

CHAPTER 3: A GENERIC SPATIAL BIOECONOMIC MODEL

This chapter provides simple and broadly relevant algebraic forms for the functions given in equations 2-3 and 2-4 above. The effects of parameter values on the shapes of the resultant profile of prey density across space and overall supply function are investigated, and inferences drawn with respect to the likely stability of the system. Some complicating factors often relevant to the harvesting of terrestrial populations are also considered, and it is shown how an explicit bioeconomic analysis resolves apparently contradictory results of previous work in regard to these.

3.1 Equations

For the purposes of a generic model, simple forms were chosen for the cost and growth functions, which accord with the classic, non-spatial Schaefer (1957) model. Hunting cost within at a single location is assumed to be inversely proportional to the local prey density (in keeping with the exploratory models of chapter 2), and the period of each hunting trip is limited by the point at which the maximum bag size is reached (i.e. no more prey can be carried) or otherwise by an absolute time limit. Hence, the cost equation, 2-3, becomes:

$$C = \frac{H}{N(x)} + \frac{xT}{\min\{B, \frac{A-xD}{L/N(x)}\}} \quad \text{Eqn 3-1.}$$

where C is the total cost per animal,

H is the local hunting cost at unit prey density (= unit cost of effort / q_0),

x is the distance from the hunters' point of origin

T is the cost of travelling one unit of distance and back,

B is the maximum number of animals a hunter can carry (bag size),

$A-xD$ is the maximum hunting time available at x , i.e. the maximum trip time minus the travel time to and from x ,

and L is the time needed to capture an animal at unit prey density.

If no constraint were applied to trip length, then hunting trips would continue indefinitely as the contribution of the fixed cost of travel to overall cost decreases with the number of animals caught.

Rational economic agents should maximise their ratio of profit to investment rather than return to cost, but the two are equivalent in the absence of differential time lags associated with investment in different factors. Where hunters use cheap or re-usable technology to catch animals and travel on foot or horseback, it is not unreasonable to assume that the predominant cost is a time cost. Equating cost with time allows a simplification of subsequent algebra, by removing L , i.e. equation 3-1:

$$C = \frac{H}{N(x)} + \frac{xT}{\min\{B, \frac{uA - xT}{H/N(x)}\}} \quad \text{Eqn 3-2.}$$

where u is the unit cost of time, i.e. $T = uD$ and $H = uL$

Prey population growth is assumed to be logistic, so the spatial growth equation is:

$$\frac{dN(x)}{dt} = rN(x)\left[1 - \frac{N(x)}{K}\right] \quad \text{Eqn 3-3.}$$

where $E(x)$ is the hunting effort at distance x

and $m(dN(x)/dx)$ describes the net immigration at distance x as a function of the spatial prey density gradient.

Algebraically, the simplest assumption to make for migration is that net flow is directly proportional to the density gradient, i.e. that it obeys Fick's Law, which describes movement by diffusion: flow at point x and time t ;

$$J(x, t) = -D \frac{\partial u(x, t)}{\partial x} \quad \text{Eqn 3-4.}$$

where $u(x, t)$ is the concentration or density at point x and time t , and D is a constant of proportionality.

Therefore the rate of change in u at point x is given by:

$$\frac{\partial u}{\partial t} = -D \frac{\partial^2 u}{\partial x^2} \quad (\text{Rothery \& Brown 1993}) \quad \text{Eqn 3-5.}$$

Including diffusive dispersal, and replacing D with the migration constant M in the notation, the growth equation becomes:

$$\frac{dN(x)}{dt} = rN(x)\left[1 - \frac{N(x)}{K}\right] - q_0 E(x)N(x) + M \frac{\partial^2 N}{\partial x^2} \quad \text{Eqn 3-6.}$$

Note that if space is modelled in discrete segments, then Fickian diffusion can be approximated by moving a fixed proportion of the population of a segment (equal to M/d^2 , where d is the width of the segment) to neighbouring segments at each time step. Hence the system of movement used in the effort distribution model in chapter 2 approximated Fickian diffusion.

Clearly, the assumption of movement by Fickian diffusion is not correct for most organisms, especially not large, motile and intelligent ones, but it can produce an adequate description of overall, broad-scale patterns of dispersal (Skellam 1973). It is satisfactory as a glib caricature of dispersal, against which

systems based on more detailed knowledge can later be compared. To get a sense of plausible figures for M , note that if a population, initially at a point location, spreads by diffusion in both directions along a single dimension, then at time t , the expected spatial distribution of the population is normal with mean displacement = 0 and variance = $2Mt$.

3.2 Implementations

Whilst much of the basic behaviour of the model, in terms of the variation in prey density with distance, could be understood analytically, in order to include migration, numerical solutions were necessary. Computer based iterative solutions were produced for a notionally unbounded linear system. It was unbounded in the sense that the maximum distance from the hunter origin included was set to twice the maximum distance at which hunting occurs, as areas beyond this would contribute very little to population growth and therefore offtake. Default parameters were set to be broadly appropriate to a large ungulate (table 3-1).

| Parameter | Value | Units |
|---------------|--------|----------------------------------|
| r | 0.4 | yr ⁻¹ |
| K | 5 | animals km ⁻² |
| M | 2 | km ² yr ⁻¹ |
| C | 50 | acu animal ⁻¹ |
| T | 10 | acu km ⁻¹ |
| H | 10 | acu km ⁻² |
| B | 3 | animals |
| distance step | 0.1 | km |
| time step | 0.0001 | yr |

Table 3-1. Default parameters for the unbounded, linear implementation of the generic spatial bioeconomic model. All costs are measured in arbitrary currency units (acu). The distance and time steps are not parameters if the fundamental model, but relate to the degree of resolution used in the numerical solution.

Decreasing the size of the time and distance steps used in the numerical solution had very little effect on the results obtained. Reducing the default time step by a factor of 1000, resulted in a change in predicted offtake of roughly 1%, and a fivefold change in the distance step yielded a 0.5% change. None of these changes affected the predicted maximum hunting distance, which agreed with analytical predictions (see eqn. 3-18 below) to the degree of spatial resolution used.

Real harvested systems are of course finite; if they were not, the backwards-bending supply curve characteristic of renewable resources would not be obtained. In order to study the effects of model parameters on the shape of the supply curve, a 2D numerical implementation was produced, based on hunting within a circular island of habitat of radius 30km, with the hunter origin located at the centre. In the modern world, villages are rarely surrounded by a sea of natural habitat, in fact the converse is often true with pockets of habitat ringed by villages. Linear or sub-linear areas of exploitation may therefore be more commonly applicable than the circular area used here, but in any case the effects of geometry on supply can be easily understood through differences in the area available at different

distances. Default model parameters were the same as those used in the linear implementation. Plotting supply curves necessitated iterative solutions at successive values of C , and so to maintain manageable run-times, the time and distance steps were reduced to 0.1 years and 1 km respectively. Again the effect on model predictions was minor, in the order of a 5% change in offtake, compared with the step sizes used in the linear implementation. Given that the aim was to examine relative effects of parameters, rather than to make detailed predictions for a single set, these differences were considered inconsequential.

3.3 Behaviour

3.3.1 Form of prey density – distance relationship

Most of the discussion of the linear behaviour of the model will be with reference to the case where hunting trips are limited by bag size. This will be contrasted with the time-limited case in section 3.3.7.

Transport cost is independent of offtake at any given locality, thus at population equilibrium, within the region where hunting occurs, prey population density is controlled solely by the cost equation. The growth equation determines equilibrium offtake at any given distance:

$$S(x) = q_0 E(x) N(x) = \frac{dN(x)}{dt} = rN(x) \left[1 - \frac{N(x)}{K} \right] + M \frac{\partial^2 N}{\partial x^2} \quad \text{Eqn 3-7}$$

Given the bag-limitation assumption, eqn 3-1:

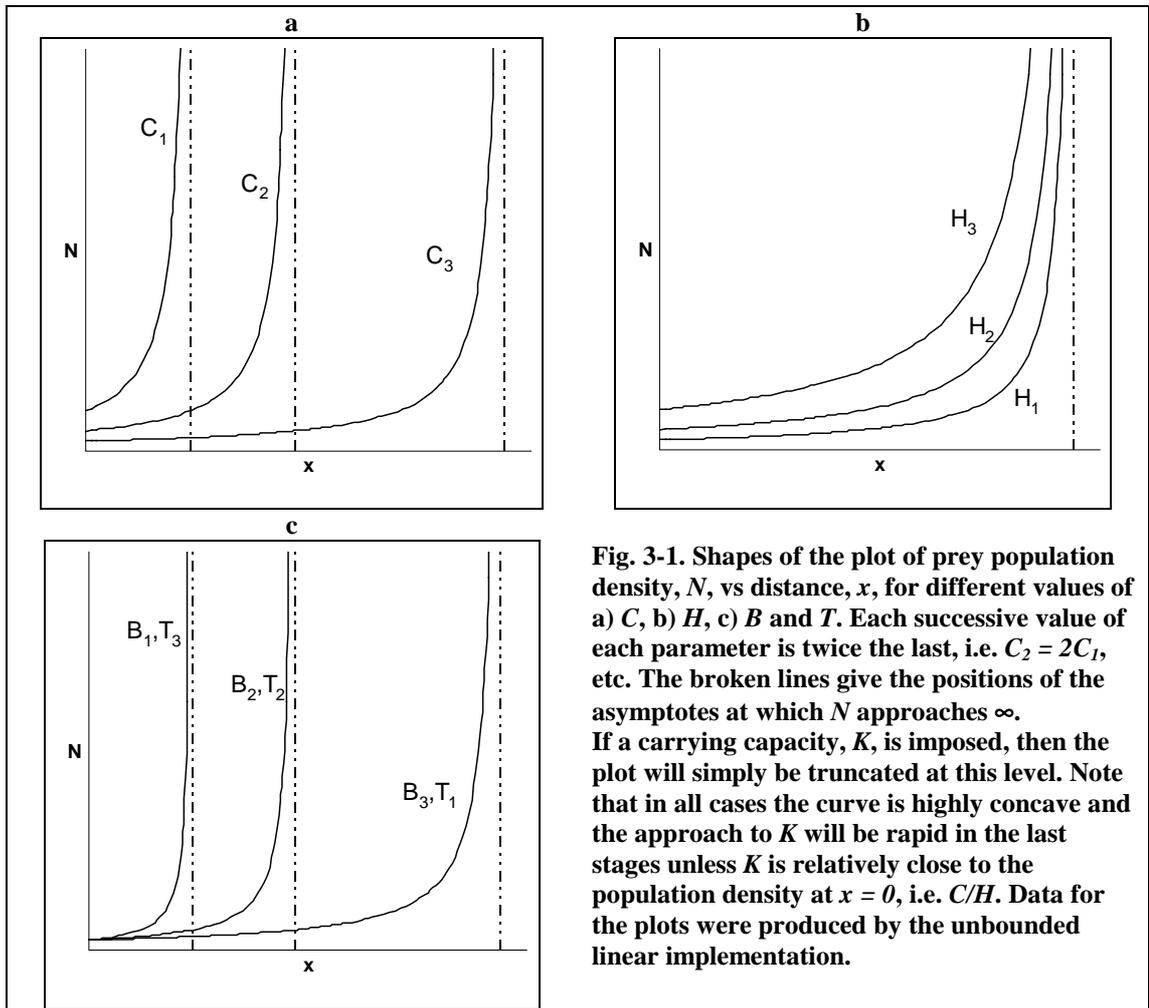
$$C = \frac{H}{N(x)} + \frac{xT}{B} \quad \text{Eqn 3-8.}$$

Therefore:

$$N(x) = \frac{H}{C - \frac{xT}{B}} \quad \text{Eqn 3-9.}$$

If $K = \infty$, then the plot of N against x traces an accelerating rise from H/C at $x = 0$, approaching infinity at the asymptote $x = BC/T$, i.e. where the total cost of a hunting trip, BC , is equal to the travel cost alone, xT . H affects the population density at the origin, T and B have reciprocal effects on the position of the asymptote, and C influences both (fig. 3-1). Increasing C does not change the shape of the curve, but simply moves the curve further to the right. For any given starting density, H/C , and end point,

BC/T , the curve can only follow one path; any change in e.g. H must be balanced by the same proportional change in C and T/B to preserve the endpoints, and would therefore cancel out in eqn. 3-9.



3.3.2 Width of the hunted region

A finite K truncates the rise in N , so that all the parameters now affect the width of the region over which prey are depleted. If there is no dispersal within the system, i.e. $M = 0$, then $N(x)$ will increase with x until hitting an abrupt plateau at K , where;

$$K = \frac{H}{C - \frac{xT}{B}} \tag{Eqn. 3-10}$$

Therefore, the distance from the hunter origin up to which hunting will occur:

$$x_H = \frac{B}{T} \left(C - \frac{H}{K} \right) \tag{Eqn. 3-11.}$$

Note that the concavity of the curve, depends only on H , C and K , as:

$$\frac{x_H}{x_{N=\infty}} = 1 - \frac{H}{CK} \quad \text{Eqn. 3-12.}$$

Hence if hunting reduces the population density to a proportion a of K at $x = 0$, then x_H will be equal to $(1-a)$ times the distance at which N would approach ∞ if prey density was unlimited. Cases of conservation concern will be those where hunting has the capacity to reduce populations to small fractions of K , at least at in the areas where hunting is most intense. This means that x_H would generally occur very close to $x_{N=\infty}$, and so K would not be reached until a point were the curve is already very steep. Hence the density profile of the resource is expected to show very low population densities in accessible areas, with a sharp transition to high densities in economically inaccessible areas.

When dispersal is added to the system, the same relationship between N and x must still hold for $0 \leq x \leq x_H$, but $x_H < B/T.(C-H/K)$. The migration term in the growth equation is proportional to the curvature of $N(x)$. The effect of migration is therefore to smooth the curvature around $x = B/T.(C-H/K)$, until the point at which the migratory flow is balanced by the difference in biological growth (fig. 3-2).

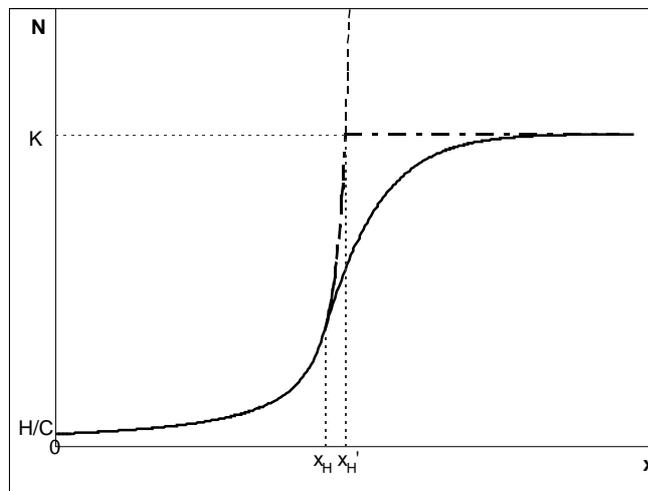


Fig. 3-2. Equilibrium prey density, N , vs distance, x , in the presence of dispersal, using default parameters in the unbounded linear implementation. The thick broken line shows the form of the relationship in the absence of migration. The thin dashed line shows the continuation of that trajectory in the absence of any limit to prey density, i.e. if $K = \infty$. The effect of migration is to smooth the approach to K , reducing local population density. The distance limit to the hunted region, x_H , is the point at which population density falls below the economically viable level for hunting due to the effect of migration. In the absence of migration, the limit of the hunted area would occur at $x_H' = B/T.(C-H/K)$.

Wherever N falls below $H/(C-xT/B)$, total cost will exceed C , so hunting will no longer occur and x_H will decline. For $x > x_H$, $N(x)$ at population equilibrium will be given by

$$M \frac{\partial^2 N(x)}{\partial x^2} + rN(x) \left(1 - \frac{N(x)}{K} \right) = 0 \quad \text{Eqn 3-13.}$$

This has a unique positive real solution for $N(x)$ over $x_H \leq x \leq \infty$ for any given value of $N(x_H)$, but cannot be solved analytically. It does, however, provide a means of calculating x_H . Given that any point change in the gradient of $N(x)$ will produce an infinite curvature of $N(x)$ at that point, at population equilibrium, x_H must satisfy the condition that $\partial N(x)/\partial x$ as given by the cost equation (equation 5) must equal $\partial N(x)/\partial x$ as given from the migration equation above (equation 6). It will also be a point of inflexion as net migration must switch from being negative to positive as x decreases across x_H (fig. 3-3). Substituting p for $\partial N(x)/\partial x$ in equation 3-13 gives:

$$\int p \partial p = \frac{p^2}{2} = -\frac{r}{M} \int N(x) \left(1 - \frac{N(x)}{K} \right) \partial N(x) \quad \text{Eqn 3-14.}$$

Therefore:

$$\frac{\partial N(x)}{\partial x} = 2 \left(\frac{-r}{M} \int N(x) \left(1 - \frac{N(x)}{K} \right) \partial N(x) \right)^{1/2} \quad \text{Eqn 3-15.}$$

Given that at $N(x) = K$, $\partial N(x)/\partial x = 0$, the constant of integration can be determined, giving:

$$\frac{\partial N(x)}{\partial x} = \left(\frac{r}{M} \left(\frac{K^2}{3} - N(x)^2 \left(1 - \frac{2N(x)}{3K} \right) \right) \right)^{1/2} \quad \text{Eqn 3-16.}$$

By straightforward differentiation, the cost equation 3-8 yields:

$$\frac{\partial N(x)}{\partial x} = \frac{TH}{B \left(C - x_H \frac{T}{B} \right)^2} \quad \text{Eqn 3-17.}$$

Equating these two expressions for $\frac{\partial^2 N(x_H)}{\partial x^2}$ at $x = x_H$, substituting $H/(C - x_H T/B)$ for $N(x_H)$ and

solving for x_H , gives:

$$\frac{K^2}{3H^2} z^4 - z^2 + \frac{2H}{3K} z = \left(\frac{T}{B} \right)^2 \frac{M}{r} \quad \text{Eqn 3-18.}$$

where $z = C - x_H T/B$.

This 4th order polynomial is extremely complex to solve analytically, but can be solved numerically, or graphically and conceptually by plotting the intercept of $(K^2/3H^2).z^4 - z^2$ with $(T/B)^2 M/r - (2H/3K).z$, which shows that there is only one real positive solution for x_H between 0 and K .

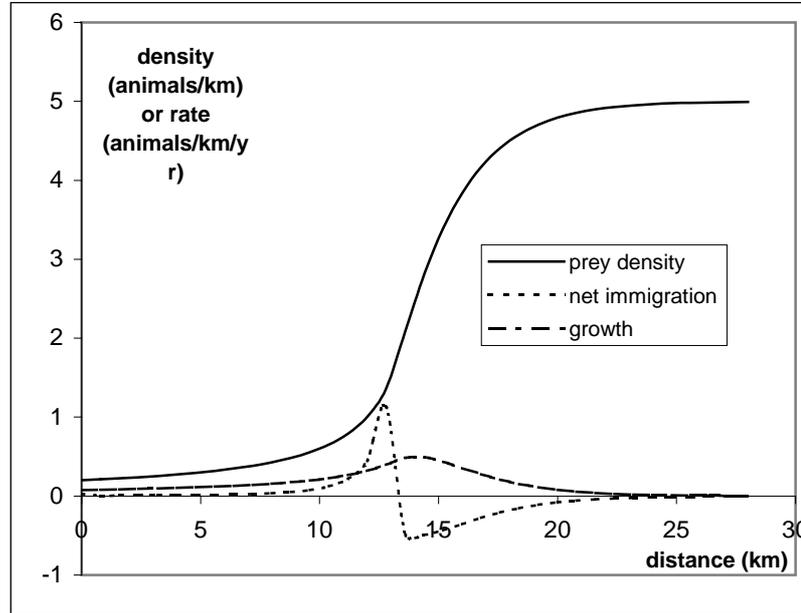


Fig 3-3. Prey density and net immigration and growth rates with distance from the hunter origin under default parameters. Offtake and hunting effort are not shown, but offtake is equal to the sum of growth and migration over the region where net immigration is positive, and hunting effort is proportional to Q/N . The hunted region is a sink and extends up to the point of inflexion on the prey density curve. The region beyond this is a source.

Hence, in the absence of migration, the width of the hunted region is directly proportional to B/T , and to the difference between the total unit hunting cost and the unit capture cost at $N = K$, $(C-H/K)$. Once migration is included in the system, the proportion of that hunted region which remains economically viable to hunt at equilibrium is largely dependent on the relative strengths of M and r . As M/r increases, the width of the hunted region decreases, until $x_H = 0$ at a threshold value derived by setting $x_H = 0$ in equation 3-18:

$$\frac{M}{r} = \frac{CB^2}{T^2} \left(\frac{K^2 C^3}{3H^2} + \frac{2H}{3K} - C \right) \quad \text{Eqn 3-19.}$$

Once M/r reaches or exceeds this threshold, it is more profitable for hunters to sit and wait for prey to diffuse towards them than to travel to capture prey. The sensitivity of x_H to proportional increases in M/r generally increases as the threshold is approached (fig. 3-4).

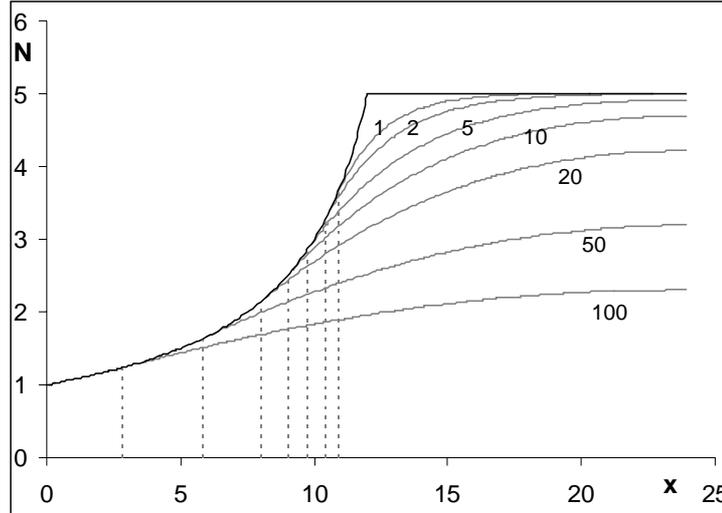


Fig. 3-4. N vs x profiles for various values of M . The black line is for the case without migration, i.e. $M=0$, and each successive grey line is for a higher value of M (values marked next to lines). The vertical dotted lines give the position of x_H in each case. Data were generated from the unbounded linear implementation with default parameters, other than H , which was set to 50 acu km^{-2} .

Figure 3-5a suggests that C , T and B have a much stronger influence on the width of the hunted region than other parameters, which will tend to be the case where the final approach to K is steep – i.e. where H/C is a small fraction of K .

3.3.3 Total offtake

Total offtake rate at equilibrium is the integral of the sum of biological growth and net migration with respect to x evaluated over $0 \leq x \leq x_H$. Substituting $H/(C-xT/B)$ for $N(x)$ in eqn. 3-7 gives

$$S = \int_0^{x_H} \frac{H}{z} \left(r \left(1 - \frac{H}{Kz} \right) + \frac{2MT^2}{B^2 z^2} \right) dx \quad \text{Eqn 3-20.}$$

where $z = C - xT/B$, as before.

Obviously the precise effects of individual and combined parameter changes on offtake are complex, but their general impact can be readily understood in terms of their effect on the shape of the $N(x)$ curve. Net production is simply a function of $N(x)$ between $x = 0$ and ∞ . The closer that $N(x)$ lies to $0.5K$, over the greater part of this range, the stronger growth will be. Increasing M will always increase production as it causes $N(x)$ to fall significantly below K over a wider range of x . Total net production beyond the harvested region is equal to the flow of immigrants at $x = x_H$, i.e. $M \frac{\partial N(x_H)}{\partial x}$. The flow is

not directly proportional to M , however, as a higher M reduces $\frac{\partial N(x_H)}{\partial x}$. It also decreases the length of the harvested region (fig. 3-5a) and therefore production from within it, so the overall response to a

change in M is relatively weak (fig. 3-5b). Figure 3-5b suggests that the biological parameters have a stronger influence on offtake than they do on x_H . Obviously, increasing r will increase offtake, but this increase will be slightly less than proportional as a higher r has opposite effects to M beyond the harvested region. Amongst the cost equation parameters, anything which (1) increases the length of the hunted region, i.e. increasing B or C , decreasing T or H , or (2) leads to a greater proportion of the population within the hunted region occurring at a density close to $0.5K$, will generally increase offtake. Figure 3-5b suggests that as H rises, the increase in population densities and hence productivities outweighs the effects of the concurrent reduction in the width of the hunted region (assuming that $H/C < 0.5K$). Again, this can be understood intuitively by looking at the shape of the $N(x)$ curves for different values of H (fig. 3-1b).

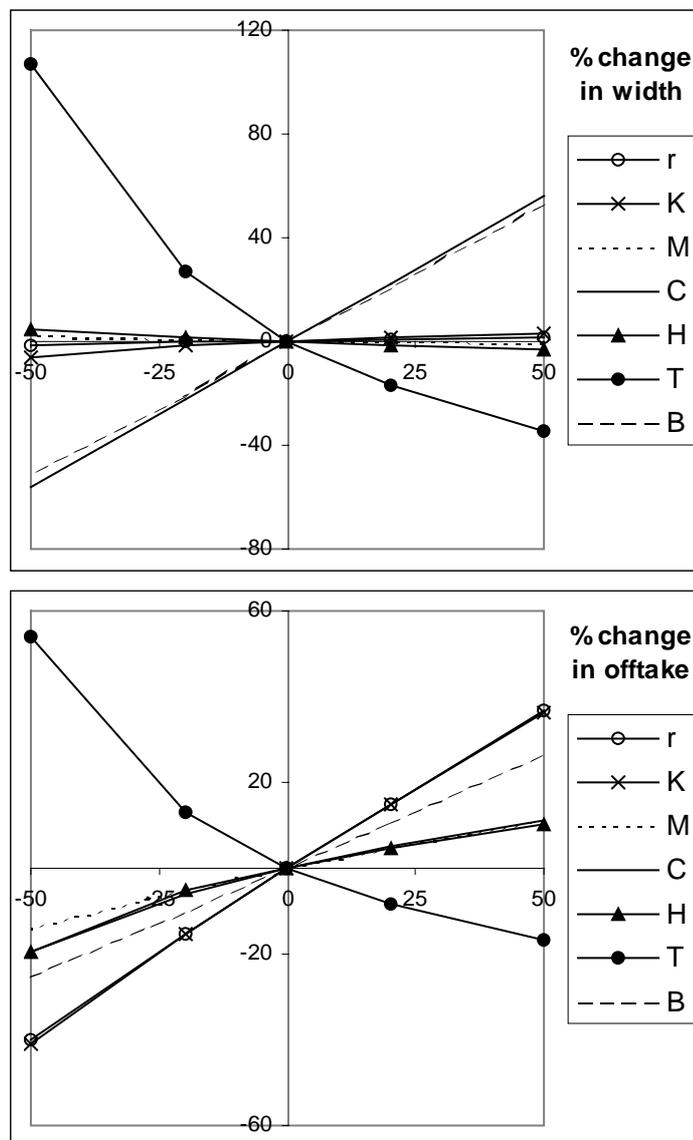


Fig. 3-5. Sensitivity of the width of the hunted region, x_H , and the total offtake at equilibrium, in response to changes in individual parameters. Percentage change in each variable is plotted against percentage change in each parameter relative to its default value; i.e. each parameter was set to 50, 80, 120 and 150% of its default value.

3.3.4 Shape of supply curve

Figure 3-6 shows variation in equilibrium prey population size, offtake and maximum hunting distance with C for the 2D circular island model. If the axes are reversed on the plot of offtake vs. C , then we obtain the familiar form for an AC curve and therefore the supply curve for a renewable resource under open-access harvesting. When there is no migration in the system, the peak in the supply curve will always occur at the point at which the most distant areas have already begun to be harvested. This is simply due to the way that the profile of $N(x)$ varies with C . As C increases the curve is shifted to the right (see fig. 3-1a), so the width of the area contributing to overall production and therefore offtake must increase. With the inclusion of migration, this is tempered by the fact that populations beyond the harvested region may be drawn down to levels below maximum productivity at $0.5K$, but the effect will not be great unless migration is very strong.

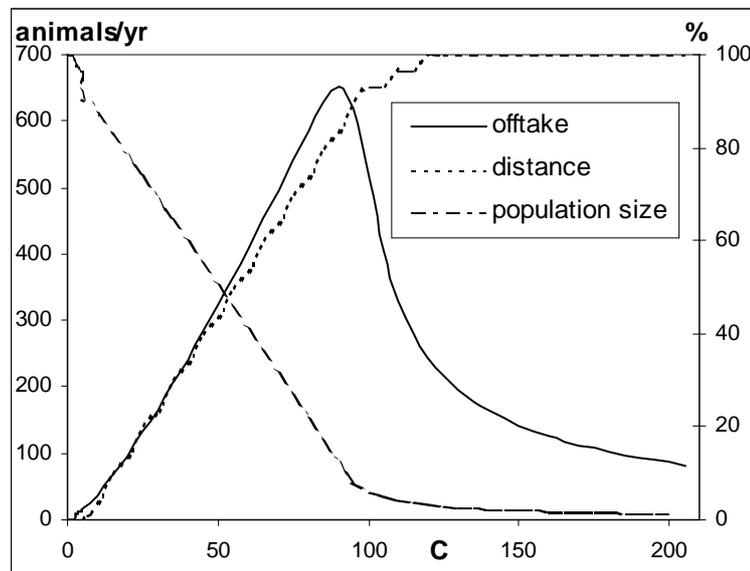


Fig 3-6. Equilibrium offtake (animals per yr), maximum distance travelled by hunters and global prey population density (% of maximum) vs. C in the 2D island implementation under default parameters. Note that, unlike in the non-spatial case, the maximum yield occurs when global population has already fallen to a small fraction of its maximum. By the point at which it becomes economically viable to hunt in even the most remote sites, the prey population is extremely small.

Figure 3-7 shows some of the effects of model parameters on the shape of the supply curve. If transport costs are an insignificant proportion of the total hunting cost, then the situation is essentially the same as for the non-spatial Schaefer model (fig. 3-7). Travel costs flatten the supply curve, producing a lower peak production at a higher unit cost. Increasing M has similar effects to reducing T (fig. 3-7a), as when M is very large, prey movement obviates the need for hunter travel. Changes to K or r alter the productivity of the system, without any significant effect on the relative shape of the supply curve.

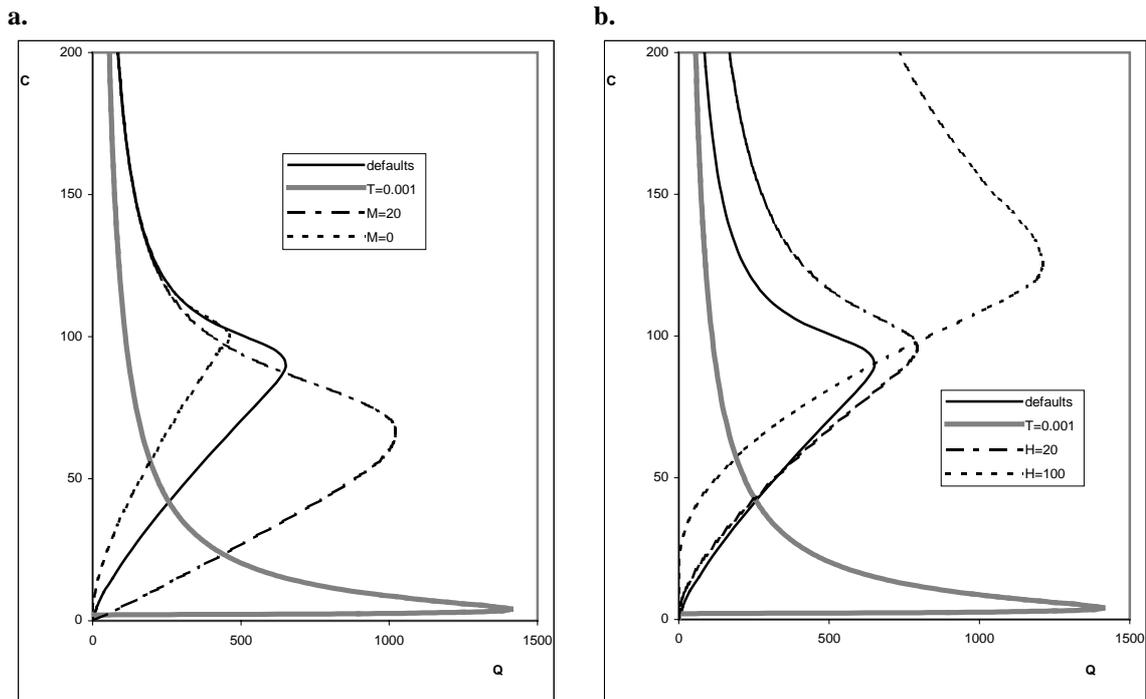


Fig 3-7. Effects of model parameters on the shape of the AC curve. Both plots illustrate the default AC curve, and that produced when travel costs are insignificant ($T=0.001$). Note that the AC curve under default parameters is the same as the C curve in fig 3-6, but the axes have been reversed to convert the graph into the standard form for a supply curve. a) Effects of removing migration and higher migration. b) Effects of higher values of H .

Increases in H naturally extend the supply curve along the cost axis, but also increase the size of the peak supply as the fall in transport cost relative to hunting cost encourages a more even spatial distribution of hunting effort. Supply under a higher H system will be lower at low C , but may overtake that of a lower H system rapidly (fig 3-7b).

3.3.5 Local extinction

If a depensatory effect is included, such that local extinction occurs wherever $N(x)$ and immigration fall below set thresholds, then the exploited region may be reduced to a very narrow band (fig. 3-8).

The effect on the supply curve is to decrease supply in general, due to the loss of prey populations in low density areas, and eventually produce a global collapse of the system as global densities fall below the extinction threshold as C rises (fig. 3-9).

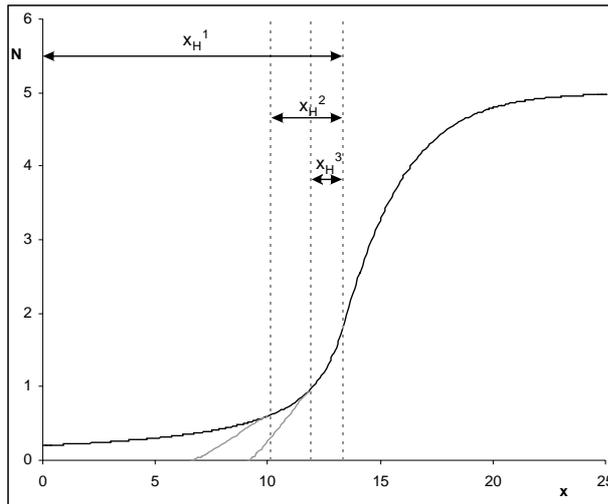


Fig. 3-8. N vs. x with local extinction. The black line shows the normal prey density profile under default parameter values in the unbounded linear implementation, and the resulting width of the hunted region, x_H^1 . The grey lines show the results of imposing increasingly severe population density and immigration thresholds at which local extinction will occur: $<10\%$ K with an influx of $<5\%$ K , and $<20\%$ K with an influx of $<10\%$ K . Local extinction produces much shorter regions of exploitation, x_H^2 and x_H^3 respectively. The figure illustrates typical values, as the implementation did not arrive at a stable equilibrium when extinction was applied. In the region where population density falls below the standard curve, dispersal gradually reduces the severity of the decline in N , i.e. the bases of the grey lines creep leftwards, until immigration falls below the threshold value simultaneously over a wide region, causing local collapse and a re-initiation of the cycle

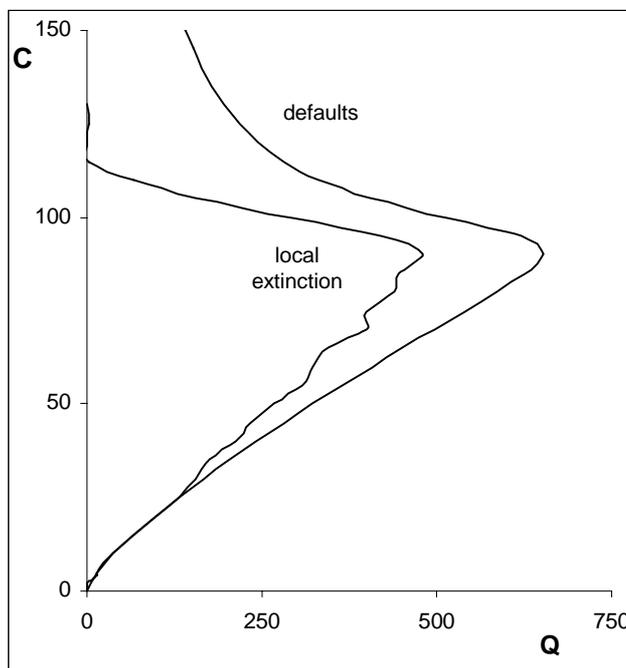


Fig. 3-9. Cost curves for the default parameters in the 2D island implementation, and for the same set of parameters with the inclusion of population density and immigration extinction thresholds of 10% and 5% K respectively.

3.3.6 Discounting and monopoly harvesting

In the case of sole-owner or socially optimal harvesting strategies, individual hunters are not necessarily in competition. Hence we can loosen the constraint that hunters should equalise the total cost of hunting across space, and C in the model becomes a function of distance, x , rather than a constant with respect to it:

$$C(x) = \frac{H}{N(x)} + x \frac{T}{B} \quad \text{Eqn 3-21.}$$

Essentially, it may be in the interests of society or a sole resource owner to subsidise hunting at a higher unit cost in certain locations if that increases overall efficiency. The sole owner is seeking to minimize his total cost $\int_x^{x_H} C(x)Q(x)dx$ at any given level of supply $\int_x^{x_H} Q(x)dx$. It will therefore be in his interest to take an animal from x_2 rather than x_1 if the increase in total cost from taking this extra animal at x_2 is less than the reduction in total cost from not taking the animal from x_1 , i.e. if

$$\frac{dC(x_2)Q(x_2)}{dQ(x_2)} < \frac{dC(x_1)Q(x_1)}{dQ(x_1)} \quad \text{Eqn 3-22.}$$

A sole owner will therefore seek to equalize the industry marginal cost, $\frac{dC(x)Q(x)}{dQ(x)}$, over space rather than the average cost, $C(x)$. Noting that industry MC is constant across space at any given level of supply, and denoting it by F , we have:

$$F = \frac{dC(x)Q(x)}{dQ(x)} = C(x) + Q(x) \frac{\frac{dC(x)}{dN(x)}}{\frac{dQ(x)}{dN(x)}} \quad \text{Eqn 3-23.}$$

Hence, in the absence of migration:

$$F = \frac{H}{N(x)} + x \frac{T}{B} - \left(N(x) - \frac{N(x)^2}{K} \right) \frac{\frac{H}{N(x)^2}}{1 - 2 \frac{N(x)}{K}}$$

Therefore:

$$N(x) = 0.5 \left(K + \frac{H}{F - x \frac{T}{B}} \right) \quad \text{Eqn 3-24.}$$

Note that if $x = 0$, then this is equivalent to Clark's (1990) result that the equilibrium population level in a monopoly-controlled fishery with perfectly elastic demand and a discount rate of zero is $0.5(K + c/pq)$, as price $p = F$, the industry MC, under these circumstances, and c/q is equivalent to H .

Figure 3-10 displays the resulting prey density vs. distance profiles under sole-owner harvesting, and figure 3-11 contrasts cost and supply curves for open-access, sole-owner harvesting, and monopoly trading with independent harvesting.

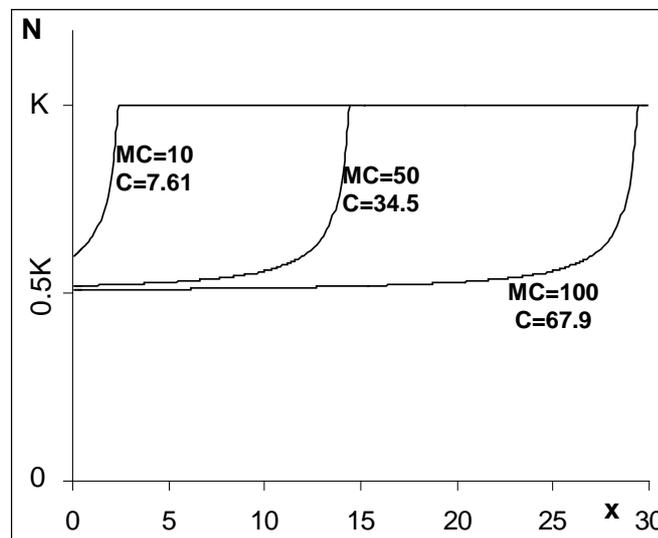


Fig. 3-10. N vs. x for different (constant) values of marginal cost, MC. Mean unit cost C is also given for each curve, but note that $C(x)$ varies with x . As MC increases, the shape of the curve remains the same, but it moves further to the right.

The addition of migration to the system has more complex effects when MC rather than unit cost is equalised over space as MC is dependent on the rate of offtake, rather than density, and hence partly on the flows of animals due to migration itself. As migration buffers the effects of increasing offtake, the industry MC will be lower for at a given N in the presence of migration. So for a given industry MC, populations will be exploited at a lower level, although offtake will also be higher, and the rise in N with x will also be steeper as the effect of migration is greatest where the curvature of the density profile is highest. An iterative solution including migration would be complicated, but in essence the effect of migration would be to make the outcome slightly more similar to the non-spatial case, as before.

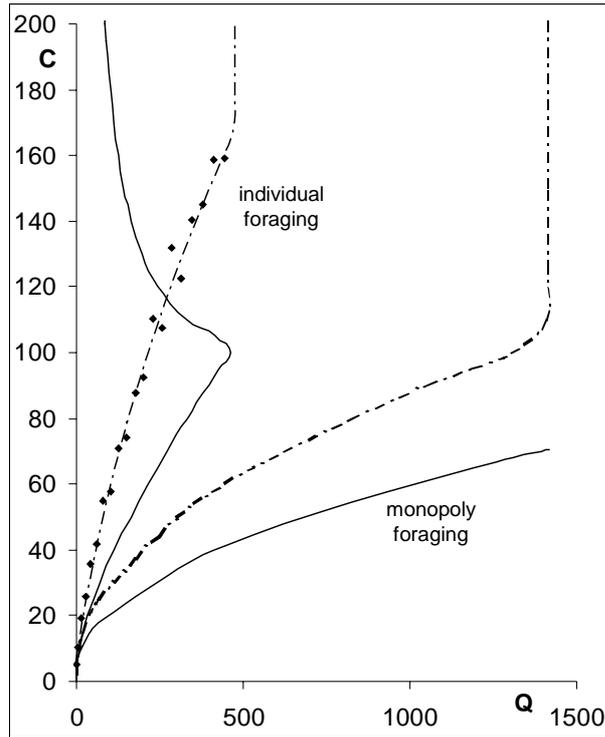


Fig. 3-11. Cost curves for individual and monopoly foraging under the default parameters of the 2D island implementation with $M=0$. Under individual foraging, C is equalised over space according to the standard model. Under monopoly foraging, MC is equalised over space as illustrated in fig. 3-10. The solid lines give the AC curves, i.e. the supply curves in a competitive market, and the broken lines give the industry MC curves, i.e. the ideal supply curve for a monopoly supplier with a discount rate of zero. The industry MC curve for individual foraging is fitted by hand to numerical estimates of dCQ/dQ generated in the computer implementation. This corresponds to the expected supply curve in a situation where there is a monopoly in the trade of the product, but the actual harvesting is carried out by independent individuals. This is also relevant to a situation in which a government tries to maximise rent from the industry through market controls, e.g. by imposing taxes on the sale of the product. The monopoly foraging supply curves are calculated from the curves of N vs x illustrated in fig. 3-10, but adjusting for the change in area that would occur at each distance in the 2D island scenario. The industry MC curve always approaches infinity at the MSY as it is impossible to increase production beyond this point. Note that in the context of the spatial model, the social gain from (socially) optimal foraging is much higher than that achieved by socially optimal supply with individual foraging.

3.3.7 Time-limited case

If the length of hunt trips is limited by time rather than by the number of prey which can be carried, the cost equation 3-2 becomes:

$$C = \frac{H}{N(x)} \left(I + \frac{xT}{uA - xT} \right) \quad \text{Eqn 3-25.}$$

As before, at equilibrium, prey density at distance x is determined solely by the cost equation:

$$N(x) = \frac{H}{C \left(1 - \frac{xT}{uA} \right)} \quad \text{Eqn 3-26.}$$

for $0 \leq x \leq x_H$.

This equation has essentially the same form as equation 3-9, with B replaced by uA/C . It produces a similarly shaped profile of the increase of prey population density with distance as before (i.e. fig. 3-1), but increasing C will not extend the position of the vertical asymptote along the x axis, it will just lower the $N(x)$ curve and increase its concavity. The length of the hunted region in the absence of dispersal will now be $uA/T \cdot (1 - H/KC)$.

If hunters are subject to both time and bag constraints, then at any one point in space only one can be limiting. The point of switching between the two types of limitation is given by:

$$N(x) = \frac{H}{C \left(1 - \frac{xT}{uA} \right)} = \frac{HB}{BC - xT}$$

$$\therefore uAx = BCx$$

$$\therefore x = 0 \text{ or } BC = uA.$$

I.e. for any given unit hunting cost, C , the profiles of $N(x)$ versus x given by the two different constraints do not cross, and hunters are limited by only one of the constraints (whichever produces the higher values of $N(x)$) throughout the entire hunted region. The two constraints produce exactly the same $N(x)$ profiles when $BC = uA$, i.e. when the cost of obtaining a full load of animals is equal to the time cost of the each trip.

When hunting trips are time- rather than bag-limited, the effect of C on the prey density / distance profile is different, as discussed above. An absolute maximum travel distance is set by the available time. Although supply will rise to a peak and then tail off slowly and factors which increase costs will stretch the supply curve out along the C axis as before, changes in H will have very little impact on the peak supply for the system. Other than the growth parameters r and K , only parameters which extend the width of the region that contributes to supply will have a significant impact on peak supply; i.e. M , and the parameters determining maximum travel distance, u , T and A .

3.4 Implications

To predict the stability of a harvested system, it is obviously necessary to specify the demand function and the manner in which harvesting effort adjusts when supply and demand are out of balance. But even if little is known about demand and the dynamic processes of industry adjustment, it is possible to infer much from the shape of the supply curve and hence the likely region in which the intersection with the demand curve will occur.

Pronounced spatial structure, i.e. where travel costs are significant and the prey dispersal rate not overwhelming, results in a flatter AC curve with its peak at a higher unit cost. For relatively elastic demand, spatial structure is therefore likely to increase the stability of the system, as the equilibrium is more likely to occur below the MSY and to leave an unexploited refuge at the farthest distances.

This gain in stability comes with a loss in renewable resource rents, however. Even harvesting across space would produce the highest prey productivity (appendix 3-1), and the effect of this is seen in the difference between the density-distance plots and overall offtake for individual and sole-owner harvesting (fig 3-11). Even if overall effort or supply can be optimally managed, rents will still be relatively poor where harvesters act independently and travel costs are significant. This is even more the case given that harvesting near the MSY in a spatial system is even more risky than in the non-spatial case, and hence the conflict between short-term productivity and stock conservation (see e.g. Roughgarden and Smith 1996) is even more acute. In the spatial system, the MSY is expected to occur at a much lower global population level, and adding local extinction to the model suggests that the long tail of the supply curve may not actually be available in reality (fig 3-9).

Hunting (as opposed to travel) cost is another area where the interests of conservationists and resource users may appear to be divergent; increasing H can be an effective conservation strategy, but deliberately introducing inefficiencies is anathema to economists. In the case of open-access harvesting, however, an increase in H could result in a social efficiency gain even if that increase represented a real social cost (i.e. was introduced through restrictions on harvesting methods or periods, as opposed to a tax). The reason is of course that due to the backwards-bending supply curve, higher production, and therefore consumer surplus, may be obtained by decreasing offtake per unit effort. The potential for social gains from increasing H is even higher in the spatial case because a higher H produces a higher peak supply, as opposed to just moving the position of the peak along the cost axis in the non-spatial case. I.e. increasing harvesting costs reduces the relative importance of travel costs, and therefore some of the social inefficiency associated with strongly spatial harvesting.

It is important to recognise, however, that these conclusions are based on equilibrium predictions of the model. In the short term, any increase in costs will initially cause offtake and hunting revenues to fall, and is therefore likely to be resisted. There may therefore be a role for short to medium term donor projects which subsidize or compensate for this loss during the adjustment period, and allow arrival at a

more profitable (and more conservation orientated) equilibrium. Bulte and Horan (2001) reached the same conclusion with a model concerning alternate land use options.

A decrease in H associated with the introduction of a new hunting technology, e.g. firearms, head-torches or steel snare wire, may have an even more damaging short-term impact than that predicted by the equilibrium model, if the adoption of the new technology involves a substantial investment which is not readily recoupable (see appendix 3-2). The consequences of non-malleable capital have been explored within the context of over-capitalisation in fisheries (Clark and Munro 2002) and in renewable resources more generally (Kumar 1997), but not specifically in the context of the introduction of new technology. Within terrestrial harvesting systems, short-term non-equilibrium stock collapses may be even more problematic than in the fisheries context, as the loss of extractive values could precipitate habitat conversion (Swanson 1994; Schultz and Skonhofs 1996; Bulte and Horan 2001).

3.5 Complications

As the brief review in section 1.1.3 made clear, density gradients in animal populations and other harvested resources are often observed in relation to distance from human settlements. The problem for the verification of the generic bioeconomic model presented here, however, is that several other processes could produce broadly similar $N(x)$ curves, and none of the studies surveyed in section 1.1.3 provides the detailed data which would be needed to distinguish between them. For instance, if hunters hunt as they travel out from a settlement, rather than hunting and travel being divided into entirely separate activities, then a sigmoidal $N(x)$ curve will be produced simply due to the fact that hunters are more frequently close to the settlement than far from it (see appendix 3-3). Amongst motile, sentient prey, avoidance behaviour alone may produce similar patterns.

Deviations from the patterns of the simple model above may also occur because substantially different economies are associated with harvesting at different distances. Clark and Kirkwood (1979) found that for any given set of bioeconomic parameters either large freezer trawlers or small brine boats were more efficient in the Gulf of Carpentaria prawn fishery. Both types of boat persisted in the fishery, however, presumably because brine boats were more efficient closer to shore and vice-versa. To give a terrestrial hunting analogy; hunters may set snares around their fields, but hunt with firearms deep within the forest. In general such effects are likely to make offtake across space more even.

Any bioeconomic model must of course account for economic alternatives available for the factors involved in harvesting. In general these can be incorporated through an opportunity cost of time and an interest rate on capital, but where these alternatives interact more directly with the stock in question, they must be considered more explicitly. Two such cases are explored in the following subsections.

3.5.1 Multiple prey species

Most consideration of harvesting from multispecies systems has been in terms of the biological interactions between species (e.g. May *et al.* 1979), and due to the potential complexity of these, the practical results have been limited. Clark (1990) did, however, consider economic interactions between harvested species in isolation from biological interactions, but assumed that prices were constant and species were fished with the same gear, which limited the range of potential economic interactions. This section focuses exclusively on economic interactions, but employs a more general and spatially explicit treatment.

Thus far the units of offtake have been individual animals. If more than one species is hunted, then it is likely that the amount of product derived from an individual of each species will, on average, differ, even if the product itself is indistinguishable. Where two species are hunted together, the familiar cost equation can be generalised to the following:

$$C = x \frac{T}{B} + \frac{c_E}{w_1 q_1 N_1 + w_2 q_2 N_2} \quad \text{Eqn 3-27.}$$

where w_1 and w_2 are the number of units of product derived from an individual of species 1 and 2 respectively,

C and B are measured in the same units as w ,

and $c_E = \text{unit cost of hunting effort} = H_1 q_1 = H_2 q_2$.

Ignoring the possibility of biological interactions between the species, the prey population equations in the absence of migration are:

$$\frac{dN_1(x)}{dt} = r_1 N_1(x) \left(1 - \frac{N_1(x)}{K_1} \right) - q_1 E(x) N_1(x) \quad \text{Eqn 3-28a.}$$

$$\frac{dN_2(x)}{dt} = r_2 N_2(x) \left(1 - \frac{N_2(x)}{K_2} \right) - q_2 E(x) N_2(x) \quad \text{Eqn 3-28b.}$$

Hence:

$$E(x) = \frac{r_1}{q_1} \left(1 - \frac{N_1(x)}{K_1} \right) = \frac{r_2}{q_2} \left(1 - \frac{N_2(x)}{K_2} \right) \quad \text{i.e.}$$

$$\frac{1 - \frac{N_1(x)}{K_1}}{1 - \frac{N_2(x)}{K_2}} = \frac{r_1}{q_1} \Big/ \frac{r_2}{q_2} \quad \text{Eqn 3-29.}$$

So the relative impact of hunting on either species is determined by the relative values of their intrinsic growth rates and catchabilities, which mirrors Clark's result that it is the "bio-technical productivity" of the species that is important, rather than their prices..

Rearrangement of eqn. 3-29 and substitution into 3-27:

$$N_1(x) = \frac{H_1 q_1}{C - x \frac{T}{B} + w_2 q_2 K_2 \left(\frac{r_1 q_2}{r_2 q_1} - 1 \right)} \Big/ \frac{w_2 K_2 r_1 q_2^2}{K_1 r_2 q_1} + w_1 q_1 \quad \text{Eqn 3-30.}$$

and vice-versa for N_2 .

Figures 3-12 and 3-13 show plots of prey density against x , and supply and demand curves for two species together in comparison to the more vulnerable of the two species in isolation. The first point to note is that unlike the single-species case, deterministic local and eventually global extinction is possible for the more vulnerable species, as the catch of the resilient species means that it remains profitable to hunt at levels where the population of the susceptible species falls to zero. The region over which the susceptible species is exploited at equilibrium is narrow as it is driven to local extinction at relatively low levels of hunting intensity, at which the other species persists at substantial densities. Where both species are hunted together, their population levels are lower than that which would occur if either one of them were hunted in isolation, as hunting of each is subsidised by the catch of the other. As the region of exploitation of the susceptible species is narrow and its productivity low, however, its presence has little impact on the abundance of the resilient species, or on the overall yield from the system.

Figure 3-13 shows that the impact of each species on the other is potentially more complicated when demand effects are considered, however. If demand is inelastic, the reduced supply in the absence of one species would lead hunters to harvest at a higher unit cost, reducing the population of the other to low levels over a greater distance. In the illustrated example, the impact on the susceptible species is much less severe in the presence of the resilient species when demand is inelastic (cf. results in section 2.3).

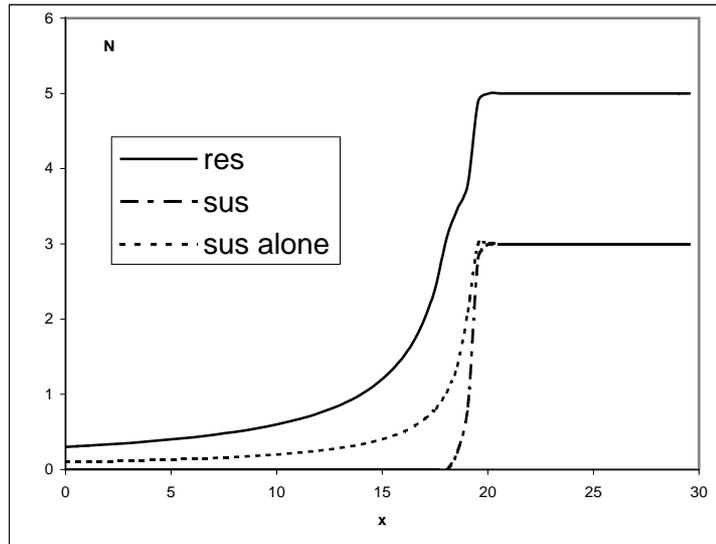


Fig. 3-12. N versus x for a resilient and susceptible species in the two species model, and for the susceptible species in isolation. The curves were derived from equation 3-30 with the following parameters – $C=1, T=10, B=200, qH=15$; resilient species: $r=0.4, K=5, w=50$; vulnerable species: $r=0.2, K=3, w=100$. I.e. the species susceptible to hunting is larger than the other, with a lower intrinsic growth rate and carrying capacity.

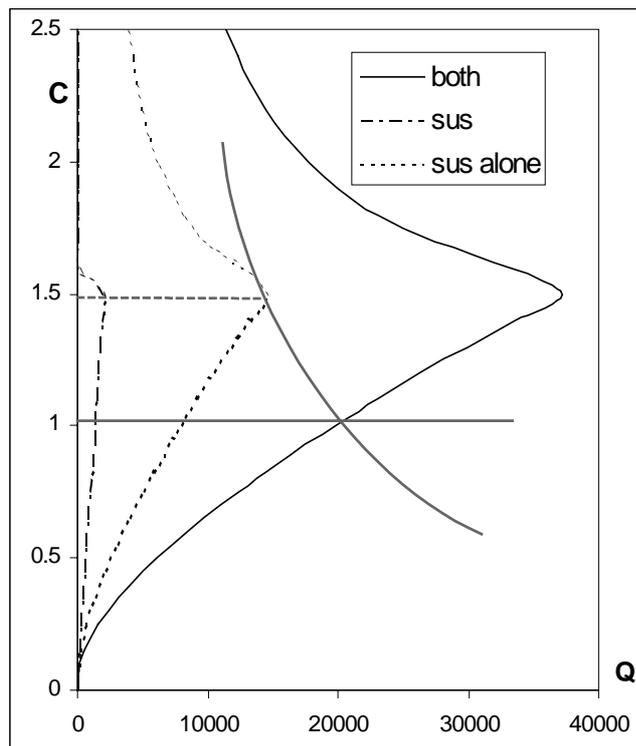


Fig. 3-13. Supply (C) curves for both species together, for the susceptible species as a component of the joint supply, and for the susceptible species alone. The thick grey lines show perfectly elastic and strongly inelastic demand functions. Under either demand function the outcome would be the same if the two species occurred in combination. If the susceptible species were to occur on its own, however, the equilibrium stock under inelastic demand would be far lower than that under elastic demand, and even lower than if it were to occur in combination with the resilient species. The supply curves were calculated by multiplying up linear results according to the area of habitat occurring at each x within the notional 30km radius island.

In the presence of migration, the results would be broadly similar, but large differences in the strength of migration between species would affect the relative abundances of the species in areas where they are hunted together. The species with the higher rate of migration would occur at relatively higher density as immigration would buffer the population of that species whilst encouraging higher hunting effort than could be supported by entirely autochthonous production.

In economic terms, prey populations interact through a subsidy effect (opportunistic by-catch of either species increases the overall return whilst hunting the other) and a crowding-out effect (supply of either species reduces demand for the other). If species are hunted together and demand is perfectly elastic (which was the case considered by Clark), then only the subsidy effect will be operative. If the species are hunted separately, hunters should equalise the unit cost of hunting between species as well as between areas:

$$C - x \frac{T}{B} = \frac{H_1}{w_1 N_1(x)} = \frac{H_2}{w_2 N_2(x)} \quad \text{Eqn 3-31.}$$

Hence at any given cost, the harvesting pattern for each species would be the same as if it occurred in isolation, so there is no subsidy effect. The strength of the crowding-out effect will depend upon the elasticity of demand as before.

Figures 3-14a and 3-14b illustrate relative prey density plots for cases where species are hunted together and separately respectively. If we relax the assumption that the values of the products derived from the two species are the same, then if the species are hunted together, a hunter should reject the lower value species where:

$$\frac{R_h}{F_h + \frac{H_h}{N_h}} > \frac{R_l}{F_l} \quad \text{Eqn 3-32.}$$

where R_h is the return from the high-value species, and R_l that from the low-value, and F is the fixed cost, i.e. transport plus any handling cost.

As the switching point is independent of the density of the low-value population, it could occur where the relative density of the high-value species is higher, or, if $H_l < H_h$, conceivably where it is lower, producing prey density plots illustrated in figures 3-14c and 3-14d respectively. Note that by eqn 3-29, in the region where they are hunted together, the relative density curves for the two species cannot cross. In the differential value scenario, however, the curves can cross at the discontinuity where the lower value species is rejected (fig 3-14d). For species with different values hunted separately, the curves become entirely independent and so may cross at any point.

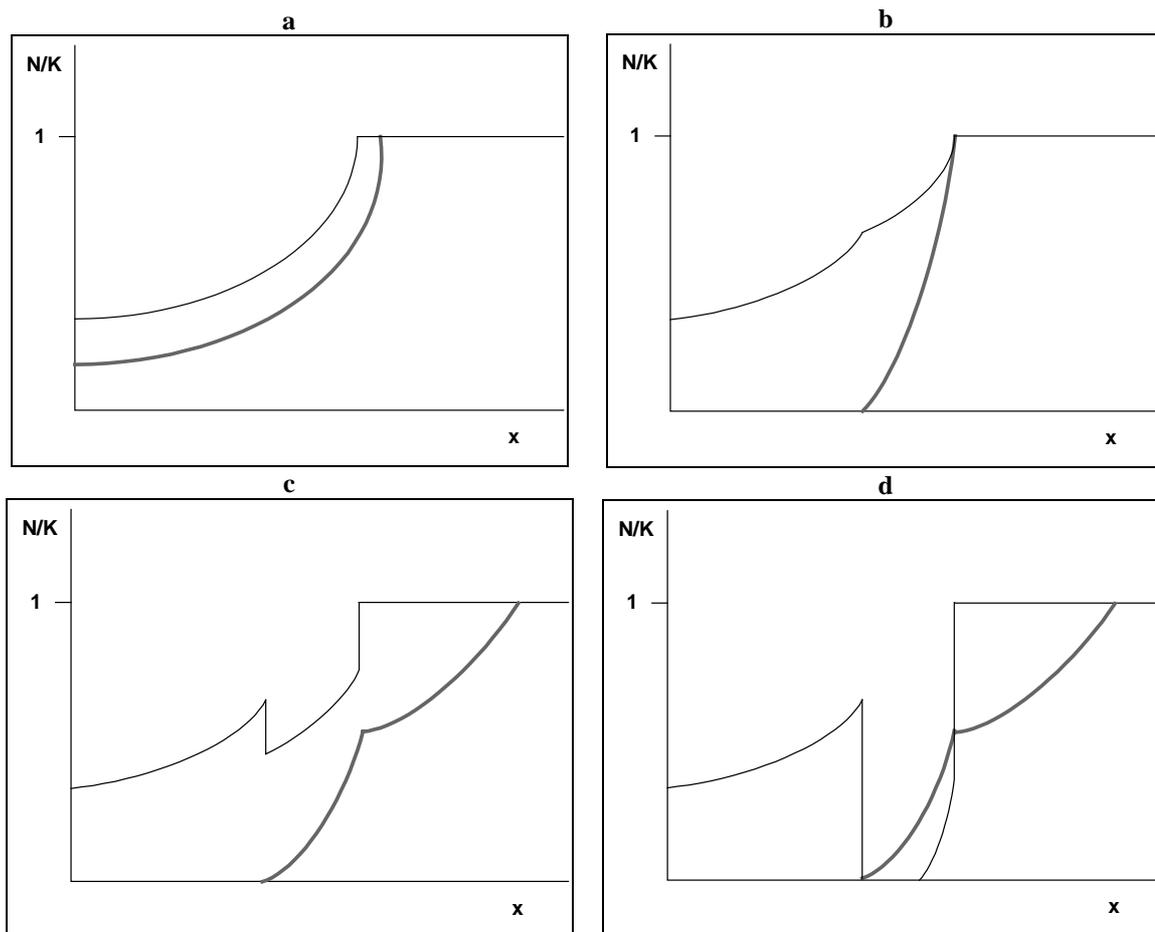


Fig 3-14. Forms of N vs x curves for a 2 species system. Note that relative population density N/K is displayed, rather than absolute density N .

a) Species yield identical products and are hunted together. The more susceptible species (i.e. that which has a lower value of r/q) is represented by the thick grey line.

b) Species yield identical products and are hunted separately. The more susceptible species (i.e. that which has a lower value of H) is represented by the thick grey line.

c) Species yield products of different value and are hunted together. The more valuable species (i.e. that for which RB is higher) is represented by the thick grey line, and has a lower value of r/q in this case.

d) As (c), but the more valuable species has a higher value of r/q .

Allowance for different product values also implies, however, that there is more than one relevant demand curve, so unless both demand functions are known to be perfectly elastic, the dynamics of the system cannot be understood in terms of a single 2D supply and demand diagram. Whether the choice is between hunting techniques or prey encountered through a single technique, adding uncertainty to the system would also increase the range of hunter decisions, and the complexity of the relationship between the species. Time-limited hunters may initially concentrate on a high-value species, but then switch to a low-value alternative if they do not have early success.

3.5.2 Alternate land uses

Several authors have previously provided case specific models of the conflict between extractive uses of wild or semi-wild area, and more intensive uses, typically agriculture, involving their conversion (Swanson 1994; Schultz and Skonhofs 1996; Bulte and Horan 2001), and concluded that in the face of alternative land uses, a form of investment in wildlands is necessary. But an explicit consideration of space and transport costs shows that there does not need to be an investment in wildlands for them to persist. In fact, because agricultural lands are usually private and wildlands public, it is generally safest to assume that there will be no investment in harvested systems, even when these are more profitable than agricultural alternatives. The extent to which habitat is exploited or converted will depend on an interplay of transport costs with demand and the availability of labour.

Consider an isolated village in a wildland area producing goods derived from hunting, or the harvest of renewable resources more generally, in natural habitat, and agricultural products derived from the conversion of that habitat. Agricultural products are characterised by a comparatively low value per unit volume, a high volume produced per unit land area, and a small area of production per unit labour. The demand for both is entirely endogenous. High transport costs place a limit on the radius of agricultural conversion; agricultural goods will be produced from a small area close to the village, and wild products harvested from a larger area at greater distance.

For a given availability of labour within the village, the amounts of each product produced will depend on the inherent preferences for them and the ratio of harvesting costs. Imagine there is a constant substitutability, s , which determines the change in the consumption ratio in response to a change in the cost ratio, such that:

$$\Delta \frac{Q_h}{Q_a} = s \Delta \frac{C_a}{C_h} \quad \text{Eqn 3-33.}$$

where Q_a and Q_h are quantities of agricultural and harvested production, and $C_{a/h}$ denotes their production costs.

Note that s is not exactly equivalent to the cross-price elasticity of demand as does not incorporate an income effect, only a substitution effect.

Agricultural production will be directly related to the area land cultivated, whereas figure 3-6 and later supply curves suggest that harvesting production is more closely related to the maximum radius over which harvesting occurs than its square. I.e.

$$Q_a = a_a \cdot x_a^2 \quad \text{and} \quad Q_h \approx a_h \cdot x_h \quad \text{Eqn 3-34.}$$

where $x_{a/h}$ is the maximum distance at which agricultural / harvested products are produced, and $a_{a/h}$ is a constant.

Note that we are ignoring harvested production from the area of habitat that is converted to agriculture as the area close to the village should contribute little (see fig 3-3).

Ignoring migration, the unit cost of harvested production at x_h will be equal to the cost of harvesting at maximum stock density plus the transport cost over the distance x_h . The marginal cost of agricultural production will similarly be equal to a constant cost of cultivation, plus the cost transport cost at the furthest distance. Thus changes in production costs at the margin are related to x as:

$$\Delta C_h = t_h \Delta x_h \quad \text{and} \quad \Delta C_a = t_a \Delta x_a \quad \text{Eqn 3-35.}$$

where $t_{a/h}$ represents unit transport cost.

If there is an increase in labour through population growth or an increase in demand (i.e. a substitution of leisure time for production), then substituting 3-34 and 3-35 into 3-33 gives:

$$\frac{a_h \Delta x_h}{a_a (x_a + \Delta x_a)} = s \frac{t_a \Delta x_a}{t_h \Delta x_h}$$

$$\therefore a_h \cdot t_h \Delta x_h^2 = s \cdot a_a \cdot t_a (2x_a \Delta x_a^2 + \Delta x_a^3) \quad \text{Eqn 3-36.}$$

From the intrinsic properties of the two products, it is expected that $t_h \ll t_a$ and $a_h \ll a_a$. Hence as long as s is not excessive, equation 3-36 would imply that the increase in the width of the region harvested will be far greater than the increase in the width of the region cultivated.

If transport links between the village and the outside world are developed over time, such that the unit cost of transport to local markets falls steadily, then the possibility for trade complicates the situation. Aggregate demand will increase, and with it production, as villagers invest more labour to produce a surplus for trade. As transport costs continue to fall, there will also be a shift in the comparative advantage of the village from harvested products to agricultural products as transport costs become less significant.

The precise outcome will of course depend on a variety of economic factors. It is likely that initially transport costs will be so high that only wild products can be traded with the exterior. Villagers will invest extra labour in harvesting a harvested surplus. Eventually, transport costs may drop to the point at which agricultural products replace harvested production in trade, depending of course on the balance of market prices for the two products. Hence the harvested area may fall back to that needed only for subsistence. Agricultural products could eventually be traded for external harvested products or their substitutes if:

$$\frac{C_a}{C_h} < \frac{P_a - T_a}{P_h + T_h} \quad \text{Eqn 3-37}$$

where $P_{a/h}$ is the market prices and $T_{a/h}$ is the unit transport cost to the market, and $C_{a/h}$ is given by the point of endogenous production at which subsistence needs for harvested products are met.

It may even become viable to trade harvested products for externally produced agricultural goods, if the reciprocal conditions of equation 3-37 are met. And eventually greater access to capital and/or labour from exterior markets may vastly increase the overall productivity of the village.

The general point is that not only are several outcomes possible, depending on economic and production factors, but that a series of switches between radically different production states and zones of cultivation and extraction could occur in response to a steady change in only one variable, transport costs to market. Time lags in the system, such as the loss of harvesting potential from habitat converted for agriculture, may mean that the end result is dependent on the precise sequence followed. And from a conservation perspective, the desirability of the various pro-agriculture or pro-extraction scenarios will depend on the nature of the conservation resources of most concern, the overall productive capacity in the different sectors, and the probability that the wild resources will be well managed. Clearly the consequences of simple, uni-directional processes such as increased market access are not generalisable without detailed knowledge of the economic circumstances.

3.6 Conclusion

The addition of a spatial aspect provides for a wider range of behaviour than that of the original Schaefer model. The preceding sections should have made clear that there are no simple generic answers to most of the questions regarding the sustainability of harvested systems. The value of an explicit spatial bioeconomic model, however, is that it makes clear the role of various assumptions which are often made implicitly. Hence contradictory results from apparently similar models can be resolved. The difference in the conclusions of Keeling *et al.* (1999) and Winterhalder and Lu (1997) with respect to the effect of the presence of a hunting-resilient species on a susceptible one is essentially due to different demand schedules. Keeling *et al.* assumed perfectly elastic demand, so only the subsidy effect was in operation (reinforced in this case by a unique transport cost function), and survival of the sensitive species was prejudiced, whereas Winterhalder and Lu examined Neolithic subsistence hunting where demand was highly inelastic, and hence crowding out enhanced the survival of more susceptible species.

Wilkie *et al.* (2000) predicted that road building in the Congo Basin would have an extremely negative impact on wildlife populations. This conclusion accords with conventional logic that increased access leads heavier exploitation over a wider area, but was actually contradicted by D. Wilkie (verbally) himself in 2002, when he suggested that one of the reasons for increased bushmeat harvests in West Africa was a decline in agricultural income due to degradation of the transport network. Section 3.5.2

shows that such contradictions should be expected because sweeping conclusions such as increasing access is prejudicial to wildlife are too facile to hold in all cases, even if generally true.

Static sustainability indices were shown to reveal little about the actual stability of a harvested system in chapter 2 partly because the relationship between offtake and stock size is not monotonic, even when the system is in equilibrium. Once spatial structure is included, however, this relationship is even more flexible and therefore an even less reliable basis for inference. In the case of two species harvested together under inelastic demand illustrated in fig 3-13, the offtake of the susceptible species is much higher when it occurs on its own, although the stock size is much greater when it occurs in conjunction with the resilient species.

Conclusions drawn in other cases are also revealed to be less clearcut once viewed in the context of the model. Comparing two indigenous communities in the Peruvian Amazon, one hunting with shotguns, and one using only traditional techniques, Alvard (1995a) concluded that new hunting technology had not had a deleterious effect on prey stocks, on the basis that per capita wild meat consumption was similar in both. There are so many potential explanations for this result, however, that it is difficult to draw any firm conclusion from the information that is provided. If demand for wild meat is very inelastic, then it would be expected that a new technology would not have a serious impact, but the conclusion should be drawn no more widely than that. Alternatively, the shotgun hunters may have depleted local prey stocks and hence be travelling farther to provide the same yield, simply substituting higher transport costs for lower hunting costs. Alvard makes the assumption that because shotgun hunting is more effective, it is therefore more efficient, failing to consider costs as well as returns. It is mentioned that amongst the community with shotguns, some members still hunt with traditional bows, suggesting that shotguns may not be clearly advantageous; use of shotguns could be for cultural rather than material reasons. Considering this case in light of a bioeconomic framework does not provide the answers, but it does reveal the questions that should be asked.

The spatial bioeconomic model is therefore conceptually useful, and chapter 2 illustrates how, with a little familiarity, it provides a way of understanding the dynamics of a complex system through a simple graphical representation. The patterns of prey density produced accord with the studies listed in section 1.1.3 that have noted spatial structure, and moreover the skewed distance-offtake-profiles is reminiscent of the data obtained by Milner-Gulland and Clayton (2002) on the origin of wild pigs sold at a Sulawesi market. But appendix 3-3 reveals that similar coarse spatial patterns do not themselves prove that the model is appropriate. It remains unclear whether the spatial structure used in the present model is generally appropriate, and whether the model is of any use in a practical, applied setting. Moreover, the work in this chapter has only considered stability implicitly, drawing inferences from the shapes and curves and therefore likely positions of equilibria. Even in the phase-plane diagrams of chapter 2, the dynamics considered explicitly are only those of the market equilibrium. In a spatial bioeconomic model there are separate equilibria associated with each of the three eponymous aspects; the equilibration of unit cost over space, of population growth and offtake, and of supply and demand.

Naturally all of these processes will interact, with abundant potential for complexity in the system as a whole.

The next three chapters develop a case study which aims to test, at least in some aspects, the practical applicability of the generic model presented in this chapter.