developing MSEs, the potential for shifts in the population selectivity should be carefully considered and where appropriate should be adequately accounted for in the operating model.

The issue of whether selectivity is asymptotic or dome-shaped is sometimes controversial in stock assessments and subsequent calculations of catch quotas (e.g., Butterworth and Rademeyer 2008). If the population-selectivity curve is highly domed, then exploitation of the oldest age classes is relatively light, with the consequence that the stock in equilibrium has a residual pool of spawning stock biomass and can therefore support higher rates of fishing. This “cryptic” biomass is unobserved in the fishery because of the low selectivity of older fish (Fonteneau 1996). If an assessment estimates that population-selectivity is domed when in fact selectivity is asymptotic, then the resulting forecasts for future total allowable catches can be much too high. If these target catches are achieved then overfishing could result. Hence there can be considerable concern when an assessment indicates a dome-shaped selection curve, especially if there are no obvious mechanisms to account for the apparent deficit of older fish in the catches. Our model for population-selectivity, however, demonstrates that across a wide range of general conditions, the simple mechanism of non-uniform fishing will tend to cause selectivity to be dome-shaped. Stock assessment scientists who assume by default that selectivity is asymptotic should reconsider the validity of such an approach.

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References

Apostolaki, P., Milner-Gulland, E.J., McAllister, M.K., and Kirkwood, G.P. 2002. Modelling the effects of establishing a marine reserve for mobile fish species. Can. J. Fish. Aquat. Sci. **59**(3): 405–415. doi:10.1139/f02-018.

Beverton, R.J.H., and Holt, S.J. 1957. On the dynamics of exploited fish populations. Fishery Investigations, London Series, **2**: 19.

Butterworth, D.S., and Punt, A.E. 1999. Experiences in the evaluation and implementation of management procedures. ICES J. Mar. Sci. **56**(6): 985–998. doi:10.1006/jmsc.1999.0532.

Butterworth, D.S., and Rademeyer, R.A. 2008. Statistical catch-at-age analysis vs. ADAPT-VPA: the case of Gulf of Maine cod. ICES J. Mar. Sci. **65**(9): 1717–1732. doi:10.1093/icesjms/fsn178.

Dahm, E., Weinbeck, H., West, C.W., Valdemarsen, J.W., and O'Neill, F.G. 2002. On the influence of towing speed and gear size on the selective properties of bottom trawls. Fish. Res. **55**(1–3): 103–119. doi:10.1016/S0165-7836(01)00301-0.

Darby, C.D., and Flatman, S. 1994. Virtual population analysis:

version 3.1 User guide. Information Technology Series, MAFF Directorate of Fisheries, Lowestoft, UK.

DeOliveira, J.A.A., Kell, L.T., Punt, A.E., Roel, B.A., and Butterworth, D.S. 2008. Managing without best predictions: the Management Strategy Evaluation framework. *In* Advances in fisheries science: 50 years from Beverton and Holt. *Edited by* A. Payne, J. Cotter, and T. Potter. Blackwell Publishing, Oxford, UK. pp. 104–134.

Deriso, R.B., Quinn, T.J., II, and Neal, P.R. 1985. Catch at age analysis with auxiliary information. Can. J. Fish. Aquat. Sci. **42**(4): 815–824. doi:10.1139/f85-104.

Engås, A., and Godø, O.R. 1986. Influence of trawl geometry and vertical distribution on sampling with bottom trawl. J. Northwest Atl. Fish. Sci. **7**: 35–42. doi:10.2960/J.v7.a4.

Fonteneau, A. 1996. Why so many very old fishes in the southern bluefin tuna catches? Preliminary modeling of the “cryptic” biomass hypothesis. *In* Proceedings of the Sixth Expert Consultation on Indian Ocean Tunas (Colombo, Sri Lanka, 25–29 September 1995). Indo-Pacific Tuna Development and Management Programme, IPTP Collective Vol. 9, pp. 279–285.

Gulland, J.A. 1965. Estimation of growth and mortality rates. Annex to Arctic Fisheries Working Group Report. ICES Doc. CM 1965 / Gadoid Fish Committee, 3.

Hampton, J., and Fournier, D.A. 2001. A spatially disaggregated, length-based, age-structured population model of yellowfin tuna (*Thunnus albacares*) in the western and central Pacific Ocean. Mar. Freshw. Res. **52**(7): 937–963. doi:10.1071/MF01049.

Hannah, R.W., Parker, S.J., and Buell, T.V. 2005. Evaluation of a selective flatfish trawl and diel variation in rockfish catchability as bycatch reduction tools in the deepwater complex fishery off the U.S. west coast. N. Am. J. Fish. Manage. **25**(2): 581–593. doi:10.1577/M04-126.1.

Madsen, N., Tschernij, V., Hansen, K., and Larsson, P.-O. 2006. Development and testing of a species-selective flatfish ottertrawl to reduce cod bycatches. Fish. Res. **78**(2–3): 298–308. doi:10.1016/j.fishres.2006.01.002.

Millar, R.B., and Fryer, R.J. 1999. Estimating the size-selection curves of towed gears, traps, nets and hooks. Rev. Fish Biol. Fish. **9**(1): 89–116. doi:10.1023/A:1008838220001.

Nedreaas, K.H., Soldal, A.V., and Bjordal, Å. 1996. Performance and biological implications of a multi-gear fishery for Greenland halibut (*Reinhardtius hippoglossoides*). J. Northwest Atl. Fish. Sci. **19**: 59–72. doi:10.2960/J.v19.a6.

Pelletier, D., Mahevas, S., Drouineau, H., Vermard, Y., Thebaud, O., Guyader, O., and Poussin, B. 2009. Evaluation of the bioeconomic sustainability of multi-species multi-fleet fisheries under a wide range of policy options using ISIS-Fish. Ecol. Model. **220**(7): 1013–1033. doi:10.1016/j.ecolmodel.2009.01.007.

Pope, J.A., Margetts, A.R., Hamley, J.M., and Akyuz, E.F. 1975. Manual of methods for fish stock assessment. Part 3 — selectivity of fishing gears. FAO Fish. Tech. Pap. 41.

Punt, A.E., Smith, A.D.M., and Cui, G. 2002. Evaluation of management tools for Australia’s south east fishery: 1. Modeling the south east fishery taking account of technical interactions. Mar. Freshw. Res. **53**(3): 615–629. doi:10.1071/MF01007.

Quinn, T.J., II, and Deriso, R.B. 1999. Quantitative fish dynamics. Oxford University Press, New York.

Rose, C.S., and Gauvin, J.R. 2000. Effectiveness of a rigid grate for excluding Pacific halibut, *Hippoglossus stenolepis*, from groundfish trawl catches. Mar. Fish. Rev. **62**: 61–66.

Sampson, D.B. 1991. Fishing tactics and fish abundance, and their influence on catch rates. ICES J. Mar. Sci. **48**(3): 291–301. doi:10.1093/icesjms/48.3.291.

Sampson, D.B. 1993. The assumption of constant selectivity and the stock assessment for widow rockfish. Fish Bull. **91**: 676–689.

Somerton, D., Ianelli, J., Walsh, S., Smith, S., Godø, O.R., and Ramm, D. 1999. Incorporating experimentally derived estimates of survey trawl efficiency into the stock assessment process: a discussion. ICES J. Mar. Sci. **56**(3): 299–302. doi:10.1006/jmsc.1999.0443.

Sun, C.L., Ehrhardt, N.M., Porch, C.E., and Yeh, S.Z. 2002. Analyses of yield and spawning stock biomass per recruit for the South Atlantic albacore (*Thunnus alalunga*). Fish. Res. **56**(2): 193–204. doi:10.1016/S0165-7836(01)00320-4.

Wileman, D.A., Ferro, R.S.T., Fonteyne, R., and Millar, R.B. 1996. Manual of methods of measuring the selectivity of towed fishing gears. ICES Coop. Res. Rep. 215.

Appendix A: Conditions producing domed selectivity

Under equilibrium conditions (constant recruitment and constant rate of fishing mortality), the population-selection curve is dome-shaped if $N_a N_{a+2} > (N_{a+1})^2$. We now prove that this condition leads directly to inequality 6 for the special case of no fish movement between the regions ($P_{i,j} = 0$ for all i and j) and identical gear-selection coefficients for three adjacent age classes ($s_a = s_{a+1} = s_{a+2} = s$). We start with the simplest case of two regions and then extend the proof to three regions. The approach can be further extended in the same manner to any number of regions.

With two regions (under the conditions given above), the following equations define population abundance for ages a, a+1, and a+2.

$$N_a = \sum_{r=1}^{2} N_{a,r} = N_{a,1} + N_{a,2}$$

$$N_{a+1} = \sum_{r=1}^{2} N_{a+1,r} = N_{a,1}\exp(-F_1 s - M) + N_{a,2}\exp(-F_2 s - M)$$

$$N_{a+2} = \sum_{r=1}^{2} N_{a+2,r} = N_{a,1}\exp(-2F_1 s - 2M) + N_{a,2}\exp(-2F_2 s - 2M)$$

In each region the fish that are a+2 years old have suffered 2 more years of mortality than the fish that are a years old. The condition for decreasing population-selectivity is $N_a N_{a+2} > (N_{a+1})^2$, equivalent to $N_a N_{a+2} - (N_{a+1})^2 > 0$.

$$N_a N_{a+2} = (N_{a,1})^2 \exp(-2F_1 s - 2M) + (N_{a,2})^2 \exp(-2F_2 s - 2M) + N_{a,1} N_{a,2} \exp(-2F_1 s - 2M) + N_{a,1} N_{a,2} \exp(-2F_2 s - 2M)$$

$$(N_{a+1})^2 = (N_{a,1})^2 \exp(-2F_1 s - 2M) + (N_{a,2})^2 \exp(-2F_2 s - 2M) + 2N_{a,1} N_{a,2} \exp(-F_1 s - F_2 s - 2M)$$

Note that the first two terms in these last two equations are the same and cancel in the difference.

$$N_a N_{a+2} - (N_{a,1})^2 = N_{a,1} N_{a,2} \exp(-2M)[\exp(-F_2 s) - \exp(-F_1 s)]^2$$

With three regions (under the same conditions) the following equations apply:

$$N_a = \sum_{r=1}^{2} N_{a,r} + N_{a,3} = A + N_{a,3}$$

$$N_{a+1} = \sum_{r=1}^{2} N_{a+1,r} + N_{a,3} \exp(-F_3 s - M) = B + N_{a,3} \exp(-F_3 s - M)$$

$$N_{a+2} = \sum_{r=1}^{2} N_{a+2,r} + N_{a,3} \exp(-2F_3 s - 2M) = C + N_{a,3} \exp(-2F_3 s - 2M)$$

The summation term in each equation represents the abundances for the first two regions. In terms of the condition for decreasing population-selectivity, these equations result in the following set of equations:

$$N_a N_{a+2} = AC + AN_{a,3} \exp(-2F_3 s - 2M) + CN_{a,3} + (N_{a,3})^2 \exp(-2F_3 s - 2M)$$

$$(N_{a,1})^2 = B^2 + 2BN_{a,3} \exp(-F_3 s - M) + (N_{a,3})^2 \exp(-2F_3 s - 2M)$$

$$N_a N_{a+2} - (N_{a,3})^2 = AN_{a,3} \exp(-2F_3 s - 2M) - 2B \exp(-F_3 s - M) + CN_{a,3} + AC - B^2$$

$$N_a N_{a+2} - (N_{a,3})^2 = N_{a,1} N_{a,3} \exp(-2M)[\exp(-F_1 s) - \exp(-F_3 s)]^2 + N_{a,2} N_{a,3} \exp(-2M)[\exp(-F_2 s) - \exp(-F_3 s)]^2 + N_{a,1} N_{a,2} \exp(-2M)[\exp(-F_1 s) - \exp(-F_2 s)]^2$$

The same process can be repeated for a system with four regions and so on.