# CHAPTER 2: EXPLORING SUSTAINABILITY AND THE BIOECONOMIC APPROACH

This chapter develops some basic theoretical models addressing the stability of harvested populations in light of considerations raised in chapter 1. It demonstrates how this leads logically to a bioeconomic approach, and reviews the distinctive aspects of bioeconomics.

## 2.1 Stability of exploited populations

Some conservation professionals still profess the opinion that hunting is unlikely to lead to extinction because the last few animals are always difficult to kill (e.g. J. van der Ven pers. comm., M. Poulsen pers comm.) From an anthropocentric perspective this is an understandable view; an individual hunter may find it very difficult to locate a last few animals. But from the perspective of the prey, the opposite conclusion may seem more obvious; the probability of encountering hunters in a heavily exploited habitat will be high. Many prey populations have clearly been reduced to low levels by hunting. Of primary importance to conservationists amongst others is to determine whether this represents a new stable equilibrium, an unstable, extinction-prone equilibrium, or simply a waypoint in a continuing decline. To examine the stability of a low-density equilibrium, we need to employ the more formal logic of population regulation.

## 2.1.1 Population regulation and density

Any source of mortality may reduce the level of a population equilibrium and is hence a limiting factor, but that does not imply it is a regulating factor. Regulating factors must show positive density dependence, i.e. the mortality rate become more severe as population density increases (see fig. 2-1). Both regulating and non-regulating factors affect equilibrium population size, but only regulating factors control population size, in the sense that a stable equilibrium cannot occur in the absence of regulating factors. Without density dependence, even if the average growth rate is zero or slightly positive, random fluctuations in the number of deaths or births will cause the population to drift to zero, and it becomes impossible to make any specific predictions about population size.
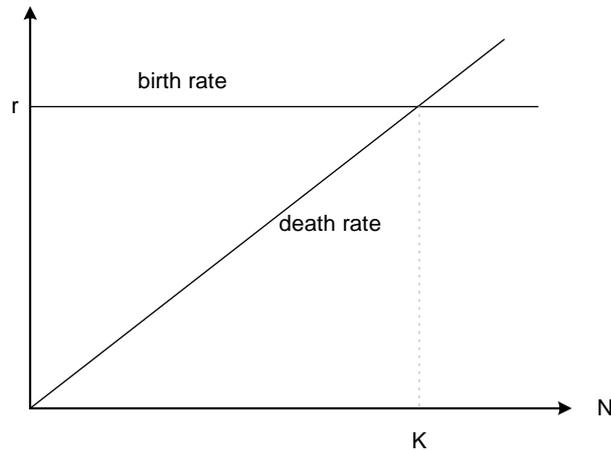
**Fig 2-1 (after Sinclair 1989). Per capita birth rate r is constant, but the per capita death rate is directly proportional to population density, *N*. The growth of this population is described by the logistic equation, *dN/dt = rN(1-N/K)*. At *N = K*, the death rate equals the birth rate, and the population reaches a stable equilibrium.**
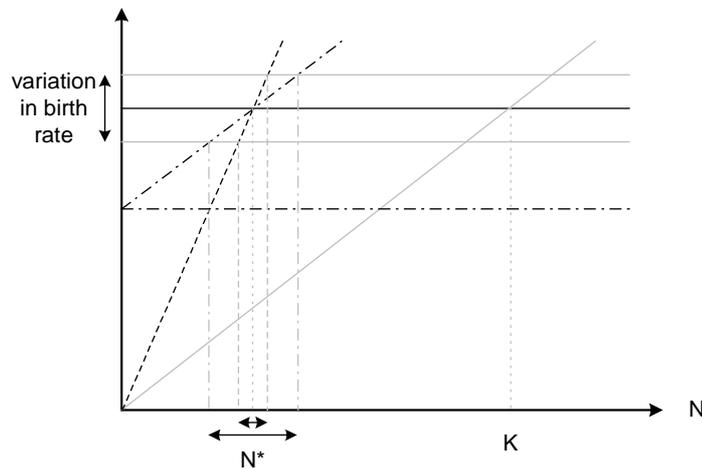


**Fig 2-2. A population has been reduced from *K* to a new equilibrium density, *N\**. This reduction could result from an increase in the severity of d.d. mortality (shown by the dashed line), or the effects of a new d.i. mortality (shown by the dot-dash lines). Given stochastic variation in the birth rate, the outcome of these two scenarios are not equivalent. The addition of d.i. mortality leads to far greater variation in the transient population equilibrium about *N\**.**

Even if an increase in the severity of a regulating (density dependent, d.d.) factor and a non-regulating (density independent, d.i.) limiting factor result in the same equilibrium population density, the behaviour at that equilibrium will not be the same, as is illustrated in figure 2-2. The equilibrium population density $N^*$ in figure 2-2 varies in response to stochastic variation in the per capita birth rate *r*. The magnitude of the variation in the equilibrium density is clearly proportional to the gradient g of the combined mortality curve, which is determined by *d*, the proportion of overall mortality that is accounted for by the d.d. factor. If *r* varies with a constant CV, then the CV of $N^*$ is given by:

$$CV_{N*} = \frac{r}{gN} = \frac{rN*}{drN*} = \frac{1}{d}$$
**Eqn 2-1.**

The variation in population density at equilibrium is not exactly the same as the variation in $N^*$ (appendix 2-1), but using the reciprocal of the variation in $N^*$ as a rough metric of stability nonetheless, it follows that population stability is equivalent to the strength of density dependence.

Note that in the simple continuous population model illustrated by figure 2-2, extinction is impossible because birth and mortality rates are relative to population density, so as density approaches zero, the rate of population change does likewise. Assuming that there exists a critical density below which the population will go extinct through the inability to find mates or other depensatory processes (or simply because it represents a level at which the absolute population size falls to <2), any reduction in equilibrium density is potentially harmful as it brings the density closer to the critical limit. If the limit does not lie particularly close to the new equilibrium, and there is no increase in d.i. mortality, then the increase in extinction risk will be trivial, however. I.e. it is a reduction in the strength of density dependence, rather than low density itself which is more prejudicial to the survival of a simulated, continuous N population.

Considering a spatially extended system where the severity of mortality factors may vary across space, the situation is more complex. Severe d.i. mortality may wipe out animals wherever it is active, but if active in only a proportion of the area, it may have a negligible effect on the survival of the population as a whole. A spatially heterogeneous mortality that was locally density independent, could in fact increase the stability of the global system if its spatial patterning served to strengthen density dependence at the metapopulation level (Hanski and Gilpin 1997), i.e. if it was more likely to act in areas where population density was high.

### 2.1.2 Hunting and population regulation

For a harvested system with variable harvesting effort or spatially heterogeneous harvesting, hunting mortality cannot be represented as a simple function of $N$ as in figure 2-2. But the stability of the system can still be understood in similar fashion as being dependent on the per capita mortality gradient at the point of equilibrium. If offtake Q at a given hunting effort level E is proportional to prey density, i.e.:

$Q = qEN$                                                         **Eqn 2-2.**
*where q is a constant of proportionality known as the catchability,*

then per capita hunting mortality $Q/N = qE$. Therefore the change in hunting mortality rate, $\dfrac{dqE}{dN}$, will depend on the response of catchability and/or hunting effort to a decrease in prey density.

As noted in section 1.1.3, spatial structure is commonly evident in harvested systems, and it is therefore appropriate to consider a spatial system, which necessitates a slight augmentation of the notation. Retaining Q, N and E as the global offtake, population and effort levels respectively, we now distinguish between three measures of catchability:

$q_0$ is the intrinsic local catchability, i.e. the offtake per unit effort per unit prey density at any given point locality, where effort only includes the resources spent on catching the prey at that locality.

$q(x)$ is the extrinsic local catchability at any given locality, adjusted for the effort involved in travelling distance x to that locality.

$q_g$ is the global catchability, accounting for all effort involved in harvesting, i.e. $q_g = Q/EN$.

There are three different processes that affect $\dfrac{dq_g E}{dN}$ :

1. Variation in $q_0$ could occur either in the presence of spatial refugia with higher intrinsic catchabilities, or if prey behavioural responses to hunting pressure caused changes in $q_0$ across the board, and therefore in $q_g$. In the former case, the areas providing better conditions for hunters would likely be exploited first, and with hunters switching to lower $q_0$ areas, and therefore lowering $q_0$, as prey became scarcer.

2. Even if $q_0$ does not vary across space, at some scale $q(x)$ will. If the spatial pattern of hunting varies in response to prey density, therefore, there will also be changes $q_g$. I.e. local changes in hunting effort could potentially impact the density dependence of the system, even without any change in global effort. References to catchability within the fisheries literature typically concern CPUE within a specified fishing ground, i.e. $q_0$, but it is recognised that when searching for dispersed stocks is an important activity, as for e.g. tuna, then the situation is more complicated (Mangel 1982).

3. Overall effort E may respond to prey densities.

Whilst it is recognised that the first category is entirely feasible, it relies upon specific characteristics of the area and species in question, rather than general processes, and will therefore not be considered further at this stage. The following section concentrates instead on examining the likelihood that spatial structure may intrinsically enhance the stability of harvested systems through changes in $q_g$. Finally the latter part of the chapter will consider how to incorporate changes in overall effort, and how these might interact with spatial structure.

## 2.1.3 Exploratory spatial models

The radial patterns of prey density suggested by the studies listed in section 1.1.3, suggested a series of simple central place hunting simulations designed to examine changes in $q_g$ with overall prey density $N$. These models were based on a square grid of cells with a hunter settlement at its centre. Hunters moved out from the settlement and captured a prey with a fixed probability when they encountered an occupied cell. At the start of each run, all cells were occupied by prey. Effort was synonymous with distance travelled by hunters, i.e. there was no difference in effort between traversing an empty or occupied cell, or making or failing to make a capture. Variations in grid size, number of prey per grid cell and the probability of capture were trialled. Random-walk prey movement and reproduction were introduced sequentially. Hunters moved according to a random walk, or in a straight line in a random direction, and later were allowed to switch between travel modes in response to prey encounters. Each hunting trip was limited to a set number of moves, or a set number of captures.

Despite the numerous variations, the patterns produced were fairly typical. Predictably, increases in prey density with distance from the settlement were always observed, with the steepness of the gradient dependent on the strength of prey migration. Catchability did vary with prey number, but rapid decreases in $q_g$ with $N$ came at the very start of the process of prey depletion, when hunters no longer found prey as soon as they moved out from their base. At intermediate stages of prey depletion, $q_g$ tended to be roughly constant as the distance travelled to catch each prey varied inversely with the number of prey remaining. For catch-limited strategies, there was if anything an increase in $q_g$ at the lowest prey levels, although this was overshadowed by the increased variation in the recorded measures of $q_g$, due to sampling effects. An increase in $q_g$ at low $N$ which could lead to stability appreciably greater than that of a non-spatial system was only achieved for distance-limited hunts when the farthest parts of the grid were inaccessible to hunters and therefore provided a spatial refuge (fig 2-3).

A set of simulations also looked at the effect of varying the length and frequency of distance-limited hunts whilst keeping the overall effort rate constant. Unsurprising, longer, less frequent hunts were more efficient when N was low, and the zone of depletion around the settlement larger. This would not aid low density stability as hunters would be more likely to switch to longer hunts as N decreased.

Developing this tactical element, a subsequent model, based on a linear array of cells at progressively greater distance from the settlement, treated travel and hunting as separate activities, each demanding effort. Hunters performed as optimal central place foragers with prior knowledge of prey densities. Each hunting trip could target only one cell, chosen on the basis of minimizing the combined travel and hunting time per prey captured. Hunter effort was initially evenly distributed across space, but was gradually shifted to lower cost cells until a steady state was reached. Prey populations within each cell grew according to a logistic function and spent emigrants to adjoining cells at a constant per capita rate.

**Fig. 2-3. Examples of variation in *q(x)* for a number of simple grid foraging simulations. Simulations took place on a 49x49 cell grid with each cell initially occupied by a single prey individual. Prey movement and, where included, (asexual) reproduction occurred with a fixed probability for each individual at each time step in the event that a empty adjacent cell was available. Hunters always moved in a straight line out from the centre of the grid. The length of each hunting trip was either set at a fixed number of moves, or a fixed number of captures. In all cases $q_g$ is given on the y-axis as the number of prey caught in 10 hunts per total distance moved during those hunts per prey remaining. The x-axis gives the number of prey remaining at the end of each set of 10 hunts.**
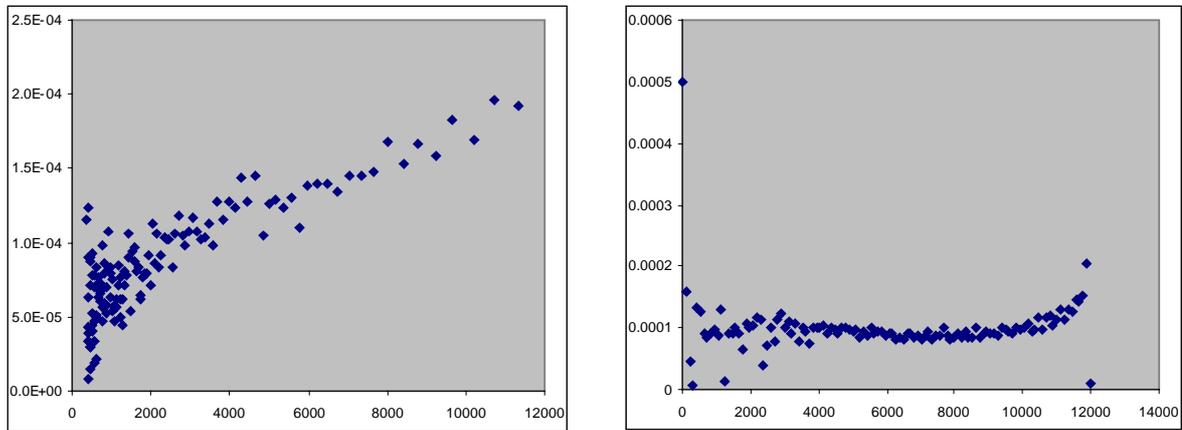


**Prey movement, but no reproduction: a) on the left, shows results for a distance-limited strategy (30 moves), b) gives results for a catch limited strategy (10 prey). The distance-limited strategy shows a decrease in $q_g$, but the effect is only strong where the hunter reaches the limit of his range. The catch-limited strategy produces a relatively constant $q_g$, it although decreases with initial prey depletion. Both plots show an increase in the variability of empirical catchability when prey numbers are very low.**
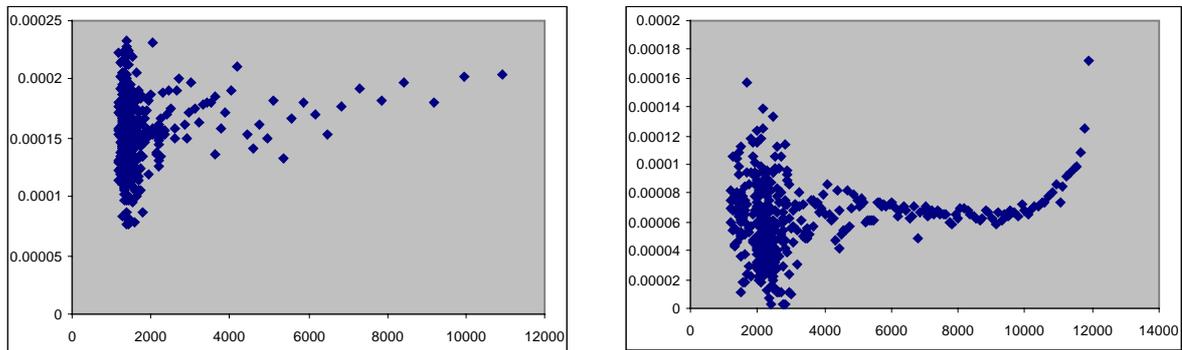


**Results with prey reproduction included: c) on the left, is for a 50-move distance-limited strategy, d) is for the 10-prey catch-limited strategy and prey reproductive rate is half of that in (c). The large cluster of points at low prey numbers represent fluctuations around a stationary point.**

The patterns of this model were again stereotypical. Hunter effort was spread fairly evenly up to a certain distance from the settlement, which was sensitive to the prey growth rate and the balance between travel and hunting costs. At around the limit of the exploited region, a transition from low to high prey density occurred, whose steepness depended on the migration rate.

The change in equilibrium $q_g$ with N was similar to that in the grid simulations; after an initial brief and small fall, $q_g$ actually rose with falling prey number, and did so rapidly at very low prey numbers (fig. 2-4a). The reason is that once the hunters are exploiting the whole area, there is very little further increase in travel effort, so further increases in effort contribute more directly to increasing offtake.

Examination of equilibrium population growth in this model also revealed that due to the spatial structure of the population, at the global level growth did not follow a logistic form, but was instead skewed, with the maximum sustainable yield MSY occurring much lower than *0.5K* (fig 2-4b). The distortion of the growth function is another deviation from the simple, non-spatial conceptual model of figure 2-2 which could affect equilibrium stability, and the skew in favour of higher growth rates at low density might suggest that this influence was positive. Within a spatially stuctured system, overall growth is always lower than that which would occur at the same N in a non-spatial equivalent, however, so it is extremely unlikely that the net effect will promote stability in comparison to the non-spatial case for a given value of *N*.
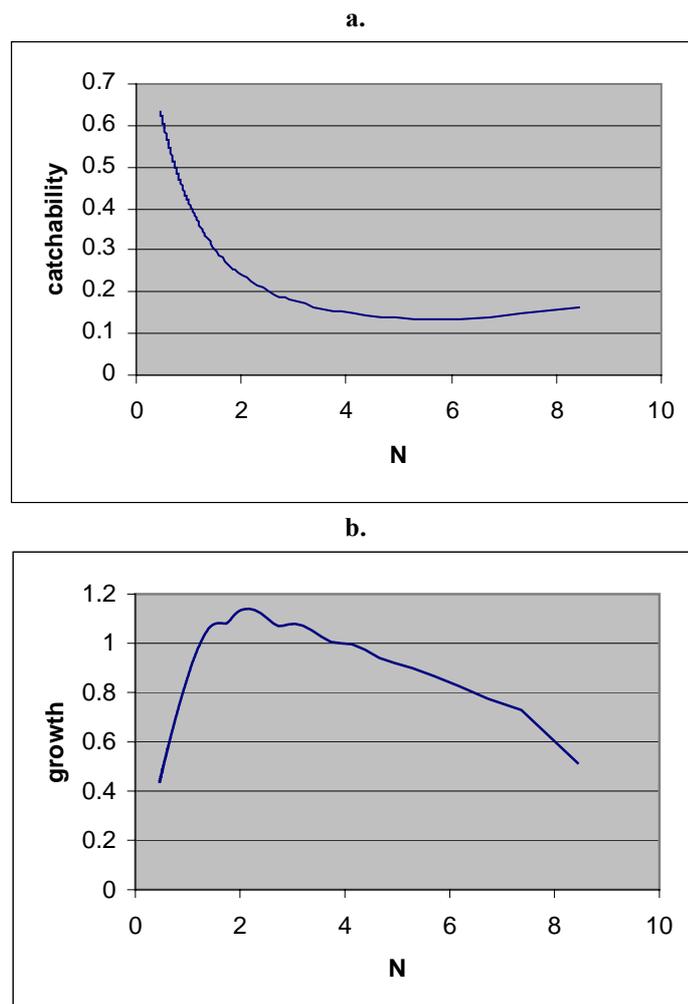
**a.**



**b.**



**Fig. 2-4. Equilibrium catchability, $q_g$ (=CPUE/$N$), (a), and prey growth rate (b) versus total prey population size in a run of the effort distribution model. The model is based on a linear array of 10 cells, each 1km in length and with K=1. The hunter origin is at one end of the array so distance to each cell increases linearly. Within each cell, prey grow according to a logistic function with $r=2$, and disperse to adjacent cells at a per capita rate of 1 per year. Offtake within each cell is proportional to the product of the population density and hunting effort exerted within that cell, with $q_0 = 10$. The effort involved in travel is 0.002 times the return distance to the cell. Unit hunting effort is re-distributed between cells until an equilibrium is reached where the total effort per trip is equal across all exploited cells, given the assumption that each hunting trip can target only one cell and lasts until 0.01 prey unit (i.e. one hundredth of the carrying capacity of a single cell) are captured.**

## 2.2 Bioeconomics

Introducing a second prey species into the effort distribution model shows that a vulnerable species (i.e. with a lower growth rate or higher $q_0$) is shielded by the presence of a species which is resilient to hunting, at any given level of effort (fig. 2-5). This is in contrast to the result of Clayton *et al.*'s (1997) model, concerning the spatial pattern and impact of hunting on two species of wild pig in Sulawesi, one of which is appreciably more susceptible to hunting. Their work and the analytical developments by Keeling *et al.* (1999) showed that the survival of the vulnerable species is prejudiced by the presence of its resilient counterpart, despite the fact that it was based on a similar framework whereby costs were equalised over space. The difference in the outcomes of these two models is informative, and its origin is most clearly explained with recourse to bioeconomics.
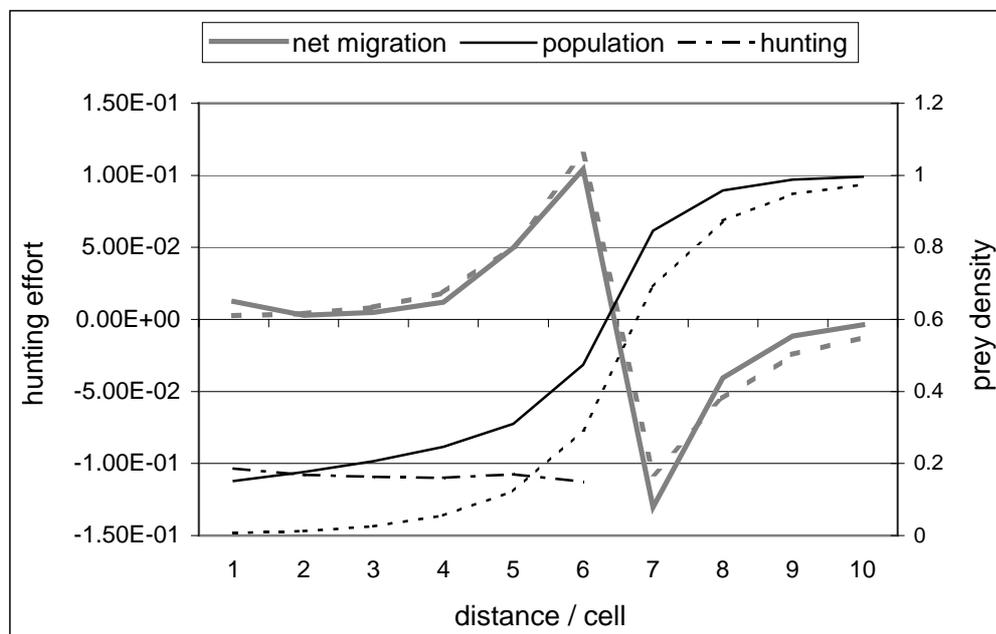


**Fig. 2-5. Migration, population and hunting effort across the 10-cell array for an example of the the 2-species version of the effort distribution model. Parameters are the same as those described in the legend to figure 2-4, except that $q_0 = 5$ for both species, and the vulnerable species has a lower intrinsic growth rate of 1.5. The solid lines give results for the more resilient species, and the dashed lines are for the vulnerable species. The vulnerable species disappears almost entirely from exploited areas, such that the length of the exploited region is determined predominantly by the resilient species. In this fashion the vulnerable species is able to persist beyond the exploited region, even though it would be driven to global extinction if it were present on its own. If the resilient species were to occur alone, the results would be almost indistinguishable from those shown here where it occurs in tandem with its vulnerable counterpart.**

Conrad (1995) defines a bioeconomic model 'as one that seeks to maximise some measure of economic value, subject to resource dynamics.' I.e. they are economic production models which take into account the fact that in the case of biological resources, production is subject to biological limitations. The study of bioeconomics stems from the pioneering work of Gordon (1954), Schaefer (1954, 1957) and Scott (1955) in relation to fisheries. These authors were concerned with static equilibrium models of

cost and offtake as a function of stock size, and were built on simple assumptions of logistic growth and linear catch per unit effort CPUE (i.e. constant $q$). Crutchfield and Zellner (1962) and later Smith (1968, 1969) recognised the time element in the system and treated optimal fishery management as a dynamic optimisation problem. The publication in 1976 of the first edition of Clark's 'Mathematical Bioeconomics: The Optimal Management of Renewable Resources', which was preceded by two high profile articles (Clark 1973a, b), rounded out and solidified the general principles of bioeconomics.

Much of the subsequent work in bioeconomics has sought to incorporate various theoretical niceties, such as stochasticity (Beddington and May 1977), ecological interactions between harvested species (May *et al.* 1979), and the opportunity costs or externalities associated with other economic activities which impact on the fishery (Swallow 1990; Swanson 1994). Returning to the early example of Beverton and Holt (1957), some authors concentrated on overcoming the 'basic reluctance of managers to treat "fishermen" as an active, responsive part of the system' (Allen and McGlade 1986), and examine fishing behaviour and the dynamics of fishing effort explicitly, eventually fitting dynamic models to real fisheries (e.g. Wilen 1976; Bjorndal and Conrad 1987; Opsomer and Conrad 1994).

Fishers have become accepted as independent agents, motivated by their individual welfare and potentially willing to deviate from social contracts to advance it, rather than an amorphous amalgamation of effort or capital perfectly plastic to the designs of optimal control theory (Hilborn 1985). This is turn has led to more earthy models examining the costs of implementing various fishery controls (e.g. Anderson and Lee 1986; Milliman 1986; Mazany *et al.* 1989; Batstone 2001), by incorporating the behavioural economics of law enforcement (see Becker 1968). This development is of clear interest to the conservation community, where the effectiveness and possible perverse incentives associated with management controls are often the prime focus, rather than an embarrassing complication. It is in this vein that bioeconomics has entered the conservation literature in models approaching hunter behaviour through the incentives that they experience (e.g. Leader-Williams and Milner-Gulland 1993; Clayton *et al.* 1997; Hofer *et al.* 2000; Bulte and Horan 2001). Bioeconomic models used in this fashion are essentially a subset of behavioural models in which all costs are expressed in a common monetary currency. Converting from the more typical currencies of behavioural ecology allows the inclusion of tactical hunting models based on optimal foraging theory (e.g. see Dreyfuss-Leon and Kleiber 2001 for where, and Rowcliffe *et al.*2003). But the novelty and power of bioeconomic models is that they can also encompass strategic processes concerned with changes in total effort and investment over time. The alternate paradigm for this within the biological sphere is predator-prey models relying on predator numerical responses (see Winterhalder and Lu 1997 for an application to hunting), but this is clearly of tenuous relevance in the modern world given the almost universal penetration of market economies.

This behavioural use of bioeconomics, in which the desired biological outcome is taken for granted, is a departure from the traditional focus on maximising economic rent from the system. Indeed under Conrad's definition above, these would not even classify as bioeconomic models, and possibly Milner-

Gulland's (1999a) distinction between ecological economics and economic ecology was in a similar light. But semantics aside, they offer a powerful tool for integrating diverse processes into a single framework and describing the dynamics of the whole system.

Clayton *et al.* (1997) and Keeling *et al.*'s (1999) model, in which the sum of unit transport cost and hunting costs for each location was equal to market price of each animal, was explicitly bioeconomic. The effort distribution model above was not as its costs were measured in terms of effort, rather than monetary equivalents. Yet its logical outcome, that unit cost should be equalised over space, was identical. It is important to note that this outcome was predicated on the assumption that hunters are independent agents, free to chose where to hunt; if spatial hunting choices were constrained then spatial cost equalisation would not be predicted. This assumption of open access harvesting is an appropriate starting point because many exploited wild populations, and especially those of conservation interest, are functionally open access. Even where ownership and exclusive use rights do exist, harvesting choices may be understood in terms of open access incentives, overlaid with the additional incentives imposed by penalties for violating social contracts.

The effort distribution and Keeling models therefore both maintain that unit cost:

$$C = h(N(x)) + t(x, N(x)) \qquad \qquad \textbf{Eqn 2-3.}$$
*for all values of x, the distance from the hunter origin,*
*where N(x) is the prey density at distance x,*
*h(N(x)) is the unit hunting cost function,*
*and t(x, N(x)) is the unit travel cost.*

Including population growth *g(N)* and migration *m(N)* functions allows the offtake at any *x* to be determined:

$$Q(N(x), E(x)) = g(N(x)) + m(N(x)) \qquad \qquad \textbf{Eqn 2-4.}$$

Integrating over x would therefore yield global equilibrium values of offtake *Q*, prey density *N*, hunting effort *E* and unit cost *C*. Note that this is essentially a spatial generalisation of the classic Schaefer model, which assumed logistic growth and the offtake function given by eqn 2-2.

Equilibrium *Q*, *N*, *E* and *C* can all therefore be related deterministically to each other, but one must be determined *a priori* in order to calculate the remaining three.

Keeling *et al.* assumed a fixed unit cost determined by the market price for wild pig meat, whereas in the effort distribution model total effort was fixed, and herein lies the contradiction with regard to multispecies results. In the Keeling model the presence of the resilient species reduced average hunting costs and therefore encouraged greater exploitation across a wider area. In the effort distribution model,

the presence of the second species encouraged greater effort at short distances which could only be provided by relieving pressure elsewhere.

Hence equations 2-3 and 2-4 do not specify a complete bioeconomic system. In fact they provide a description of the relationship between unit cost and equilibrium offtake, i.e. they allow an average cost AC curve for the extraction of the resource to be plotted, although this is not done for either of the two models discussed as they concerned a single equilibrium solution where one of the determinants was already known. To describe a complete, self-contained system, it is also necessary to specify the market conditions (i.e. the relationship between the supply curve and the AC curve), the shape of the demand curve, and, in order to examine non-equilibrium behaviour, the industry participation dynamics.

Setting unit cost equal to a fixed market price is equivalent to assuming a perfectly competitive market with perfectly elastic demand. This conflicts with Keeling *et al.*'s statement that, "Evidence from the markets suggests that demand may be inelastic to price," but in reality there is little data available on the elasticity of demand in their study area, and it is probably the statement, rather than the assumption which is in error (E.J. Milner-Gulland, pers. comm.). Fixed effort, as in the effort distribution model, would be more appropriate to an obligate subsistence hunting scenario.

Before specifying forms for the functions in equations 2-3 and 2-4, and examining the behaviour of the model in detail in chapter 2, it is appropriate to review the economic peculiarities of the exploitation of renewable resources, as distinct from typical economic production models, which have necessitated the separate field of bioeconomics.

### 2.2.1 Shape of the open access supply curve

The first point to note is that in an open access system, the supply curve lies along a social AC curve (which is the AC curve calculated from eqns 2-3 and 2-4), not a social cost marginal cost MC curve, as would be the case for a typical industry (appendix 2-2). This engenders a production externality, which has profoundly negative implications for both industry profits and resource stock size. It was the realisation that this externality would lead to rent dissipation, and hence might explain the widespread economic failure of laissez-faire fisheries, which was the foundation for the whole field (Gordon 1954).

The other peculiarity of the supply curve is that it is not monotonic under most appropriate growth functions. Under logistic growth, the MSY occurs at $N = 0.5K$, so if the stock size is depleted below this then supply must fall, producing a humped curve. Figure 2-6 illustrates the AC/supply curve for the Schaefer model.

**Fig. 2-6. Clark's supply curve (price P against yield Y) is actually the AC curve for harvesting from a non-spatial population with logistic growth and constant catachability (i.e. the Schaefer model). This will also be the equilibirum supply curve if there is open access to the resource and a perfectly competitive market. (Reproduced from Clark 1990.)**

The externality and the humped supply curve each exacerbate the negative impact of the other. In the absence of the hump, the externality could produce a reduction in efficiency, but not in the absolute supply, and in the absence of the externality, the resource would never be exploited beyond the MSY, whereas with it, exploitation may occur beyond the hump and even down to the point of stock extinction.

The economic equilibrium is of course given by the point at which the demand curve intersects the supply curve, and as location on the supply curve is related to the state of the stock, the shapes of the supply and demand curves can tell us much about the expected equilibrium stock level at a glance. Figure 2-7 shows a generic supply curve for a renewable resource. Given low, elastic demand, an equilibrium occurs at $Q_2$ below the MSY with a low hunting cost, and this is likely to represent a stable harvested population. A low, inelastic demand curve also produces a stable, low cost equilibrium at $Q_3$, but another unstable equilibrium point occurs for this system at $Q_1$. Given high, elastic demand, an economically stable equilibrium occurs at $Q_1$, but this probably occurs at a point at which the stock level is already very low and is unlikely to be biologically stable. Given the very high, inelastic demand curve, no economic equilibrium is possible, and under open access eventual prey extinction is inevitable.

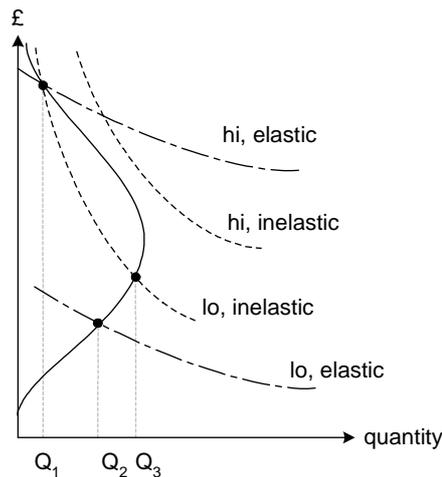The effect of system parameters on the shape of the supply curve will be a major theme of chapter 3.

**Fig. 2-7. AC curve for hunting (solid line) with four possible demand curves, representing high or low, and elastic or inelastic demand.**


### 2.2.2 Ownership and supply

If the exploited resource in question is controlled by a sole owner, then basic microeconomics suggests that he would supply according to the marginal cost of harvesting in order to maximise revenues. In the case of a renewable resource, however, because rents derived from the future growth of the exploited population cannot be obtained immediately, these are liable to be time-discounted, and the size of the discount rate will affect the optimal equilibrium stock size and supply. Clark's (1990, p.137) 'discounted supply curves' for the Schaefer model are effectively discounted industry marginal cost curves, i.e. plots of $C - (Q \frac{dC}{dN} \big/ (\delta - \frac{dQ}{dN}))$ versus $Q$, where $\delta$ is the discount rate. At discount rate $\delta = 0$, this reduces to the instantaneous MC curve, $\frac{dQC}{dQ}$; at $\delta = \infty$, it is the same as the AC curve given by the equilibrium value of $C$. The curves for all finite positive values of $\delta$ lie between these two extremes (fig 2-8).

A sole owner's optimum is to supply at the point where demand intersects the discounted MC curve. The societal optimum is the same, but note that the social discount rate may well differ from that of an individual sole owner. Appropriate societal discount rates are generally considered to be much lower than commercial discount rates, especially where issues of intergenerational equity are involved (Price 1993; Portney and Weyant 1999). If the sole owner has a monopoly over the total market supply, rather than just the supply from the area in question, then his optimal strategy is to supply at the point at which the discounted MC curve is intersected by the marginal revenue MR curve (see appendix 2-2). Hence in the case of an industry monopoly the social and monopoly optima will diverge even if the appropriate discount rates are identical, although the monopolist's optimum will actually be more conservative with regard to equilibrium stock size. Although the sole owner or monopolist's optimum is usually treated as the expected outcome, it should be recognised that the actual outcome in specific

cases of sole ownership may deviate from it. In a competitive market, competition serves to enforce the predicted outcome, so if all the assumptions of perfect competition are met, the competitive equilibrium must eventually be reached. In the case of a sole producer, however, there is no such mechanism and the outcome will be influenced by his individual ability to discover his optimal strategy.
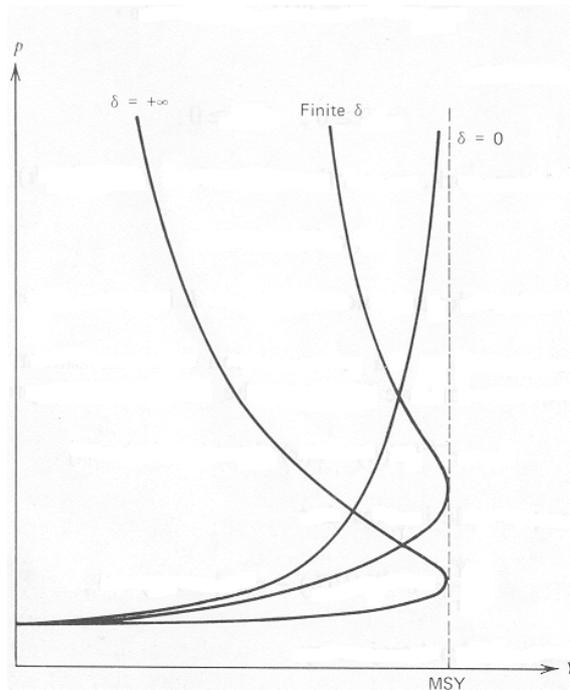


**Fig. 2-8. Discounted MC curves for harvesting from a non-spatial population for different discount rates δ. (Reproduced from Clark 1990.)**

### 2.2.3 Supply and demand dynamics

Another peculiarity of the supply and demand diagram for open access harvesting of a renewable resource, again due to the influence of stock size on cost and equilibrium offtake, is the fact that it may be used to infer the dynamics of the system in addition to the equilibrium outcome. Given that the AC curve describes the population equilibrium offtake at any given cost, it must also be a cost null-cline. If there is no change in population size then there can be no change in average cost. If the point of supply does not lie on the demand curve, however, then either a profit or loss is being made by harvesters and the competitive market theory requires that there will be a corresponding change in production effort. The demand curve therefore represents an effort null-cline. But if the point of supply does not lie on the AC curve, then the system cannot be in biological equilibrium; stock size must change and cost and offtake with it, even if effort remains constant. The supply null-cline does not therefore lie on the demand curve. Instead it must lie somewhere between the supply and demand curves where the contrary effects of changes in stock size and effort cancel out. If the relationship between profit and the change in effort is known, therefore, then the trajectory of the system can be determined for any point of supply on the supply and demand diagram (fig 2-9).
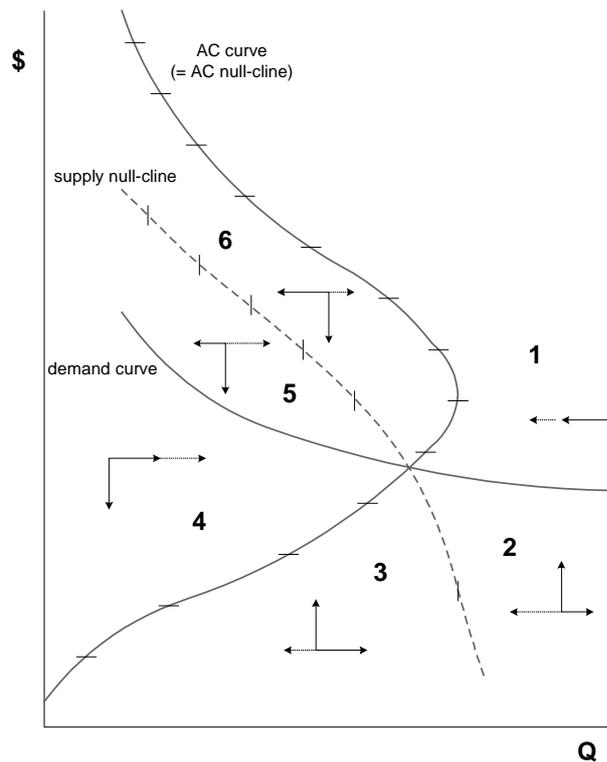
**Fig. 2-9. Phase-plane behaviour of supply and demand diagram for an open access renewable resource. The vertical vectors show the change in AC; the solid horizontal vectors show the change in supply due to changing effort, and the dotted horizontal vectors show the change in supply due to the change in the prey population. In sectors 2, 3, 5 and 6, the processes affecting supply act in opposite directions. In sectors 2 and 5 (closer to the demand curve), the change due to the change in prey density is stronger than that caused by changing effort; in sectors 3 and 6 (closer to the population equilibrium AC curve) the situation is reversed. The supply null-cline occurs where the two tendencies balance each other. Its position is determined by the relative speed with which the market adjusts, and hence the dotted line in the figure is illustrative only.**

Clearly the position of the supply null-cline will depend on the relative strength of the effects of stock size and profit on production. If industry response to the profit incentive is very rapid, then it will lie close to the demand curve, and close to the AC curve otherwise. The dynamic behaviour of the system is therefore determined by the shapes of the supply and demand curves and the relative speed of industry adjustment. Figure 2-10 illustrates some of the possibilities.

Previous authors have represented dynamic bioeconomic models in terms of phase-plane diagrams of effort versus stock size (e.g. Conrad 1995; Bulte and Horan 2001). These have been restricted to cases in which price is treated as a constant, however, as in the absence of perfectly elastic demand, there is no intrinsic relationship between stock size and profit, and so the location of the effort null-cline is not conceptually obvious. Recognizing the potential of the supply and demand plot to serve as a phase-plane diagram provides a visual means of understanding the effects of component processes on overall system dynamics fairly readily, as well as describing these in terms of properties that may be more readily measurable.
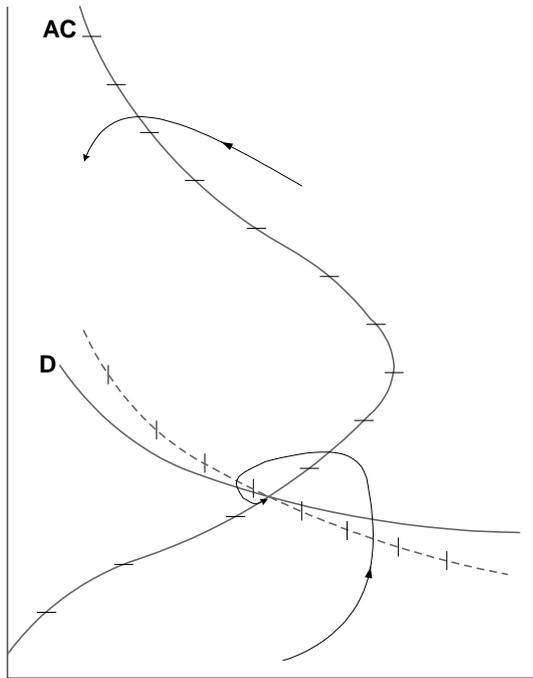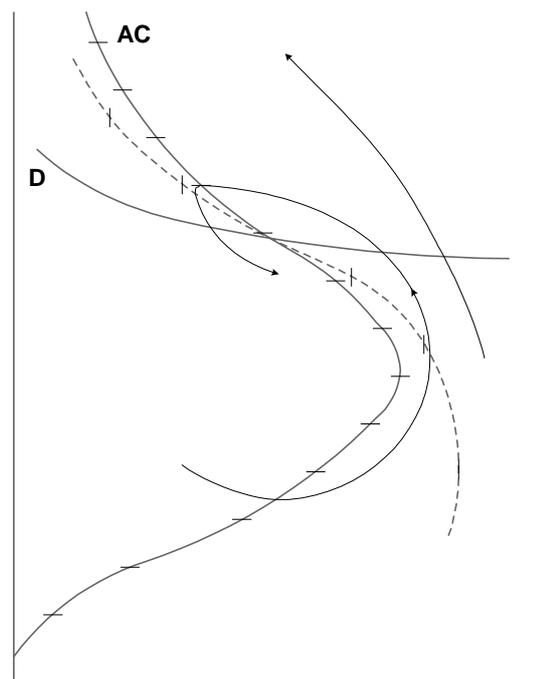
**a) low demand, fast market adjustment: focus.**
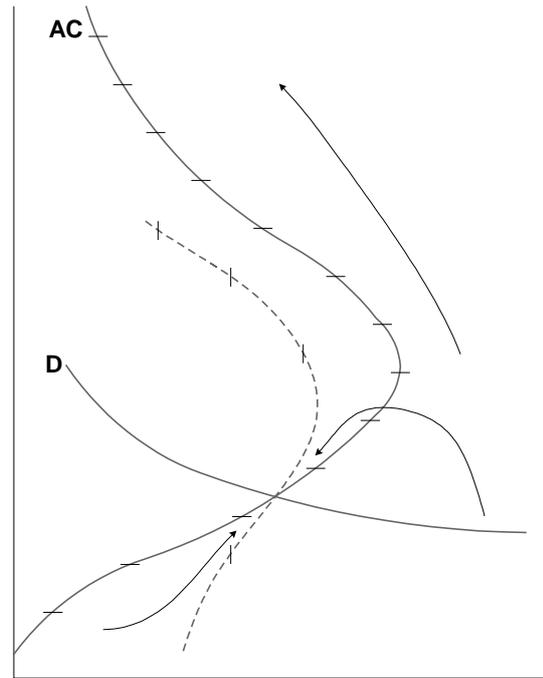
**b) low demand, slow market adjustment: node.**
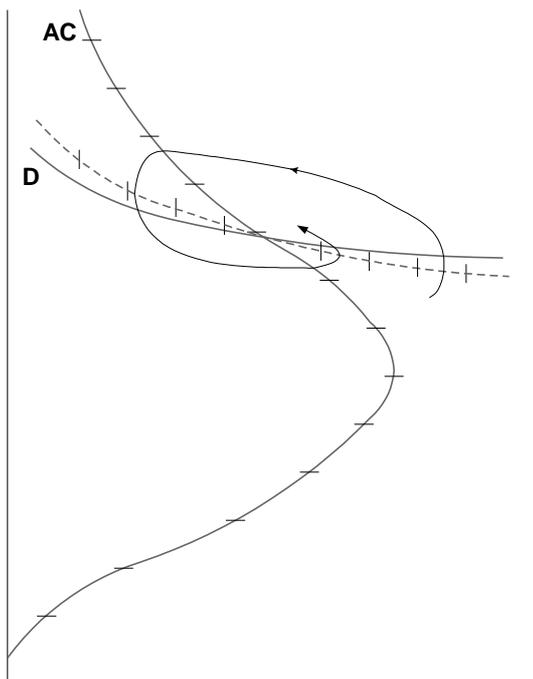
**c) high demand, fast market adjustment: focus.**

**d) high demand, slow market adjustment: focus.**

**Fig. 2-10. Examples of possible trajectories for different market conditions. Where market adjustment is slow, the situation is generally less stable with more risk of supply overshooting the population equilibrium level. Situation (d) is least stable; even when supply and cost are initially low, the dynamic trajectory may come close to dramatically overshooting the equilibrium.**

**2.3 Conclusions**

Hunting is an important threat to many species, particularly large vertebrates, many of which occur at very low and highly uneven densities even where substantial areas of habitat remain. Basic population ecology concepts suggest that the prospects for stability and therefore persistence of low density populations are not high unless the mortality factors responsible for reducing their densities are strongly density dependent. Constant effort harvesting is not generally considered to produce density dependent mortality. Recognition of spatial structure associated with transport costs in harvested systems can introduce some density dependence, but the indications are that it is unlikely to have a strongly stabilising effect. Increases in mean travel distance with stock depletion should be expected to produce a decrease in $q_g$, but the effect appears to be very weak once the majority of the resource is already being exploited, and may even be reversed at very low N. In a spatial context, low density populations may be stabilised by in-migration from an adjacent source, and hence a system with spatial refugia can be more stable than a non-spatial system of identical global population size. If all areas are exploited, however, within a simple Ricardian framework whereby hunters chose foraging areas so as to minimise their overall costs, spatial structure is unlikely to contribute intrinsically to the stability of the system. Theoretically, it could only do so, if there was some form of over-adjustment to local prey density whereby copycat hunters followed the spatial harvesting choices of others beyond the point at which these ceased to provide a greater than average return. Such a system would parallel rotational harvesting and might potentially be relevant to situations in which the resource was aggregated and ephemeral, and exploration costs were significant.

In general, however, understanding the capacity of hunting mortality to regulate an exploited population will depend upon incorporating changes in hunting effort in response to stock levels. Within this context, spatial structure may be very important as it can fundamentally affect the form of the relationship between global stock levels, offtake and intrinsic population stability. The appeal of bioeconomics is that it allows prey population dynamics, tactical elements of hunter behaviour and broad-scale industry responses to be combined in a single framework. In addition, supply and demand diagrams provide a way of understanding both the equilibrium and dynamic behaviour of a complex system within a straightforward visual medium.

To date, the only widely practised method of assessing the sustainability of hunting has relied upon estimating the MSY of the harvested area (see Robinson and Redford 1991) and the current offtake. If offtake is less than the MSY, then this is taken as some indication that the harvest is sustainable, and vice versa. Leaving aside the practical problems of estimating these quantities, stochasticity and the desirability of some form of 'natural insurance' (Roughgarden and Smith 1996), viewing hunted systems as a dynamic spatial system reveals at least three reasons why this approach tells us little about sustainability:

1.  The MSY is typically calculated for the prey population as a whole, i.e. assuming that offtake is even across the population. Over large hunting ranges, where travel costs are significant, it is unlikely that open access harvesting will be applied evenly across space, and so MSYs calculated on a non-spatial basis will always be overestimates.

2.  Even if offtake is well below the theoretical MSY, it could still be drive the prey population to extinction if that population has already been depleted beyond the MSY level. If a population is at a critical level, an offtake of one animal may doom it to extinction, although this is likely below the MSY.

3.  The approach uses instantaneous indices to describe what is in reality a dynamic system. Offtake and even effort are not fixed quantities. Even a cursory consideration of system dynamics will reveal that it is perfectly possible for a dynamic trajectory leading to deterministic stock extinction to incorporate supply points below the MSY, and a trajectory leading to a stable equilibrium to incorporate supply points above it. Theoretically, the optimal management system for a renewable resource is to 'bang-bang control', i.e. to harvest at an infinitely high rate when the stock is above the target size, and not to harvest at all when it falls below the target size (Clark 1990). This is not to suggest that such a perfect system will occur in the real world, but it clearly illustrates that the instantaneous rate of offtake tells us little about sustainability: it could be either zero or infinite within an optimally managed system.

The framework offered by equations 2-3 and 2-4 in combination with a description of demand and industry dynamics is essentially a spatial generalisation of existing bioeconomic models. Sanchirico and Wilen (1999) also offered a spatial generalisation of basic bioeconomics models, but based it on a metapopulation structure. They found that patterns of effort distribution responded in predictable fashion to costs of harvesting in and dispersal rates between distinct patches, and later used this to define the circumstances under which marine no-take zones might produce both stock and yield gains (Sanchirico and Wilen 2001). This is the first time in which a general spatial bioeconomic model has treated space as a continuous quantity, and looked explicitly at the role of transport costs in structuring spatial patterns, supply and dynamics of resource exploitation within a single continuous area. It therefore combines dynamic bioeconomic models with the principles of landscape economics revealed in models such as those of Stone (1998a, b) that describe spatial patterns of timber exploitation. The next chapter will explore the behaviour of the model assuming simple and general forms for the growth and cost functions involved.