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Author: Arne Eide

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A bioeconomic MPA study based on  
cellular automata population growth and distribution

by Arne Eide

Norwegian College of Fishery Science, University of Tromsø, Norway

Email: arne.eide@uit.no

**Highlights:**

- Uniform distribution of effort on irregularly distributed fish is less stock conservative than when systematically approaching fish dense areas.
- Small marine sanctuaries may have significant impact on stock conservation and economic performance.
- Compared with the cellular automata model, the logistic model underestimates the stock biomasses in case of diffusion

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5 by Arne Eide

6 Norwegian College of Fishery Science, University of Tromsø, Norway

7 Email: arne.eide@uit.no

8 Phone: +47 47 27 94 93 Fax: +47 77 64 60 20

9  
10 **Abstract**

11 This paper investigates possible biological and economic effects of using marine sanctuaries as a  
12 management tool, employing cellular automata techniques to model biological growth and area  
13 distribution, assuming open access to the fish stock resources outside the protected area. The cellular  
14 automata model incorporates a fish harvest model based on standard assumptions. In agreement with  
15 previous studies this study confirms that large protected areas are necessary for significant impact on  
16 stock conservation, given standard assumptions. The conclusion may however not be equally  
17 unambiguous when employing more realistic scenarios, assuming non-uniform distribution of biomass  
18 and fishing effort. This study shows that significant stock conserving effects could be obtained even  
19 when less than 10% of the total distribution area of the stock is protected from fishing activities.

20 *Keywords:* Marine Protected Area, Cellular Automata Modelling, Fisheries management,  
21 Bioeconomics

## 22 1. Introduction

23 As the word suggests, the idea behind Marine Protected Area (MPA) is to protect marine ecosystems  
24 from human activities which may cause destruction or other undesired impacts on environment or  
25 species located in the area. Such destructions may have negative economic consequences not only for  
26 the environment and ecosystem, but also for fisheries, tourism or other industries depending on the  
27 natural resources. How these industries are affected depend on the biological properties of the  
28 ecosystem, how the MPA is implemented, control and surveillance, as well as the economic dynamics  
29 of industries exploiting the natural system. Controversial issues may be placement and size of the  
30 protected area, type of protection, and restrictions on economic activities within the protected area.  
31 Given the complex and dynamic interrelation between natural systems and economic activities and the  
32 uniqueness of each such relation, it is challenging to establish general solutions fitting all cases. This  
33 paper presents a theoretical study of an idealised system including fish migration along a coastline  
34 where a part of the coast line may be closed for fishing while there are open access fisheries  
35 elsewhere.

36 Marine protected areas involves different issues within different disciplines, consequently a number of  
37 different modelling approaches are found. A vast number of publications on MPA related issues are  
38 found in resource economics and conservation biology, but there are few influential contributions  
39 aiming to merge the different disciplinary traditions. Several papers refer however to these differences  
40 in modelling approaches. Fisheries biologists have been criticised for including harvest in a simplified  
41 manner, excluding economic dynamics (Smith and Wilen, 2003), while economists may express  
42 biological growth and spatial dynamics too simplified. Crafton et al. (2005) points at some of these  
43 problems. Interesting attempts of cross-over models exists, as by Hilborn et al. (2006), including fleet  
44 dynamics though excluding economic behaviour, or Smith and Wilen (2003) who include spatial  
45 distribution of biomasses, but not the important interaction between spatially distributed fishing  
46 activities and the spatial distribution of fish biomass. While biologists of obvious reasons emphasise  
47 the biological dynamics, the interests of economists of equally obvious reasons are on the economic  
48 dynamics (or rather equilibriums). The first (biological dynamics) may be studied in greater details

49 when simplifying the fishing activity to a single fishing mortality rate, while the latter (economic  
50 dynamics) may lead to conventional biological modelling within the framework of standard  
51 bioeconomics.

52 Most bioeconomic publications on MPA issues assume MPA to be no-take zones. Several studies  
53 based on deterministic models, indicate that MPA in fact has limited value as a management tool  
54 (Hannesson 1998; Conrad 1999). The use of MPA reduces the net revenues, and the conservation  
55 effect seems to be weak unless very large areas are included in the marine sanctuary. Conrad (1999)  
56 argues however that deterministic models are less useful to reveal the true value of MPA regulation.  
57 He therefore introduced a model with stochastic growth and found the variance of fish stock  
58 biomasses to be reduced after introducing marine sanctuaries. Hannesson (2002) arrived at the same  
59 conclusion, using a stochastic spatial distribution of stock components inside and outside the MPA.

60 From a methodological point of view the spatial component appears to be most challenging when  
61 studying the economic effects of MPA regulation. Nevertheless the spatial dimensions in most  
62 bioeconomic studies has been largely ignored or highly simplified. The most common modelling  
63 approach has been to define two homogeneous stock components, one within the MPA and the other  
64 within the open area; assuming an interaction between the two areas through density driven migration  
65 (metapopulation modelling). Different solutions exist on how to handle the environmental carrying  
66 capacity of the two stock components and differences in the final conclusions seem in some extent to  
67 reflect differences in modelling approach and basic assumptions. Previous bioeconomic studies  
68 include continuous and discrete time models and investigate the effects of open access fisheries as well  
69 as regulated fisheries maximising present value of net revenues over time.

70 A even wider range of modelling approaches are found in biological studies on stock-harvest  
71 interaction in cases of protected areas, also including the use of cellular automata modelling  
72 techniques. Moustakas et al. (2006) utilise cellular automata methodology to model spatial distribution  
73 while including stochastic elements, to evaluate the effects of closed areas. Fishing is included as a  
74 learning process by vessel movements between neighbouring cells based of fish stock densities. Apart

75 from harvest production, economic modelling is not included and the fleet dynamics is controlled by  
76 presence of fish, willingness to move and fleet density constraints, not by economic performance. A  
77 recent study by Silvert and Moustakas (2011) discusses the performance of using one large versus  
78 several small MPAs while employing a 1D cellular automata model with similarities to the one  
79 presented in this study. Moustakas and Silvert (2011) presents a corresponding 2D model assuming, as  
80 in Moustakas et al. (2006), the objective of the fishing fleet to be to maximise catch. Based on  
81 bioeconomic theory and assuming an open access fishery (Gordon, 1954), the objective of each fishing  
82 unit is in this study assumed to be to maximise net revenue.

83 Different modelling traditions have developed alongside each other in fisheries biology and  
84 economics, both dealing with the same fisheries management issues, including the use of MPA, from  
85 the angle of different disciplines. The relationship between the two regarding the impact of MPA  
86 regulations has been the focus of several papers. Grafton et al. (2005) aims to bridge the divide  
87 between the two traditions, but do not address the modelling challenge of spatial distribution in  
88 particular, even though this part appears to be one of the core problems of bridging the gap between  
89 the traditions. The spatial behaviour is however the main focus of Smith and Wilen (2003) in their  
90 case study of a sea urchin diving fishery. They criticise biological models for not including economic  
91 behaviour and illustrate in their case study how the effect of economically rational behaviour differs  
92 from the results while ignoring these dynamics. In an empirical study of a snow crab fishery Swain  
93 and Wade (2003) describe how fishing effort are more intense in areas closer to home port, than in  
94 other areas with similar or higher densities of crab. Obviously they are observing an effect of  
95 economically rational behaviour. Salthaug and Aanes (2003) also discuss and model the spatial  
96 distribution of a fleet on the basis of the relation between catchability, fish density and fleet  
97 concentration, rather than including economic measures directly. There is an assumption of rational  
98 behaviour, but these models have not been capable of expressing this in economic terms.  
99 Unfortunately they have not been offered much help from the bioeconomic literature, since the  
100 modelling tradition there more is into dynamic optimisation and metapopulation modelling than  
101 integrating more complex biological dynamics and sophisticated spatial distribution models.

102 Cellular automata methodology is a relatively new approach in the modelling of complex systems,  
103 utilising certain arbitrary rules specifying how the automaton develops (Wolfram 2002). The cellular  
104 automaton consists of cells and an initial state of each cell. The state variables of a cell evolve over  
105 time due to predefined rules and the initial state of the cell and its neighbouring cells. Simple rules  
106 may create complex patterns as the automaton defined by a fixed number of cells evolves by each  
107 computational step. The theoretical idea of cellular automata (CA) dates back to Neumann (1966) and  
108 was developed further by Stephen Wolfram and others in the early 1980s as a discrete time model with  
109 stages of evolution in space and state (Wolfram, 2002). The basic idea of stepwise development  
110 through computational calculations also opens for the inclusion of continuous state variables within  
111 each cell, referred to as continuous cellular automata (CCA; see Wolfram 2002).

112 Darwen and Green (1996) claims that cellular automata methodology is a better approach to model a  
113 population in a landscape than models based on partial differential equations are. CA and CCA models  
114 are consistent with empirical experiences of spatially heterogeneous population densities with local  
115 extinctions and local booms (Darwen and Green 1996). The simplicity of cellular automata  
116 methodology also reduces the computing time compared with corresponding models based on  
117 numerically solving differential equations. Balzer et al. (1998) provides an overview over the first  
118 decades of development of cellular automata ecological models. During recent years there has been a  
119 vast number of publications within this field and cellular automata models now are virtually covering  
120 all areas of biological modelling as well as, in fact, most other modelling areas. This development also  
121 offers new possibilities of including economic rational behaviour of harvesting units, utilising  
122 economic theory and merging the two modelling traditions.

123 This study is an early attempt on moving in this direction, presenting deterministic models where the  
124 fish stock biomass essentially develops through simple CCA rules, also influenced by fishing  
125 activities. Fleet dynamics is related to economic performance, following standard assumptions of  
126 bioeconomic dynamics where the marginal changes of fishing effort are proportional to net revenue of  
127 previous time period.

128 The two alternative biological growth models are presented 1) a model proposed by Wolfram (2002;  
 129 page 157, here referred to as CCA) and 2) a straight forward cellular automata representation of a  
 130 discrete time logistic growth equation (here referred to as LCA). A slightly different representation of  
 131 logistic growth was also studied by a cellular automata rule in Darwen and Green (1996). Their model  
 132 was however a 2D lattice while the models presented here is a 1D row of cells evolving over discrete  
 133 computational steps.

134 In this study the expression MPA is used on an area where fishing activities are prohibited, while open  
 135 access to the fish resources is assumed outside the protected area. This simplification means that MPA  
 136 here is employed in its most extreme version, together with the other extreme, the open access fishery.  
 137 The term MPA is chosen because it is commonly used in the literature, but the only type of MPA  
 138 considered in this study is marine sanctuaries.

139

## 140 **2. Biological model**

141 Assume a finite number of cells in a row and connect the first and last cell, resulting in a circular  
 142 representation of cells as illustrated in Figure 1. The cells may represent the coast line of an island.  
 143 Each cell holds a specific fish biomass, being the state variable of the cell. The total stock biomass  
 144 then is the sum of biomasses in the finite number of cells. The initial biomass vector with  $n$  elements  
 145 (cells) is

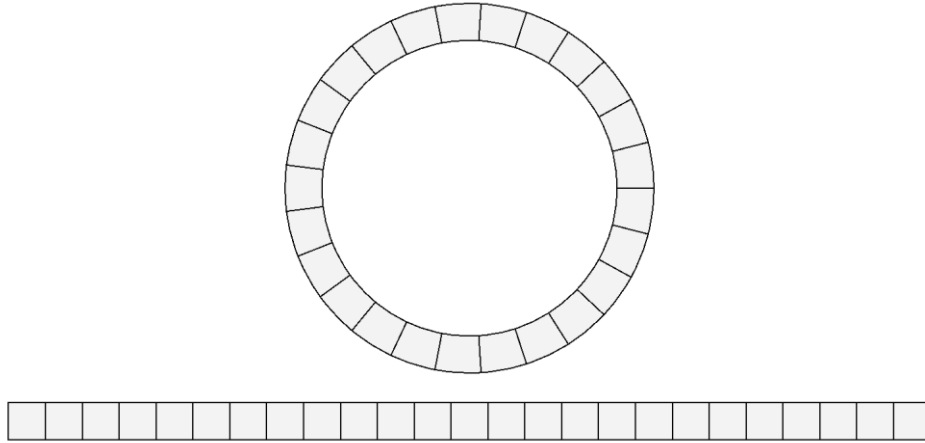
$$\mathbb{b} = (b_1, b_2, b_3, \dots, b_n) \quad (1)$$

146

147  $\mathbb{b}$  evolves over time as a function of a simple CA rule involving a growth rate ( $g$ ) and assumed  
 148 diffusion pattern. The diffusion pattern is controlled by the range parameter  $r$  which determines the  
 149 number of neighbouring cells involved when calculating the new state variable of each cell (Wolfram,  
 150 1984). If  $r$  for example equals 1, the biomasses of 1 neighbouring cell on each side of the current cell,



151 together with the current cell itself, determine the new biomasses of the cells. More specifically  
 152 implies the CCA rule employed here that biomass  $b_2$  (state variable of cell 2) next step with range  $r =$   
 153 1, is one third of  $b_1 + b_2 + b_3$  plus the growth given by the growth rate  $g$ . In the CCA model only the  
 154 fractional part of the new biomass will remain in the cell, therefore



155

156 **Figure 1.** A finite number of cells (here 25 cells) in a circular connection (above) illustrates the  
 157 spatial distribution and relationship in the model. In the following graphics the circle is represented  
 158 by a row of cells (below), assuming the first and last cell to be connected.

159

$$0 \leq b_i \leq 1 \quad (2)$$

160 for  $1 \leq i \leq n$ . The growth rate ( $g$ ) gives the percentage growth per unit of time. The biomass growth  
 161 then is expressed by

$$b_{i,t+1} = \left\{ \frac{g+1}{2r+1} \sum_{j=i-r}^{i+r} b_{j,t} \right\}, \quad (3)$$

162  $\{ \_ \}$  representing the fractional part of the expression within the brackets ( $0 \leq \{ \_ \} < 1$ ; example:  $\{ 1.2 \}$   
 163  $= 0.2$ ); while  $b_{n+1,t} = b_{1,t}$  (connecting the circle, see figure 1),  $g \geq 0$  (a non-negative growth rate)  
 164 and  $r \geq 0$ . As the growth rate ( $g$ ) is constant, biomass growth is linear until the collapse level of  $b=1$

165 is reached, where only the fractional biomass value remains within the cell. Hence the long term  
 166 average biomass (in absence of fisheries mortality) is  $1/2$ .

167 Natural mortality is expressed indirectly by the remaining fractional part, reflecting a density  
 168 dependent mortality determined on cell level (local collapses). The biomass vector is a discrete  
 169 function of time at given initial biomass value ( $\mathbb{b}_0$ ), here on the basis of (3) expressed by the  
 170 continuous cellular automata rule

$$\mathbb{b}_t = CCA(\mathbb{b}_{t-1}) \quad (4)$$

171 The corresponding discrete logistic growth equation is

$$b_{i,t+1} = \frac{g+1}{2r+1} \left( 1 - 2 \sum_{j=i-r}^{i+r} b_{j,t} \right) \sum_{j=i-r}^{i+r} b_{j,t} \quad (5)$$

172 represented by the cellular automata rule

$$\mathbb{b}_t = LCA(\mathbb{b}_{t-1}) \quad (6)$$

173 Total biomass at time  $t$  is

$$B_t = \sum_{i=1}^n b_{i,t} \quad (7)$$

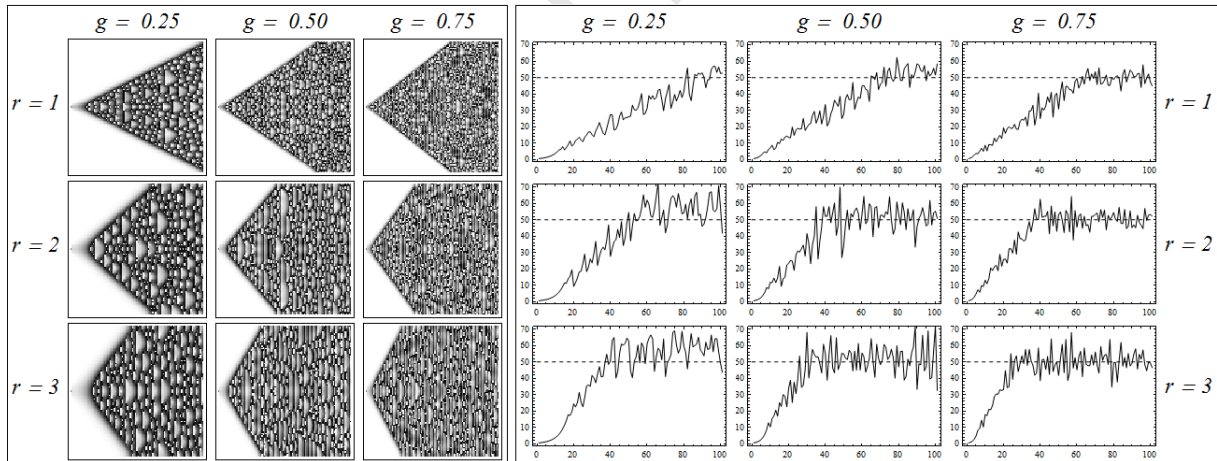
174 According to Wolfram (2002) CCA has its equilibrium biomass  $B_\infty = \frac{n}{2}$  when  $r > 0$ . Biomasses  
 175 calculated by Model (4) are presented in Table 1 for the case of 13 cells,  $g = 1/2$  and an initial biomass  
 176 of 1 is placed in the mid cell. Table 2 displays the corresponding biomasses of Model (6) distributed  
 177 on 7 cells and with  $g = 3/5$ .

178 **Table 1.** Cellular biomasses calculated by Model (4) for  $g = 1/2$ ,  $r = 1$  and  $b_0$  given by the first row  
 179 ( $t=0$ ). The table corresponds to the first period of the pattern shown in the mid column of the first row  
 180 of Figure 2.

$t$	$b_1$	$b_2$	$b_3$	$b_4$	$b_5$	$b_6$	$b_7$	$b_8$	$b_9$	$b_{10}$	$b_{11}$	$b_{12}$	$b_{13}$	$B$
0	0	0	0	0	0	0	1	0	0	0	0	0	0	1
1	0	0	0	0	0	1/2	1/2	1/2	0	0	0	0	0	3/2
2	0	0	0	0	1/4	1/2	3/4	1/2	1/4	0	0	0	0	9/4
3	0	0	0	1/8	3/8	3/4	7/8	3/4	3/8	1/8	0	0	0	27/8
4	0	0	1/16	1/4	5/8	0	3/16	0	5/8	1/4	1/16	0	0	33/16
5	0	1/32	5/32	15/32	7/16	13/32	3/32	13/32	7/16	15/32	5/32	1/32	0	99/32
6	1/64	3/32	21/64	17/32	21/32	15/32	29/64	15/32	21/32	17/32	21/64	3/32	1/64	297/64

181

182



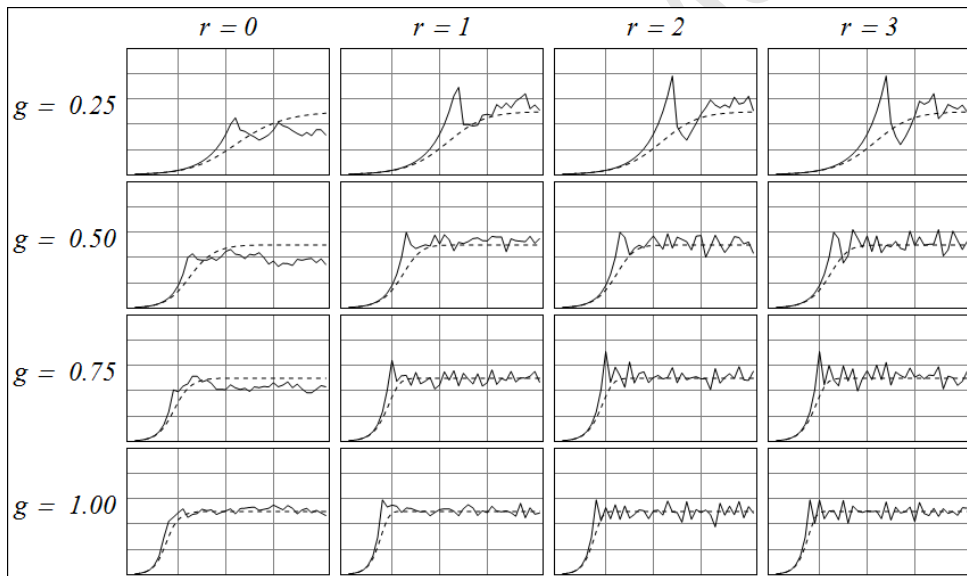
183

184 **Figure 2.** CCA model (4) of varying diffusion properties at constant growth with an initial condition  
 185 of one single biomass ( $b_{49}=1$ ) in the centre cell of 99 cells ( $n = 99$ ). The growth rate ( $g$ ) is 0.5 and the  
 186 diffusion property given by the range parameter  $r$ , indicating number of influenced neighbouring  
 187 cells. The figure includes 100 computational steps ( $t=100$ ) displayed in the horizontal axes. The left  
 188 panel shows the biomass of each cells distributed vertically, while the right hand panel shows the total  
 189 biomass of each computational step in the nine cases.

190 Graphical examples of model (4) when varying growth rate ( $g$ ) and diffusion pattern ( $r$ ), are shown in  
 191 figure 2 when a initial biomass in a single cell of a total of 99 cells develops over 100 time steps for  
 192 different growth and range parameters. One of the cases displayed in figure 2 ( $r = 1$  and  $g = 1/2$ ) is  
 193 shown numerically in Table 1.

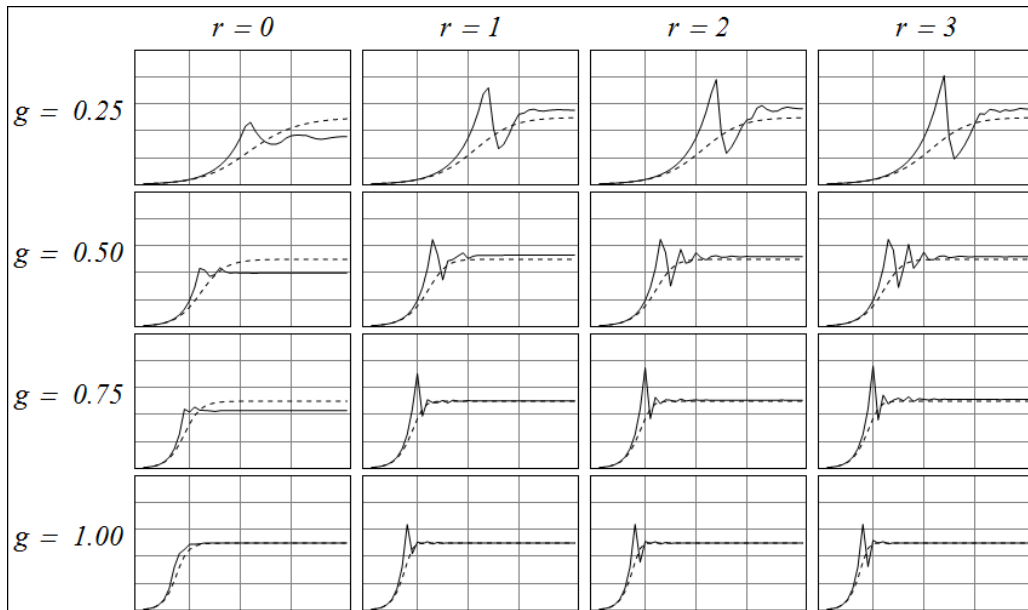
194 Growth model (4) is displayed in Figure 2 both as biomass patterns (left hand panel) and as total  
 195 biomass development over time ( $B_t$ ) in a more traditional way (right hand panel). Corresponding  
 196 biomass developments are shown in Figures 3 and 4 for Models (4) and (6), with a randomly  
 197 distributed initial low biomass (In Figure 2 the initial biomass is placed in a single cell). The figures  
 198 show how diffusion and growth properties affect biomass variations over time for 100 (Figure 3) and  
 199 one million (Figure 4) cells.

200



201

202 **Figure 3.** Biomasses over time in a CCA model (4) (solid curves) and LCA model (7) (dashed curves)  
 203 of varying diffusion properties ( $r$ ) at growth rates ( $g$ ) with the same random initial cell biomasses and  
 204 100 cells ( $n = 100$ ). The vertical axes of each case measures biomass and the horizontal axis time. The  
 205 figure includes 100 time steps ( $t=100$ ).



206

207 **Figure 4.** Biomasses over time in a CCA model (4) (solid curves) and LCA model (7) (dashed curves)  
 208 of varying diffusion properties ( $r$ ) at growth rates ( $g$ ) with the same random initial cell biomasses and  
 209 1,000,000 cells ( $n = 1,000,000$ ). The vertical axes of each case measures biomass and the horizontal  
 210 axis time. The figure includes 100 time steps ( $t=100$ ).

211

212 If the number of cells ( $n$ ) is increased and time span ( $t$ ) prolonged, the graphical presentation displayed  
 213 in the left hand panel of Figure 2 soon proves to be less useful than more traditional graphical  
 214 presentations of the development of the total stock biomass over time, as shown in the right hand panel  
 215 of Figure 2. The solid curves in Figures 3 and 4 represent the CCA model, while the dashed curves  
 216 represent the logistic growth model LCA. The figures reveal lower stock biomasses in Model (4) than  
 217 in Model (6) for  $r = 0$ , while increased biomass fluctuations seem to be associated with increasing  $r$   
 218 values. These fluctuations may further to be damped by increasing growth rates ( $g$ ). For  $r = 0$  the stock  
 219 biomasses of Model (4) do not reach the levels of Model (6) unless  $g$  is having very high values  
 220 (beyond 0.75 in the given parameter setting). The simple explanation is that without diffusion ( $r = 0$ )  
 221 the effect of additional growth (based on a fixed percentage) in cells with low biomasses in biomass  
 222 terms are less than the corresponding growth of cells with large biomasses. While diffusion efficiently  
 223 levels out this asymmetry, it becomes apparent when there is no diffusion. It may be regarded more as

224 a theoretical issue than a real problem since there will always be some diffusion, not only due to the  
225 biological properties of the species, but there will also be physical reasons for diffusion to certain  
226 extent be present. While Figure 3 displays total biomass development over time with a spatial  
227 distribution over 100 cells, Figure 4 displays the corresponding picture in the case of one million cells.  
228 The impacts of increasing growth rates and diffusion ranges are striking. Increasing the number of  
229 cells makes the curves smoother, comparing Figure 3 with Figure 4. Increased diffusion increases  
230 biomass fluctuation, while mean biomass equilibrium is not affected by the diffusion properties,  
231 except in the case of  $r = 0$  (no diffusion).

232 From a biological point of view diffusion of fish stocks may be explained as behavioural adaptation to  
233 varying environmental conditions, as the experienced prey densities may increase and (or) the  
234 corresponding predator densities decline by proper migratory behaviour. Both causes (targeting food  
235 and avoiding predators) involves relations to fish of the same species as well as well as to other  
236 species. As previously indicated the only significant difference in overall performance of the two  
237 models is found in the case of no diffusion ( $r = 0$ ). Increasing positive  $r$  values increased the rate of  
238 adaptation and adapting capacity, but in order to link this to the dispersal abilities of different species,  
239 it has to be related to the physical basic cell size, since the range number refers to number cells on  
240 each side of the cell which initially holds the migrating biomass.

241 Model (4) and (6) express biomass growth as discrete time processes on micro level, within and  
242 between cells. The total biomass is indirectly determined by the growth functions at micro level, but in  
243 a non-transparent and pseudo-random manner, though the average biomass of neighbouring cells in  
244 the long run may be a good proxy of the overall total biomass of the stock (at least when harvest is not  
245 included). Diffusion (determined by the range parameter  $r$ ) contributes in the long run to level out  
246 biomass differences between cell clusters placed in different areas, reaching a relatively stable total  
247 biomass level. In the present study all cells are assumed to share the same local carrying capacity of  
248 0.5, with a collapse limit of 1.

249

250 **3. Fishing regulated by closed area**

251 The CCA and LCA models presented above represent biological growth and spatial distribution. Now  
 252 fishing is introduced to the model, restricted by the marine protected area (MPA) and market  
 253 economic constraints. The control of compliance with the regulations is assumed to be perfect and no  
 254 cost of control and surveillance are considered.

255 The stock biomass within a MPA is given as a subset of the biomass vector  $\mathbb{b}$ ,

$$\mathbb{b}_{\text{MPA}} = (b_s, \dots, b_{s+m-1})$$

256 where  $s$  is the first cell and  $m$  is the number of cells included in the MPA. Absence of protected area is  
 257 regarded being a special case of MPA regulation (no closed area;  $m = 0$ ). The model circularity makes  
 258 the choice of  $s$ -value insignificant, hence  $s = 1$  is assumed in the following. The MPA biomass vector  
 259 then simplifies to

$$\mathbb{b}_{\text{MPA}} = (b_1, \dots, b_m), \quad (8)$$

$$0 \leq m \leq n \text{ and } s = 0 \text{ when } m = 0.$$

260 Fishing activities target biomasses in the non-protected area (NPA), represented by the complementary  
 261 subset of  $\mathbb{b}_{\text{MPA}}$  in the biomass vector  $\mathbb{b}$

$$\mathbb{b}_{\text{NPA}} = (b_{m+1}, \dots, b_n). \quad (9)$$

262 Total targeted biomass at time  $t$  then is

$$B_{\text{NPA},t} = \sum_{i=m+1}^n b_{i,t} \quad (10)$$

263 A common assumption in harvest production models is that the stock-output elasticity is equal one  
 264 (Eide et al., 2003). A useful property which follows as a consequence of this assumption is a linear  
 265 relationship between the fishing mortality rate and fishing effort per unit of time. Most studies on  
 266 stock-effort-harvest relationships indicate however that this relationship seldom is linear, and  
 267 empirical studies suggest that the stock-output elasticities are more likely to be around 1/2 than close  
 268 to 1 (Hannesson, 1983; Eide et al., 2003). Fish harvest production is therefore in this study assumed to  
 269 have a stock output elasticity of 1/2, while harvest ( $h$ ) is assumed to be linear in fishing effort

$$h_{i,t} = q e_{i,t} \sqrt{b_{i,t}} , \quad (11)$$

270 when  $b_i \in \mathbb{D}_{\text{NPA}}$  and  $e_i$  is the fishing effort of cell  $i$ . Total fishing effort is the sum of the fishing effort  
 271 of all cells

$$E_t = \sum_{i=m+1}^n e_{i,t} \quad (12)$$

272 and total harvest is given by

$$H_t = \sum_{i=1+m}^n h_{i,t} \quad (13)$$

273

274 The spatial dimension in the cellular automaton opens for different ways of spatial distribution of  
 275 fishing effort. A distribution rule based on stock biomass distribution is given by the expression

$$e_{i,t} = \frac{b_{i,t}^d}{\sum_{i=1+m}^n b_{i,t}^d} E_t , \quad (14)$$

276 where distribution parameter  $d$  (where  $d \geq 0$  is expected) controls to what extent biomass distribution  
 277 affects the distribution of fishing effort. The special case  $d = 0$  gives a uniform distribution of fishing



278 effort independent of biomass distribution. The case of  $d = 0$  is in line with most of the published  
 279 bioeconomic MPA studies published, usually separating the stock into two components (open and  
 280 closed to fishing). Uniform distribution of fishing effort ( $d = 0$ ) simplifies the expression of the fishing  
 281 effort with each cell to the constant ratio

$$e_{i,t} = \frac{b_{i,t}^0}{\sum_{i=1+m}^n b_{i,t}^0} E_t = \frac{E_t}{n-m} \quad (15)$$

282 while  $d = 1$  gives an effort distribution perfectly reflecting the stock biomass distribution. The cases of  
 283  $d > 1$  which could be called smart fishing, where the distribution of fishing effort takes advantage of  
 284 the biomass clustering, successfully targeting the most biomass dense cells, In the extreme situation of  
 285  $d = +\infty$  all fishing effort is placed in the single cell holding the highest biomass.

286 More sophisticated distribution rules (or simple cellular automaton, for example as proposed by  
 287 Moustakas et al., 2006) may take into consideration distribution histories (of biomass and/or effort)  
 288 and include constraints on local densities and growth of effort. It could be argued that the distribution  
 289 model proposed above (equations 14) connects to history through the time path of total fishing effort,  
 290 as will be explained in the following.

291 Including harvest model (11) in the biological growth model (3) yields

$$b_{i,t+1} = \left\{ \frac{g+1}{2r+1} \sum_{j=i-r}^{i+r} b_{j,t} \right\} - h_{i,t} \quad (16)$$

292 Equation (4) is adjusted accordingly and the complete CCA model including harvest (by the fishing  
 293 effort  $E$ ) and MPA regulation (by the MPA size variable  $m$ ), is expressed by

$$\mathbb{b}_t = \text{CCA}(\mathbb{b}_{t-1}, E_{t-1}, m) \quad (17)$$

294  $m$  being the number of MPA cells and  $E$  the total fishing effort. Corresponding expression in the  
 295 logistic case is from equation (5) found to be

$$b_{i,t+1} = \left( \frac{g+1}{2r+1} \left( 1 - 2 \sum_{j=i-r}^{i+r} b_{j,t} \right) \sum_{j=i-r}^{i+r} b_{j,t} \right) - h_{i,t} \quad (18)$$

296 and rule (6) is modified accordingly,

$$\mathbb{b}_t = \text{LCA}(\mathbb{b}_{t-1}, E_{t-1}, m). \quad (19)$$

297

298

#### 299 **4. Economic model**

300 The harvest equation (11) involves fishing effort ( $E$ ) which is assumed to have a fixed unit cost  $c$ . The  
 301 unit cost  $c$  also is assumed to include the sum of opportunity costs of all input factors in the production  
 302 of fishing effort. Further a constant unit price of harvest ( $p$ ) is assumed. The net revenue of harvest  
 303 ( $NR$ ) then is

$$NR = pH - cE. \quad (20)$$

304 Since normal profit is included in the unit cost of effort,  $NR$  more precisely is the total economic rent  
 305 (abnormal profit) obtained in the fishery. If an equilibrium solution exists,  $NR$  represents the resource  
 306 rent of that equilibrium; outside equilibrium a large part of the rent obtained may be labelled *quasi*  
 307 *rent* following the definition by Marshall (1893).

308 The dynamics of an open access fishery is determined by the economic performance of the fleet and  
 309 how fast it adjusts its fishing effort and how fast the stock biomass adjusts to the changes in fishing  
 310 effort. The marginal changes in fishing effort may be positive or negative depending on positive or

311 negative fleet net revenue. Since normal profit already is included in the total cost of effort, normal  
 312 profit is obtained from the harvest production process when  $NR = 0$  while economic rent is earned  
 313 when  $NR > 0$ . In case of the latter the fishing effort should increase, as input factors earns higher pay-  
 314 offs in the fishery than outside. In this study marginal changes in fishing effort is assumed to be  
 315 proportional to  $NR$ , expressed as a discrete time process by

$$E_{t+1} = E_t(1 + a NR_t) \quad (21)$$

316  $a$  is the adjustment (stiffness) parameter and represents an intrinsic rate of change in effort. The value  
 317 of  $a$  is determined by a number of factors, first of all at which rate capital can be replaced to adjust for  
 318 market perturbations. A further discussion regarding the parameterisation of  $a$  is however outside the  
 319 scope of this study.

320 Cost of fishing effort ( $c$ ) is decomposed on cells by fishing effort (equation 14) and net revenue of the  
 321 cell. Hence net revenue (economic rent) of cell  $i$  is

$$nr_i = ph_i - \frac{b_i^d}{\sum_{i=1+m}^n b_i^d} E \quad (22)$$

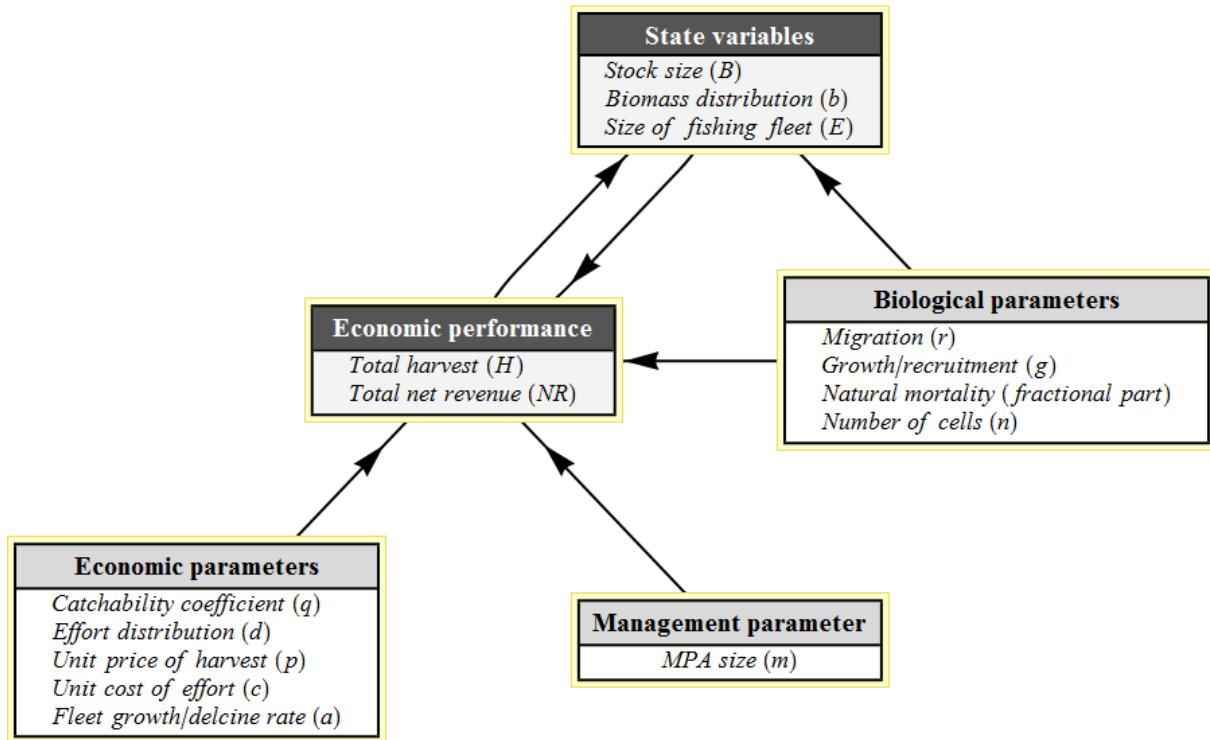
322 or simply

$$nr_i = ph_i - \frac{E}{n - m} \quad (22)$$

323 in case of  $d = 0$  (also seen from equation 15). Global net revenue is expressed by

$$NR = \sum_{i=1}^n nr_i \quad (23)$$

324



325

326 **Figure 5.** Basic flow of Models (17) and (19), based on parameter setting and the initial value of the  
 327 state variables.

328

329 The parameter values used in the simulations are shown in Table 2. Initial biomass vector in all the  
 330 performed simulations includes 100 cells evolving over 2000 time steps. Time unit and cell size is not  
 331 defined, hence the simulations may cover a wide range of different annual growth rates and actual  
 332 migratory performance.

333

334

335

336

337

338 **Table 2.** Parameter values used in the simulations displayed in Figures 6 and 7.

Parameter	CCA and LCA	Description
$r$	2	Range, number of affected neighbouring cells on each side
$g$	0.5	Biological growth rate
$n$	100	Number of cells
$q$	1	Catchability coefficient
$d$	0, 1, 8	Parameter controlling fishing effort distribution
$p$	10	Unit price of harvest
$c$	5	Unit cost of effort
$a$	0.002	Fishing effort stiffness parameter

339

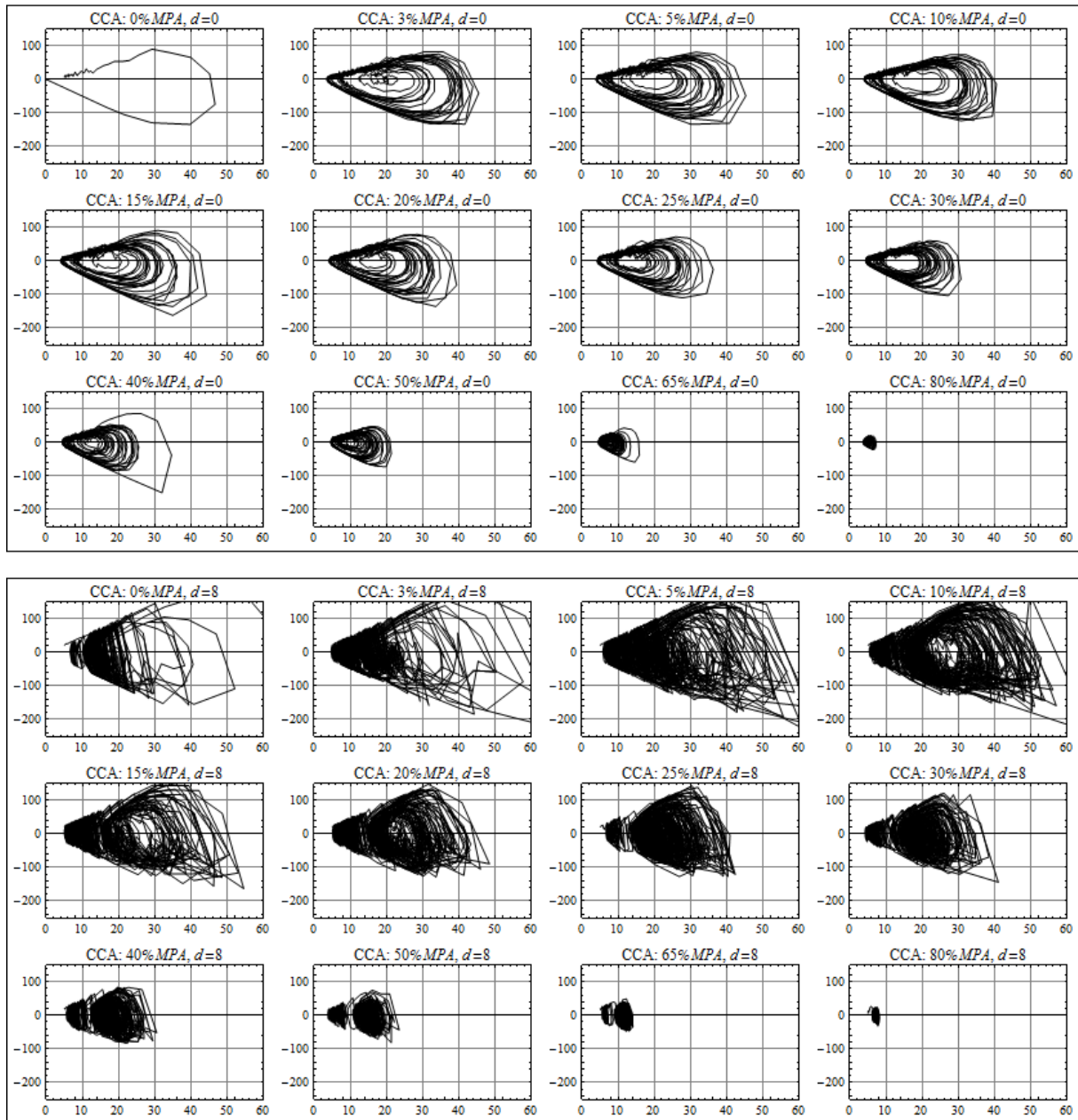
340 **5. Results**

341 The biological models presented above (CCA and LCA, equations 17 and 19) include the biological  
342 and spatial parameters  $g$ ,  $r$ ,  $d$  and  $n$ . The economic part of the bioeconomic model includes the  
343 parameters  $q$ ,  $p$ ,  $c$  and  $a$ , while the MPA-size parameter  $m$  represents the management tool of this  
344 study.

345 Let the two state variables (biomass vector  $\mathbb{b}$  and total fishing effort  $E$ ) have initial the values  $\mathbb{b}_0$  and  
346  $E_0$ . Figures 6 (CCA) and 7 (LCA) display how fishing effort (horizontal axes) develop over time due  
347 to changing economic rent (vertical axes), for different MPA sizes and effort distributions by two  
348 different values of  $d$ ; 0, representing a uniform distribution of fishing effort and 8, representing smart  
349 fishing or effort clustering.

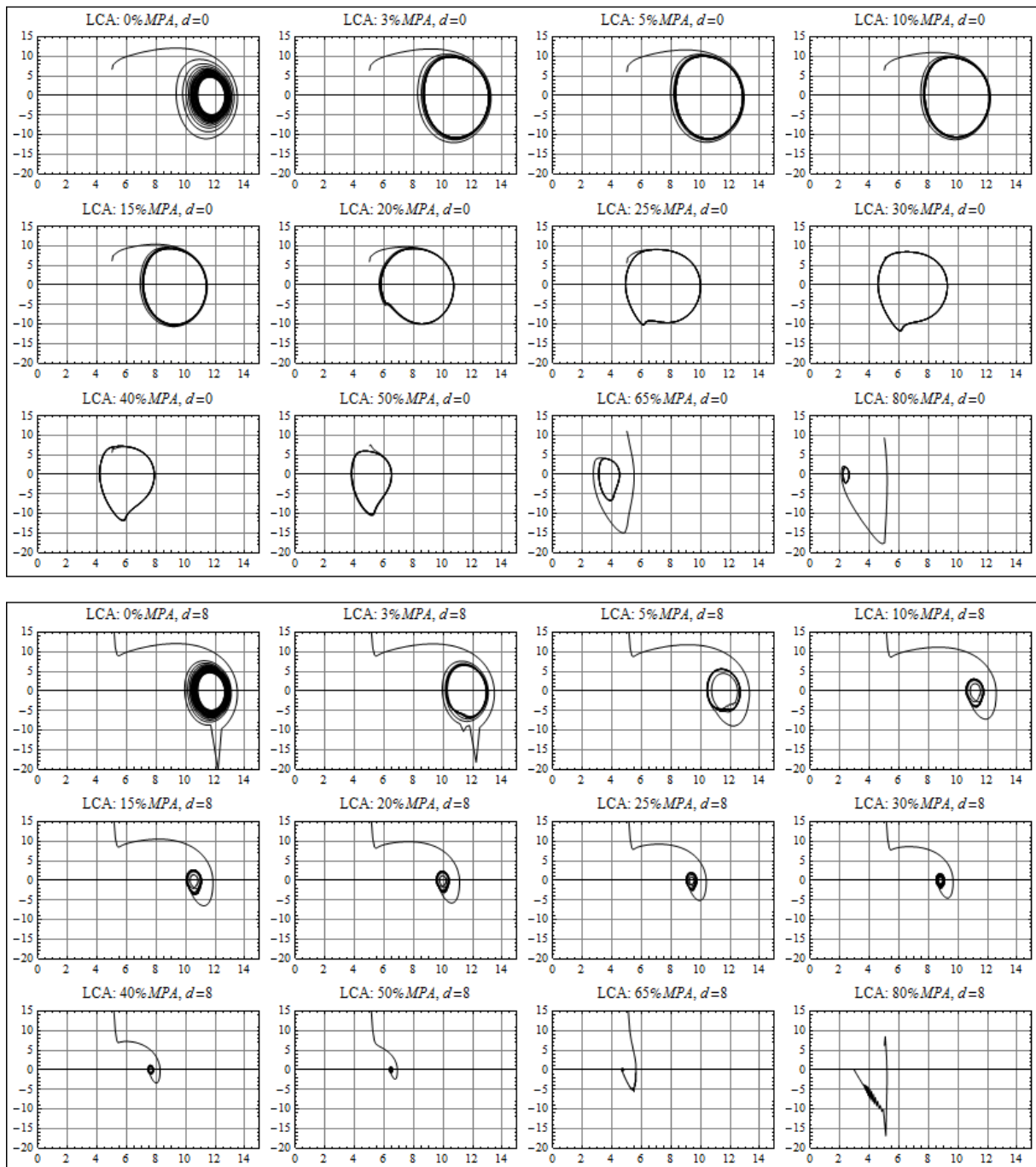
350 Figure 8 presents some statistical properties of the time series of effort, harvest, biomass and net  
351 revenue, from Figures 6 and 7 (for  $d = 0$  and  $d = 8$  while  $r = 2$ ), as Box-Whisker plots with connected  
352 median values. The figure indicates a trend of increasing biomass by increased percentage closure  
353 (increasing MPA size) in an open access fisheries and a corresponding decline in fishing effort and

354 harvest in both the CCA and the LCA model. The changes seem to be more pronounced in the case of  
355 LCA and more vague in the CCA case. In addition to the two  $r/d$  combinations (2/0 and 2/8) displayed  
356 in Figure 8, Figure 9 also includes combinations (0/0) and (2/1). From the figure it is easy to see that  
357 in the LCA case of  $r = 0$  and  $d = 0$  the open access fishing effort becomes zero at a MPA sizes beyond  
358 70%, and a corresponding negative biomass impact on MPA sizes just below this level. In all other  
359 cases the open access solutions implies positive fishing efforts and a almost a linear increase in stock  
360 biomass by increasing MPA size in an open access fishery. While the values on  $r$  and  $d$  seem to have a  
361 significant impact on the slope of this linear relationship in the CCA cases, this is not so in the LCA  
362 cases (except for the special case of  $r = 0$  and  $d = 0$ ). Interestingly, though not unexpected since  
363 uniform effort distribution of both biomass and effort is assumed in non-spatial models, the biomass  
364 development of the LCA and the CCA cases of  $d = 1$  (where effort distribution exactly is reflecting the  
365 distribution of biomass) show the same pattern.



366

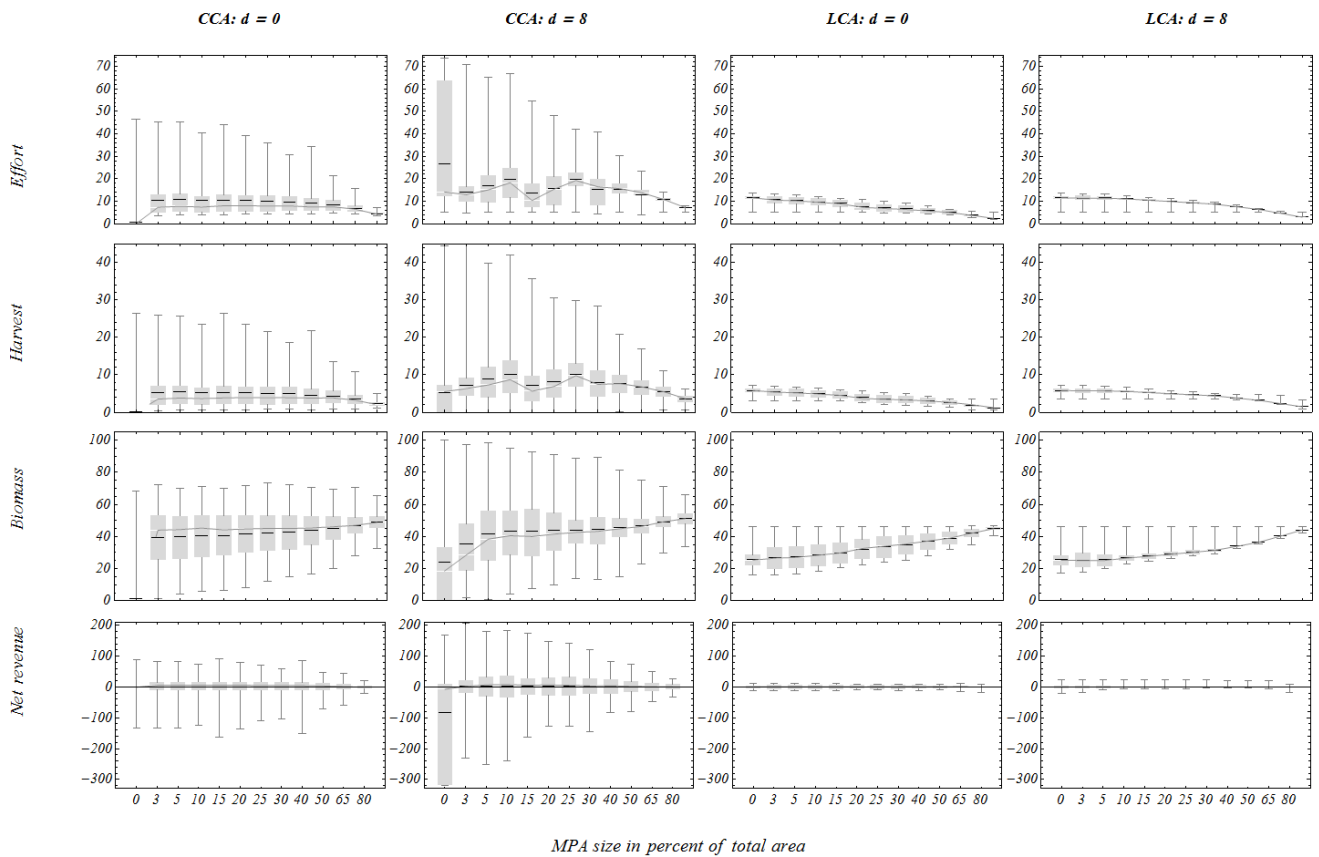
367 **Figure 6.** CCA model (17) on varying percentage of MPA cells and two fishing effort distribution,  $d=0$   
 368 (upper panel) and  $d=8$  (lower panel). The range parameter  $r$  is 2 in all cases. Parameter values used  
 369 are displayed in Table 3. In all graphs the horizontal axis measure total fishing effort ( $E$ , covering the  
 370 range of 0 to 60), while net revenue ( $NR$ , the range of -250 to 150) is measured by the vertical axis.  
 371 The period displayed in each graph counts 2000 time steps.



372

373 **Figure 7.** LCA model (19) on varying percentage of MPA cells and two fishing effort distribution,  $d=0$   
 374 (upper panel) and  $d=8$  (lower panel). The range parameter  $r$  is 2 in all cases. Parameter values used  
 375 are displayed in Table 3. In all graphs the horizontal axis measure total fishing effort ( $E$ , covering the  
 376 range of 0 to 15), while net revenue ( $NR$ , covering the range of -20 to 20) is measured by the vertical  
 377 axis. The period displayed in each graph counts 2000 time steps.

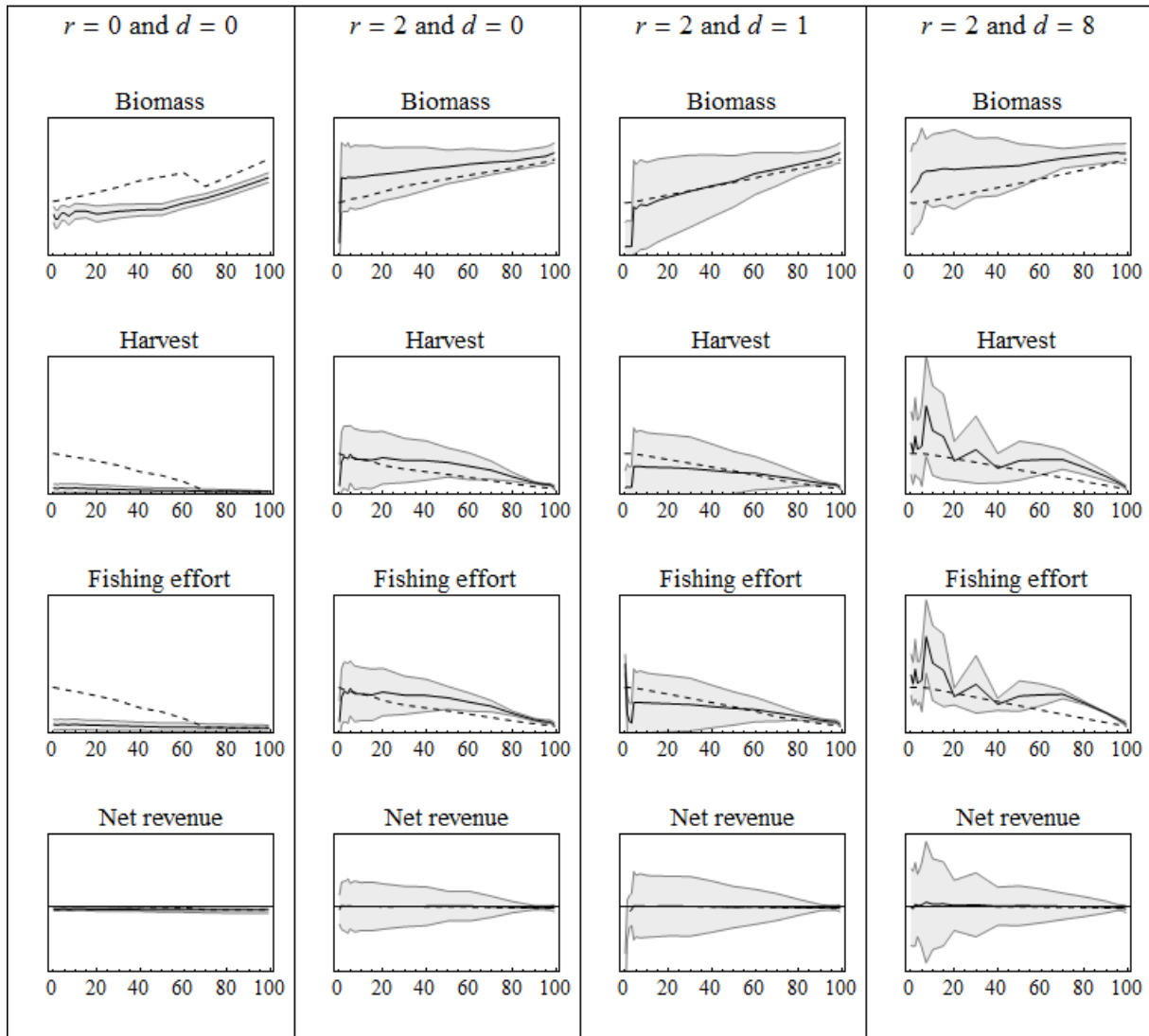




378

MPA size in percent of total area

379 **Figure 8.** Box-Whisker plots of the time series presented in Figures 6 and 7, showing trends and  
 380 variances in fishing effort, harvest, biomass and net revenue for different MPA size in Models (17) and  
 381 (19), respectively the CCA and the LCA model. The range parameter  $r = 2$  in all the simulations. The  
 382 curves connecting different MPA sizes in each plot shows median values, while the mean values are  
 383 indicated by horizontal black lines. Each box includes 50% of the sample and the range covered by  
 384 box and lines includes 95% of the data sample.



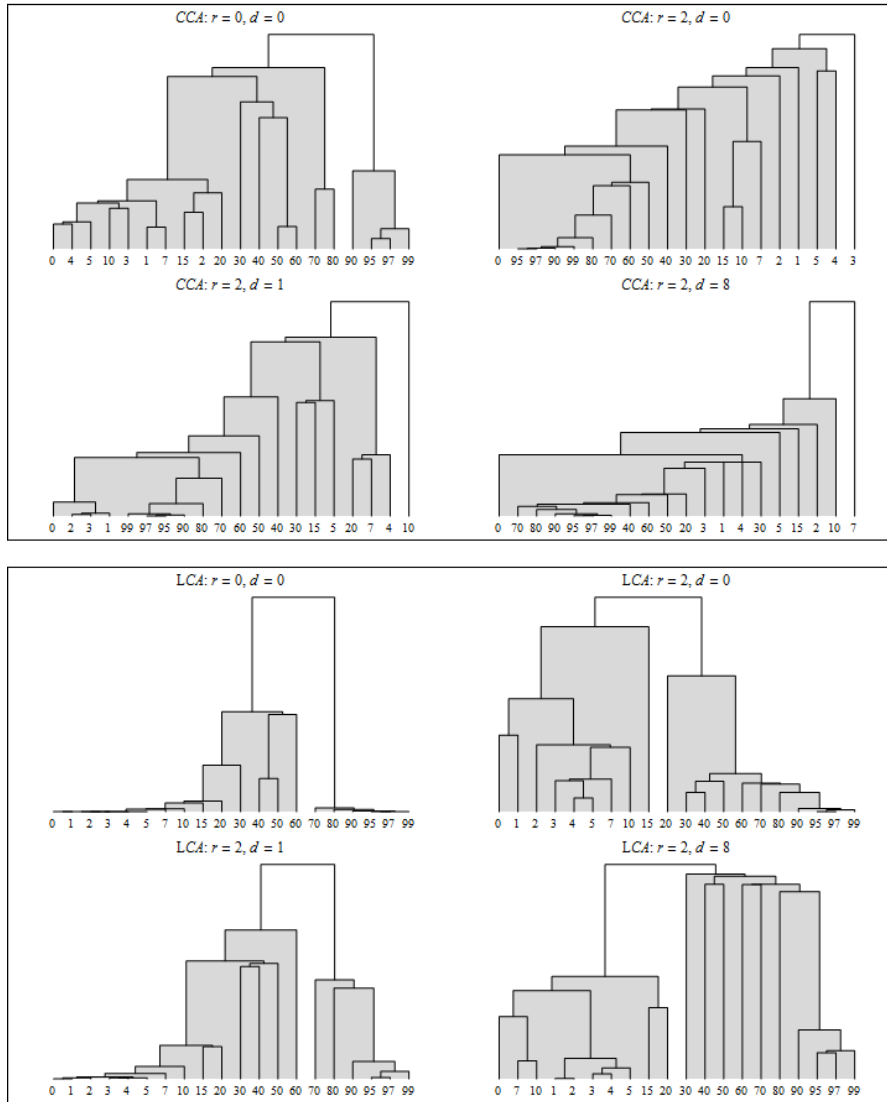
385

386 **Figure 9.** Average values of biomass, harvest, effort and net revenue of each of the four cases  
 387 (columns) obtained by CCA model (17) (solid curves) and LCA model (19) (dashed curves) from  
 388 simulations running over 500 time steps. The shaded areas indicate the standard deviations of  
 389 simulations by the CCA model (19). Parameter values are found in Table 2, except for  $r$  and  $d$  which  
 390 values are indicated in the figure.

391

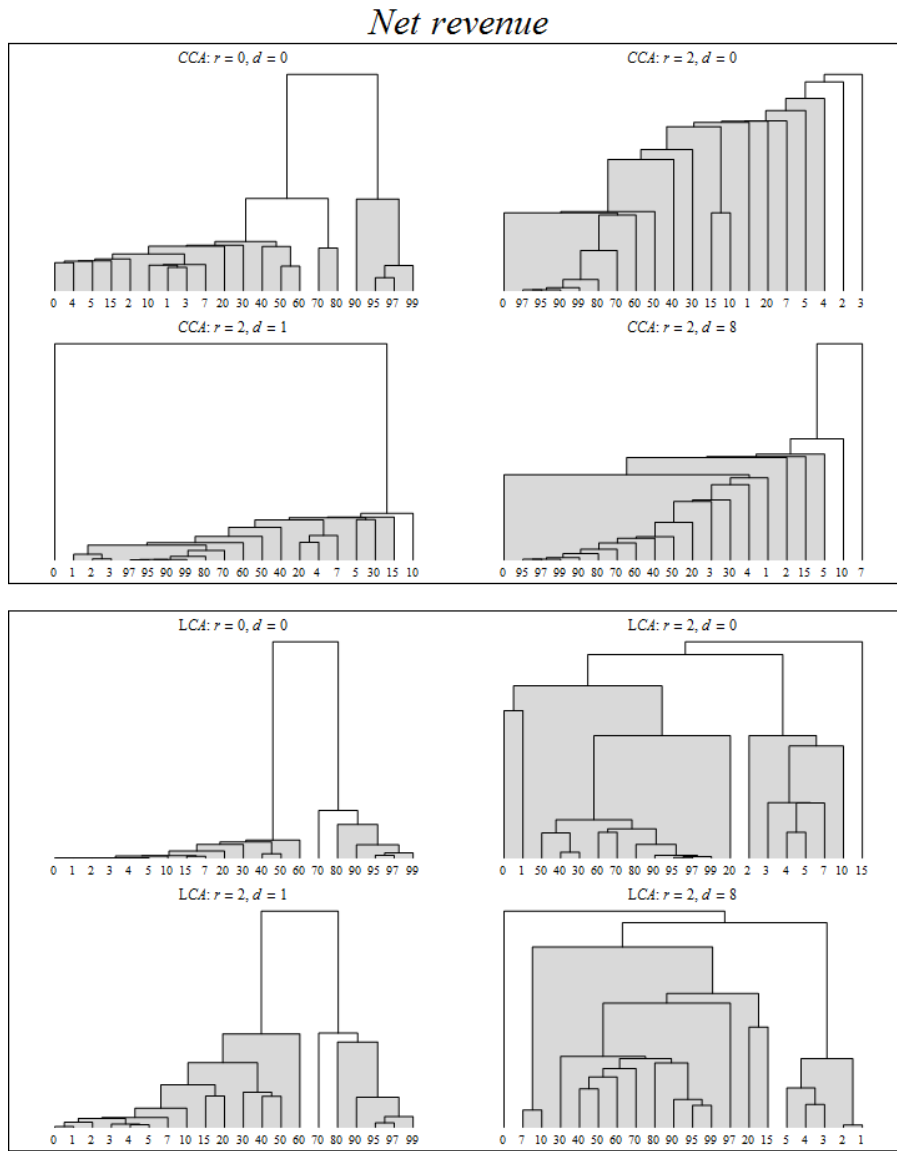
392 Figures 10 and 11 display how respectively biomass and resource rent cluster according to MPA size.  
 393 The chosen values of  $r$  and  $d$  also connects to the simulation results shown in Figure 9. The clusters  
 394 are presented as dendrogram plots involving different  $r$ - $d$ -combinations of the CCA model (the upper  
 395 panels) and the LCA model (the lower panels).

## Stock biomass



396

397 **Figure 10.** Dendrogram plots showing clustering on MPA size (horizontal axis) of the biomass data  
 398 from the simulations presented in Figure 9. The numbers at the horizontal axes represent the  
 399 percentage area closed by MPA regulation. The upper panel shows clustering on MPA size in the  
 400 CCA model (17), while the lower panel shows the corresponding clustering pattern in the LCA model  
 401 (19). The simulation includes 500 time steps (data set length) and 100 independent runs of each of the  
 402 8 cases shown in the graph. The vertical axes indicate the squared Euclidean distance between the  
 403 measured data sets.



404

405 **Figure 11.** Dendrogram plots showing clustering on MPA size (horizontal axis) of the resource rent  
 406 data (including catch and effort data) from the simulations presented in Figure 9. The numbers at the  
 407 horizontal axes represent the percentage area closed by MPA regulation. The upper panel shows  
 408 clustering on MPA size in the CCA model (17), while the lower panel shows the corresponding  
 409 clustering pattern in the LCA model (19). The simulation includes 500 time steps (data set length) and  
 410 100 independent runs of each of the 8 cases shown in the graph. The vertical axes indicate the squared  
 411 Euclidian distance between the measured data sets.

412 Further analysis of the model, also in other areas of the parameter space, could be done by utilising  
413 the online version of the model, published at Wolfram Demonstration Project  
414 (<http://demonstrations.wolfram.com/CellularAutomataModelOfAnMPAFishery/>).

415

## 416 **6. Discussion**

417 This paper presents a deterministic spatially-heterogeneous model (according to the categorisation  
418 proposed by Sumaila and Charles, 2002) based on simple principles of cellular automata modelling  
419 combined with a more traditional harvest production model under the assumptions of open access to  
420 the fish stock resources and MPA management. Fishing effort is distributed on the basis of biomass  
421 distribution, controlled by a knowledge or smartness parameter,  $d$ .

422 Standard deviation of the average biomass (shown for the CCA model in Figure 9, but visible for both  
423 the CCA and LCA model in Figures 7 and 8) is decreasing by increasing MPA size, suggesting larger  
424 stock biomass fluctuations by smaller MPA size. This is consistent with the findings by Conrad (1999)  
425 for the stochastic model he applied, where also variance differences between open and closed areas are  
426 discussed. It is not obvious how the effect of increased smart fishing (higher  $d$  values) is in this  
427 respect. Probably there are two counteracting effects, since increased  $d$ -value reduces the fishing area  
428 by concentrating the fishing activity, but over time the fleet may cover a large area since the biomass  
429 density varies, also as a function of previous fishing. The open access fishery also creates effort  
430 fluctuations since no equilibrium solution is established, also influencing the causes of this. The fleet  
431 increases and decreases as a function of profitability in the fishery, which generates biological  
432 consequences in different areas. As the area open to fishery diminishes the fluctuations also are  
433 reduced, as a function of the reduced probability space of fluctuating effort and biomass. Decreasing  
434 biomass variance related to increasing MPA size in particular causes corresponding changes in  
435 fluctuations of harvests and net revenues (economic rent) in the CCA case. The average values remain  
436 however quite stable over large ranges of MPA sizes, different from in the LCA case (see Figures 7, 8  
437 and 9).

438 Fleet dynamics related to net revenue fluctuations causes limit-cycle patterns in the LCA model (19)  
439 (Figure 7), while the CCA model (17) displays pseudo-random patterns (Figure 6), with decreasing  
440 fluctuations by increasing MPA sizes. Similarly the limit-cycles displayed in Figure 7 increase in  
441 ranges by increasing MPA size up to a closed area of about 25%, from which the limit-cycles contract  
442 by increases closed area. Figure 8 suggests that a similar pattern may be found in the CCA model (17),  
443 though less visible due to the pseudo-random feature of CCA.

444 Figures 6 and 8 also display interesting internal differences in the open access dynamics between the  
445 two distribution of effort ( $d = 0$  and  $d = 8$ ). While  $d = 8$  fishing activities effectively are targeting areas  
446 with high biomass densities aiming to almost maintain the level of fishing effort by increasing MPA  
447 size. In the case of a uniform distribution of fishing effort ( $d = 0$ ) the open access effort exhibits larger  
448 fluctuations and lower average values. Obviously the assumption regarding effort distribution is  
449 critical for the model results. It should be noted, as previously mentioned, that results obtained by  
450 models which are not including any spatial dimension in principle corresponds to the current results of  
451  $d = 1$ , rather than  $d = 0$  (if  $r > 0$ ), since the lacking spatial dimension also implies a uniform  
452 distribution of biomass.

453 Optimal size of the protected area has been the focus of many authors, both from a biological  
454 (conservation) perspective and from an economic point of view. As biologists tend to emphasise the  
455 biological system in empirical studies and since economists put more weight on human behaviour and  
456 theoretical models, it seems to be more common in biological MPA studies to discuss the actual  
457 physical size of the protected area (typically in terms of  $\text{km}^2$ , see for example Claudet et al., 2008 and  
458 Halpern, 2003), while economists more or less in unison measure MPA size in percent of total area. A  
459 biodiversity study by Rodrigues and Gaston (2001) links the two concepts of physical and relative size  
460 to number of species and number of sites. Their study is based on bird distribution, but the complex  
461 relationships between absolute size, relative size, number of species and local communities they  
462 describe, are probably equally relevant for aquatic ecosystem. Economic utilisation of such ecosystem  
463 further complicates the picture.

464 It appears to be a considerable gap between the empirical biological MPA studies and bioeconomic  
465 studies based on metapopulation dynamics modelled by systems of differential equations. To include  
466 all this aspects in a modelling exercise is however neither easy nor particularly useful. A range of  
467 modelling approaches, with varying focuses and simplifications, may all represent valid and useful  
468 ways forward, depending of the aim of the exercise. There is no need for including all aspects, in fact  
469 it would not lead to a useful model. But when spatial issues are the focus of a study, it appears to be a  
470 doubtful approach to simplify the spatial aspect to only be represented by two biomass points (units)  
471 interacting with each other through density driven migration. Nevertheless this appears to be the most  
472 common approach in bioeconomic MPA studies (see Conrad, 1999; Armstrong and Reithe, 2001;  
473 Hannesson, 1998 and 2002; Lauck et al., 1998). Migration between the two areas is not a border  
474 phenomena propagating into the two areas causing gradients, biomass clusters and empty locations,  
475 but is modelled as if it was liquid placed into two connected chambers. When removing some liquid  
476 from one chamber, its filled in from the other by gravitation rather than by individual decision  
477 behaviour by the elements (in the liquid molecules which in an aquatic system could be individual  
478 fishes, constituting the total stock). Vessel distribution becomes no issue, as the open area in the model  
479 has no distribution.

480 It seems to be a rather robust conclusion of a number of bioeconomic MPA studies utilising the  
481 modelling approach described above, that the MPA area needs to be rather large in order to benefit the  
482 soundness of the stock and the economy of the fishery. Armstrong and Reithe (2001) and Boncoeur et  
483 al. (2002) are examples of this, Beattie et al. (2002) present a review over several other studies  
484 arriving at the same conclusion, suggesting large MPAs. The hypothesis of the modelling exercise  
485 presented in this paper, is that the finding that MPAs need to be large to do the work, to a large degree  
486 could be influenced by the lack of spatial resolution in the applied models. This hypothesis could not  
487 be rejected by this study. On the contrary, this study shows that in cases where biomass and fishing  
488 effort is equally distributed, both the CCA and the LCA models arrive at the same conclusion. But in  
489 other cases this conclusion is altered.

490 The spatial distribution of biomass in the cellular automata models are controlled by the range  
491 parameter  $r$ . In the case of no biomass diffusion between cells ( $r = 0$ ) it is clearly seen from Figures 2,  
492 3 and 4 that the stable biomass level of the CCA model never reaches the theoretical equilibrium level  
493 of number of cells divided by two (0.5 in each cell) as in the LCA model.

494 Uniform effort distribution combined with a heterogeneous distribution of biomass may have  
495 devastating negative stock effects, causing even small MPA sizes to have significant conservation  
496 effects, as seen in the CCA model of this study and reflected both in Figures 8 and 9. The negative  
497 stock effect of covering the complete open area by fishing activities is shown to be dramatic, but  
498 equally unrealistic, first of all by economic reasons. Technological development makes the fleet  
499 increasingly efficient in catching efficiency and fish finding capacity, the latter is probably increasing  
500 the value of  $d$  far beyond 1, as indicated by other studies (Swain and Wade, 2003 and Ellis and Wang,  
501 2007).

502 Increasing growth rate ( $g$ ) improves the fit of the CCA model, moving the stable biomass closer  
503 towards the equilibrium level and reducing the time of recovery. The LCA model seems to be more  
504 robust towards changes in fishing patterns controlled by the parameter  $d$  (Figures 6 and 7), while the  
505 CCA model displays significant changes by varying values of  $d$ . It is simply easier to take advantage  
506 of increased knowledge about biomass distribution when this distribution is non-uniform. The biomass  
507 distribution of the LCA model is a priori expected to be less heterogeneous than what is found in the  
508 CCA model since it follows a continuous growth pattern within each cell, while the CCA model  
509 embeds local collapses and recoveries (booms and blasts). These expectations are also confirmed in  
510 the performed simulations. This difference between the two models vanishes in the case of  $d = 1$  where  
511 the distribution of fishing effort perfectly reflects biomass distribution and the average biomasses in  
512 the CCA model get very close to the biomasses obtained by the LCA model. For other values of  $d$  the  
513 CCA model seems however always to come up with larger biomass values than those found by the  
514 LCA model. This result may question the effect of partial area closure as an effective mean of stock  
515 conservation, often put forward as one of the main concerns when implementing MPA regulation. The



516 stock conservation effect of MPA regulation comes out to be less, and in some cases almost negligible  
517 in the CCA model compared with the LCA model.

518 Smart fishing and high expertise in targeting areas of high fish density ( $d > 0$ ) contributes in stabilising  
519 the stock and reducing the risk of stock depletion, increasingly so with increasing values of  $d$ . In  
520 addition to the positive stock effects of effort clustering, there are also economic benefits up to a  
521 certain point. As the value of  $d$  is approaching infinity, the whole fishing fleet will be placed into the  
522 single cell currently holding the largest biomass. Hence the total catch could not exceed the stock  
523 biomass of this cell, illustrating that increased fish finding capacity not necessarily leads to increased  
524 catches, even in the short run. The immediate (short run) catch therefore reaches a maximum value at  
525 some value of  $d$  within the range  $0 < d < \infty$ . It should be noted that there also is a positive stock  
526 effect in the long run even though the economic benefits contribute in increasing the level of open  
527 access effort and hence increasing the stock pressure.

528 The seemingly stock conserving effect of increased ability to target and approach the fish dense area  
529 (cells) compared with uniform distribution of fishing effort origins from the fact that the latter  
530 represents a situation where all cells are targeted, even though the fishing effort distributed on each  
531 cell is low. When the fishing effort is concentrated in some cells, biomass growth in the other cells is  
532 not negatively affected. The distributing of increased biomass from these cells contributes to recovery  
533 in the cells which depleted biomass by previously high fishing pressure. The increased fishing pressure  
534 in some cells caused by smart fishing also leads to reduced fishing pressure in less attractive areas.

535 The total effect of this needs to be studied in greater details and it seems to be crucial to include  
536 fishing effort distribution in fisheries models not only because of the biological effects, but also for the  
537 impact it may have on the economic performance of the fleet. In a new not yet published study by this  
538 author, the distribution of fishing effort is linked to the economic performance in a 2D model,  
539 including biomass distribution (relevant for income) as well as distance from port and other costs of  
540 fishing. The same pattern is obtained while increasing the value of  $d$ , as described above. This present  
541 study indicates that the performance of MPA regulation in both aspects (stock conservation and

542 economic benefits) has to be understood as functions of fish and fishers' behaviour, the latter  
543 including fish finding activities and effort clustering in areas with high fish densities.

544 As further seen from Figures 6 and 7, as well as in Figure 8, net revenues fluctuate between positive  
545 and negative values (quasi rent due to the definition by Marshall, 1893). In the long run periods of  
546 positive rent may more than compensate for the losses in the periods of negative rent. The stiffness  
547 parameter  $a$  determines the rate at which the fishing effort adjusts according to the economic  
548 performance of last period. The adjustment rate depends on how easily input factor in production may  
549 be moved from one place to another. As labour increasingly is substituted by capital in effort  
550 production, the stiffness parameter is expected to decline, since labour more easily is moved than  
551 capital items (vessel, gears, etc.) Changing the stiffness parameter  $a$  within a realistic range of course  
552 changes the absolute values, but the main pattern caused by the permanent adjustment to changing  
553 economic performance remains as long as  $a > 0$ .

554 The fluctuations in net revenues are reduced by increased MPA size. Since an open access equilibrium  
555 is characterised by no rent (as only normal profit is obtained), the rent obtained in the open access  
556 dynamics is accidental rent when the level of fishing effort is adjusting to constantly changing stock  
557 biomass. This quasi rent causes the effort to increase or decrease with a rate determined by how fast  
558 capital could be moved into or out off the fishery. In the models presented here this rate is given by the  
559 stiffness parameter  $a$ , assuming equal entry and exit rates. In the real world it is probably easier to  
560 enter than to leave a fishery, as the entrance may come from all capital sources, while the capital  
561 already bound into a specific fishery has limited possibilities of other placements in the short run.

562 Based on the findings in Eide (2007) a higher entry rate than exit rate seems however not to alter the  
563 finding of this study. Fluctuating biomasses give reason for corresponding changes in fishing effort,  
564 depending on these entry and exit rates. Even slow growing species outstrip the speed of growth in  
565 effort both when increasing and decreasing biomass. Since the fishing effort in some sense is running  
566 after the stock biomass, the effort is less than corresponding open access effort when biomass level is  
567 peaking (causing positive rent) and higher when the biomass is reaching low level (causing negative  
568 rent). The negative rent in the real world of economic rational behaviour however has a minimum

569 level where the contribution margin becomes zero and the fleet is better off staying in harbour. While  
570 this possibility is considered in Eide (2007), it is not included in this study. By correcting for this error  
571 the quasi rent obtained in the open access fisheries of this study could be even higher.

572 The cluster analyses displayed in Figures 10 and 11 represent inputs in the discussion on determining  
573 the optimal MPA size. As previously mentioned most bioeconomic studies on this issue conclude that  
574 the MPA size needs to be considerable to give stock conservation effects corresponding to rent  
575 maximisation (see for example Lauck et al., 1998; Armstrong and Reithe, 2001; Boncoeur et al., 2002;  
576 Beattie et al., 2002 and Helvey 2004). These results are confirmed in Figures 10 and 11 for the LCA  
577 model in cases fitting the common assumptions of uniform effort distribution ( $r = 0$ ) as well as in the  
578 case of  $r = 2$  and  $d = 1$ , which actually also represents the case of uniform distribution of effort (since  
579 the biomass is actually uniformly distributed even at range 2 in the LCA model). In both these cases  
580 there are a two large clusters divided at MPA sizes below and above 70-80% of the total area, which  
581 confirms the findings of the previous bioeconomic studies mentioned above. Also the CCA model  
582 displays a similar pattern for  $r = 0$  and  $d = 0$ , under which parameter setting the CCA model has an  
583 almost uniform distribution of biomass and effort. In this case the stock biomasses and net revenues in  
584 the CCA model cluster at the extreme MPA sizes of below and above 80-90% of the total area.

585 More interesting though is that except for the rather unrealistic cases referred to above, none of the  
586 other findings from the CCA model support the hypothesis that a large fraction of the total area need  
587 to be protected in order to obtain an optimal economic performance while utilising MPA as a way of  
588 regulating the fishery. On the contrary, the effect of closing relatively small areas (3-15% of the total  
589 area), is significant on both stock biomass and economic performance. This indicates that the common  
590 assumption of uniform distribution of stock biomass and effort outside the protected area dramatically  
591 affect the evaluation MPA sizes.

592 The concept of cellular automata represents a simple way of modelling spatial distributions. A range  
593 of other ways of modelling spatial distribution exists, and a number of previous MPA studies have  
594 utilised some of these methods. There is however another special feature of cellular automata

595 modelling which is not equally easy achieved by other modelling techniques. Cellular automata  
596 implements micro dynamics at cell levels and is a bottom-up modelling approach. The biological  
597 models proposed in this study could also include cell specific parameter values in addition to the state  
598 variables. Varying environmental capacity of different cells could be implemented by varying cell  
599 specific growth rates and/or saturation levels (biomass maximum). A further study of the robustness of  
600 MPA regulation under different environmental conditions and distribution rules should also include  
601 spatial environmental variation. The models presented in this study represent a possible way forward  
602 to perform such investigations.

603 The theoretical study presented in this paper is not linked to any specific real fishery. The aim has  
604 been to investigate some theoretical concepts regarding model design and common issues regarding  
605 implementation of MPA regulation in relation to fisheries, the issue of MPA size being the most  
606 important. In principle any real fishery could be represented by the model, taking in consideration that  
607 the parameter space is larger than the few single points investigated in the simulations presented here.  
608 A large range of different fisheries could however be covered by the fraction of the parameter space  
609 utilised in this study, first of all since cell size and time unit is not specified here. A time unit of  
610 several years could in principle cover slow growing species. Cell size combined with the range  
611 parameter  $r$  could be specified to fit the theoretical physiological and physical diffusion range a  
612 species may have within the chosen time frame, or a more accurate distribution area based on  
613 empirical studies may be used to specify cell size. The total distribution area is covered by increasing  
614 the number of cells sufficiently.

615 A further development of the model is now in progress. An extension from a 1D row to a 2D lattice  
616 also involves a shift in the effort distribution proxy from being biomass distribution to be theoretical  
617 (possible) net revenue distribution. This follows from the fact that there will be differences in cost by  
618 approaching different areas in the 2D lattice, by varying distance from home port. By such minor  
619 changes a very flexible and general model may be available, which because of its simplicity makes it  
620 possible to investigate issues which normally represent major modelling challenges, like seasonal  
621 growth, seasonal fisheries and seasonal variations in markets.

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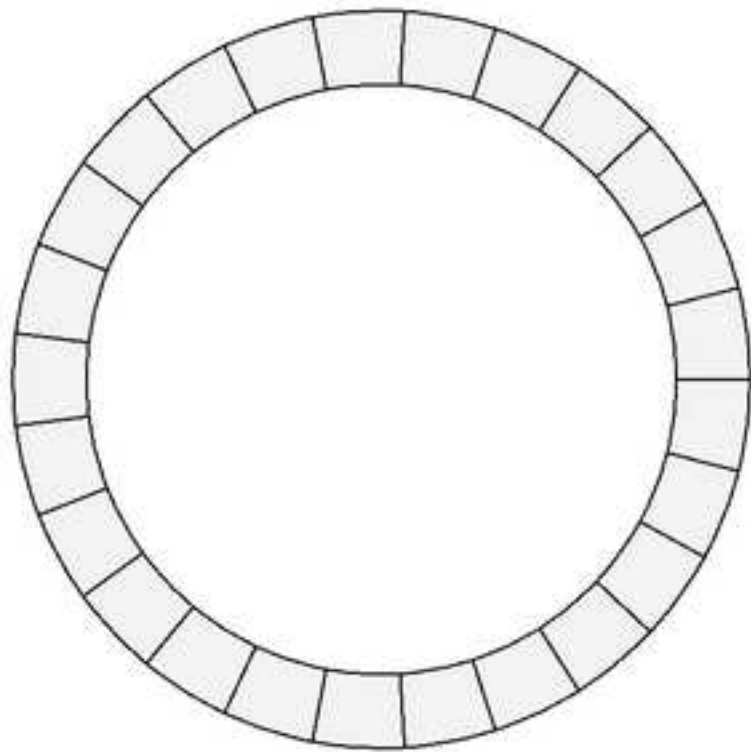
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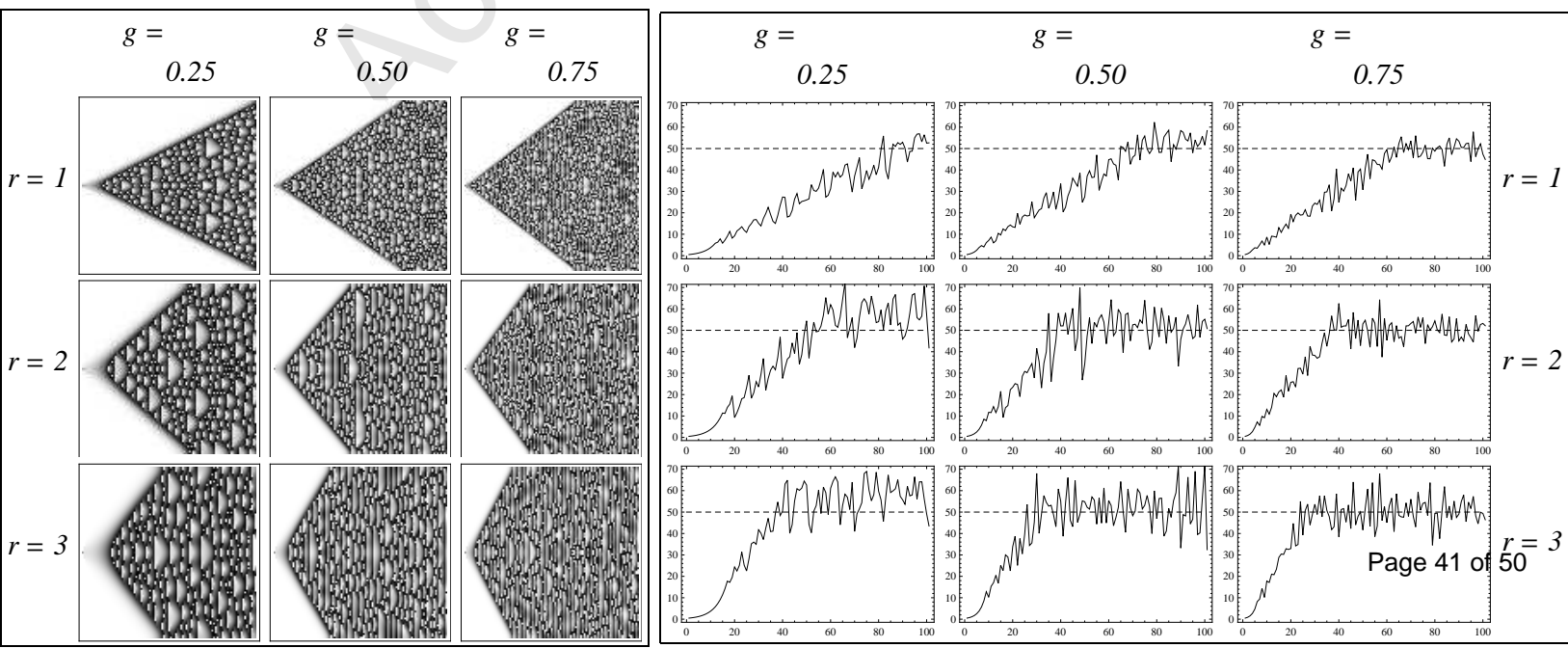
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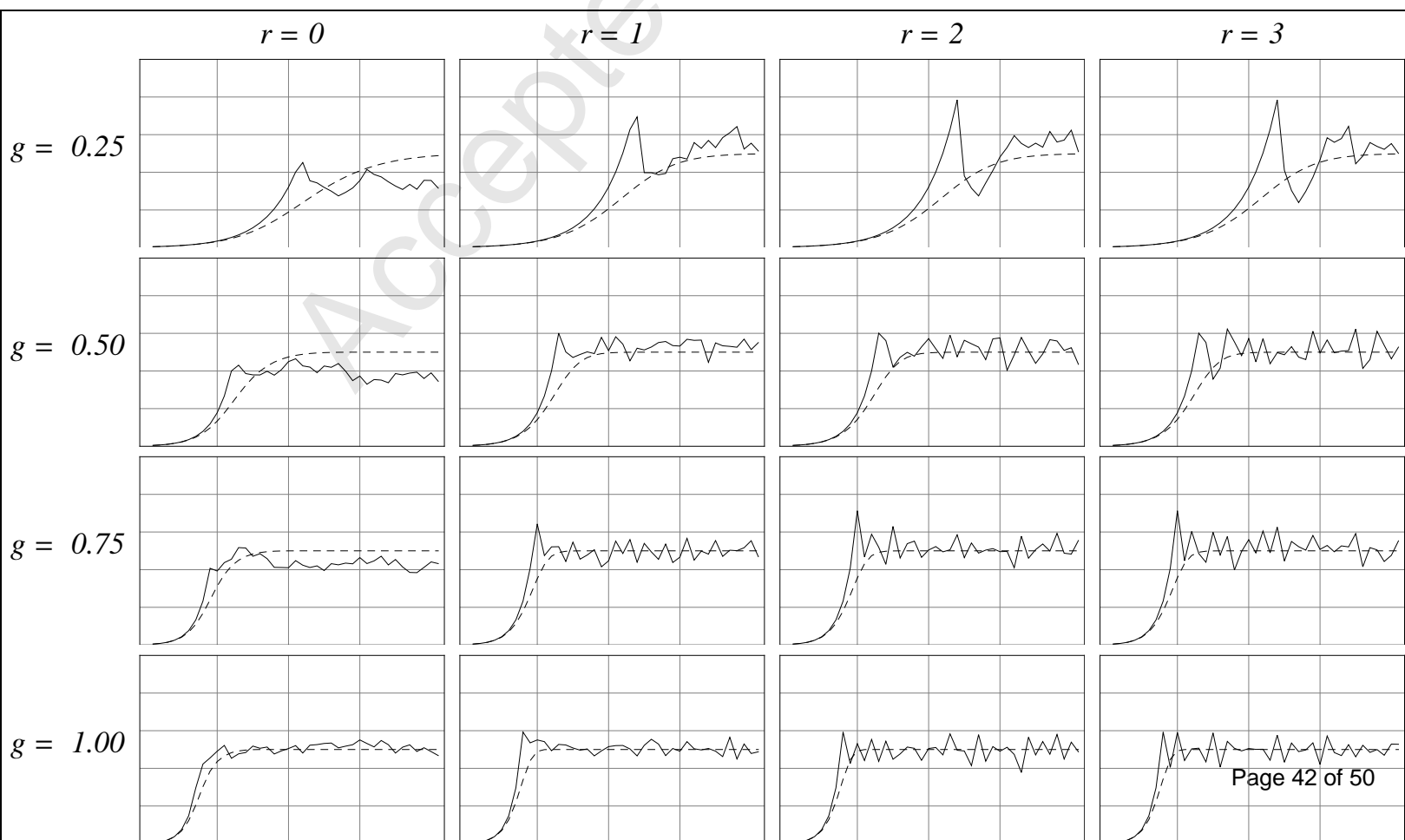
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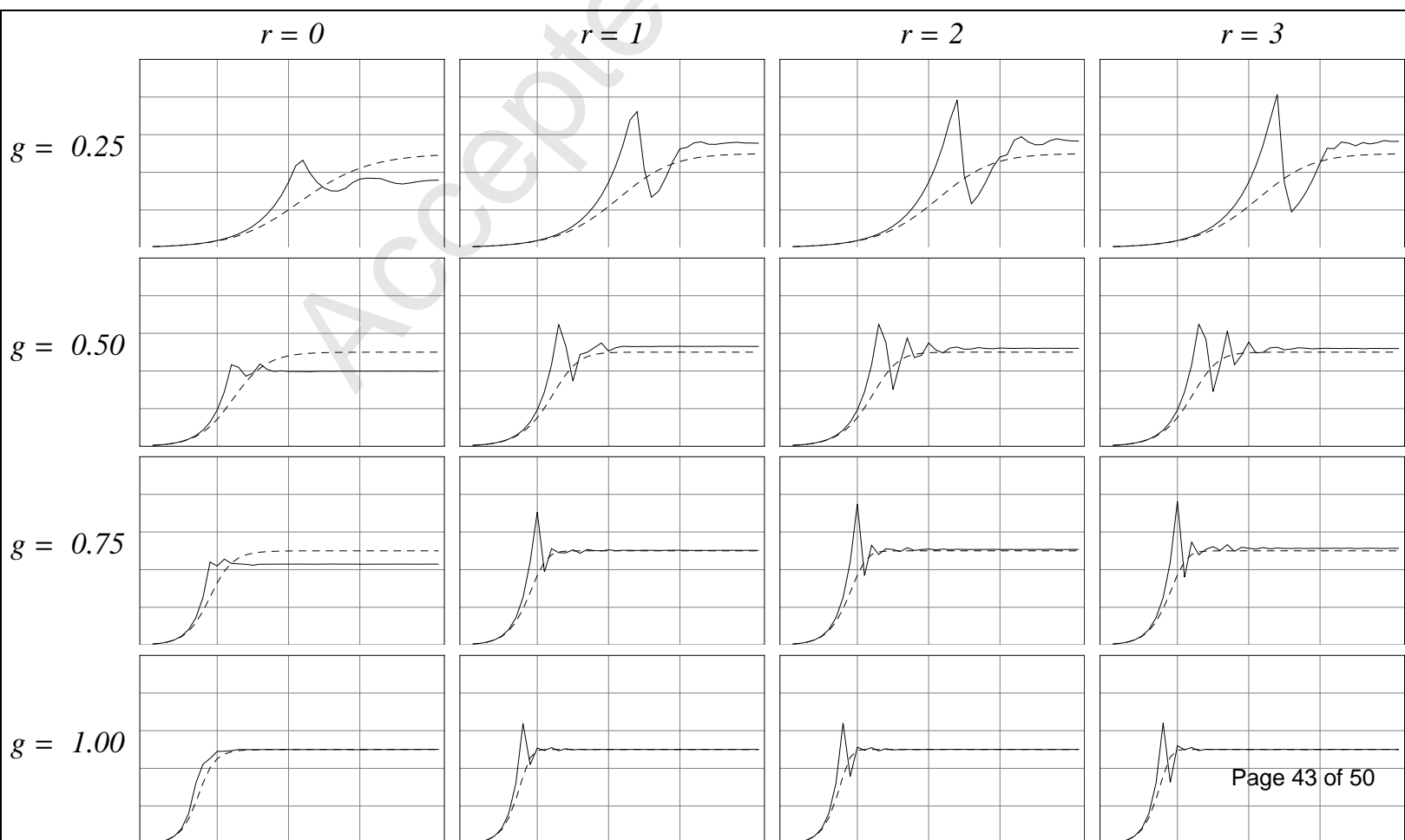


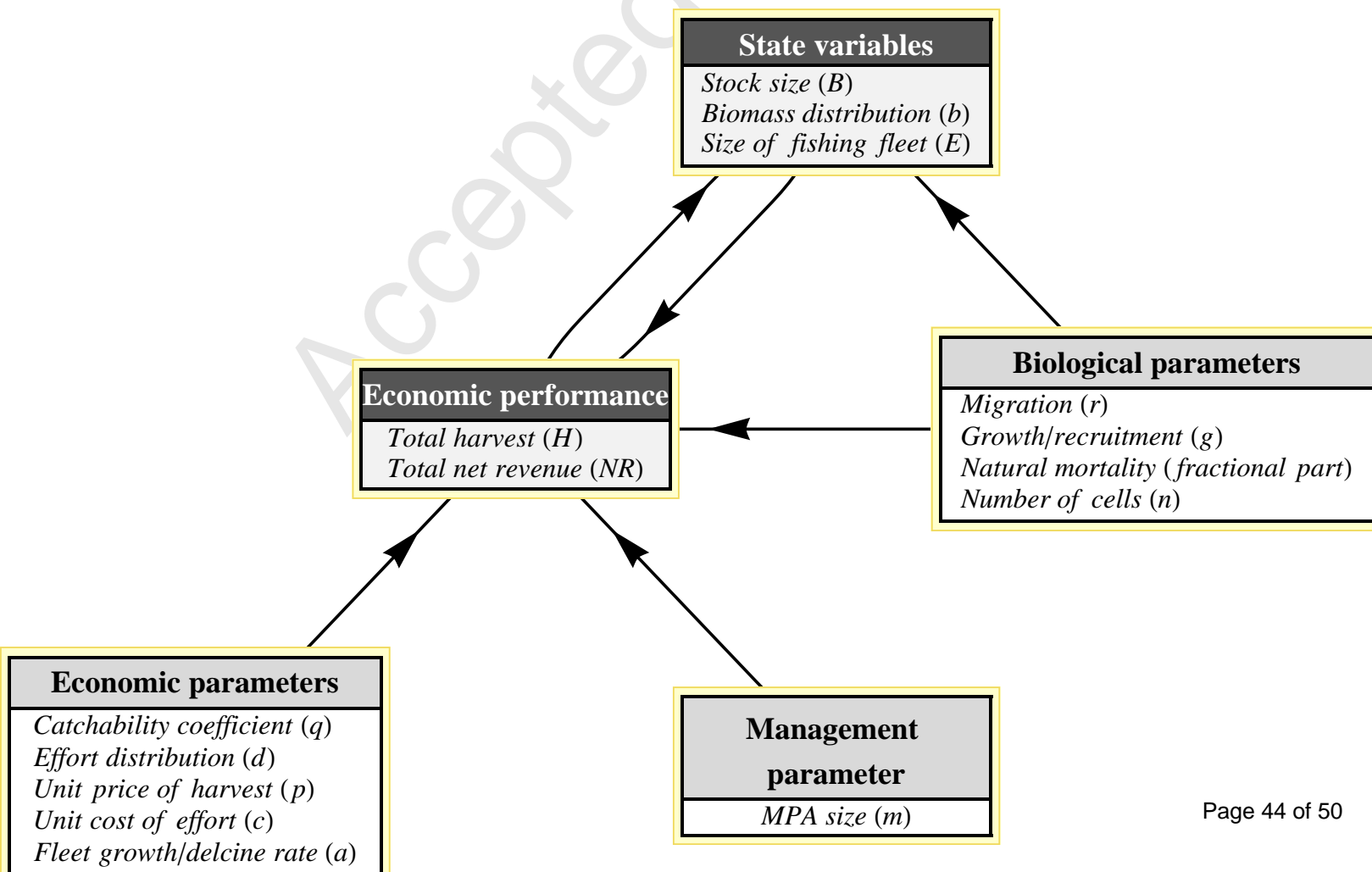
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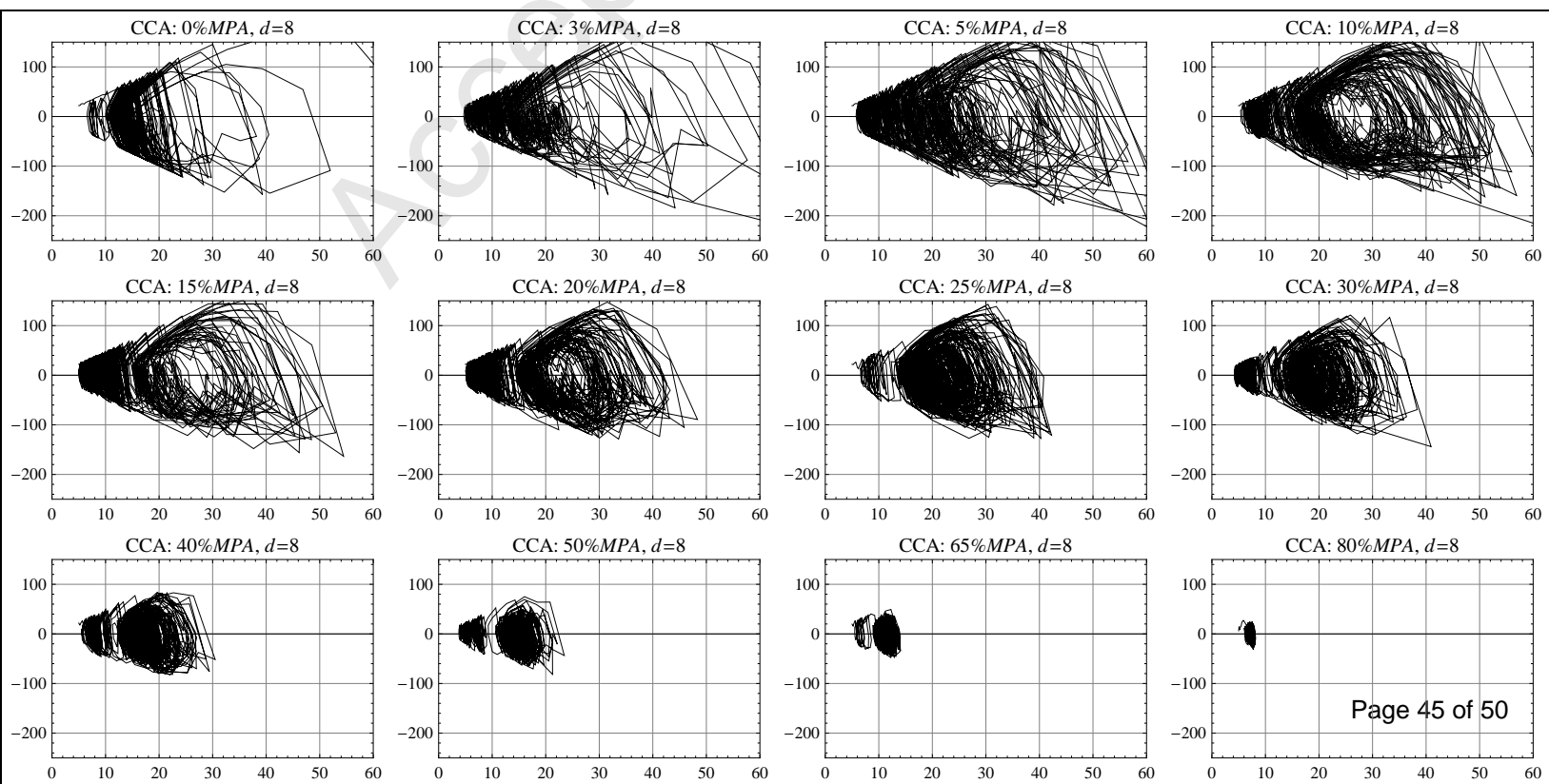
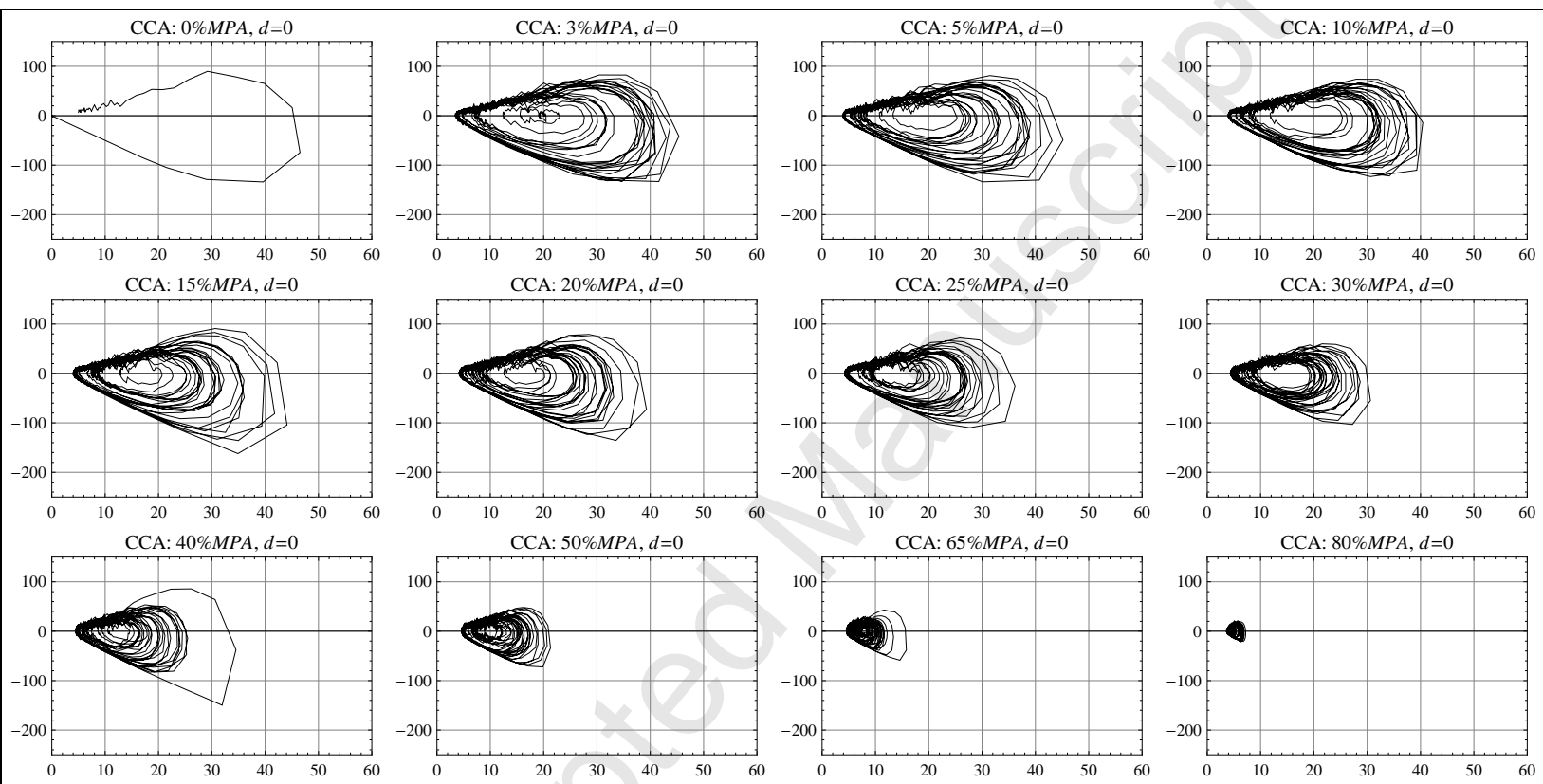


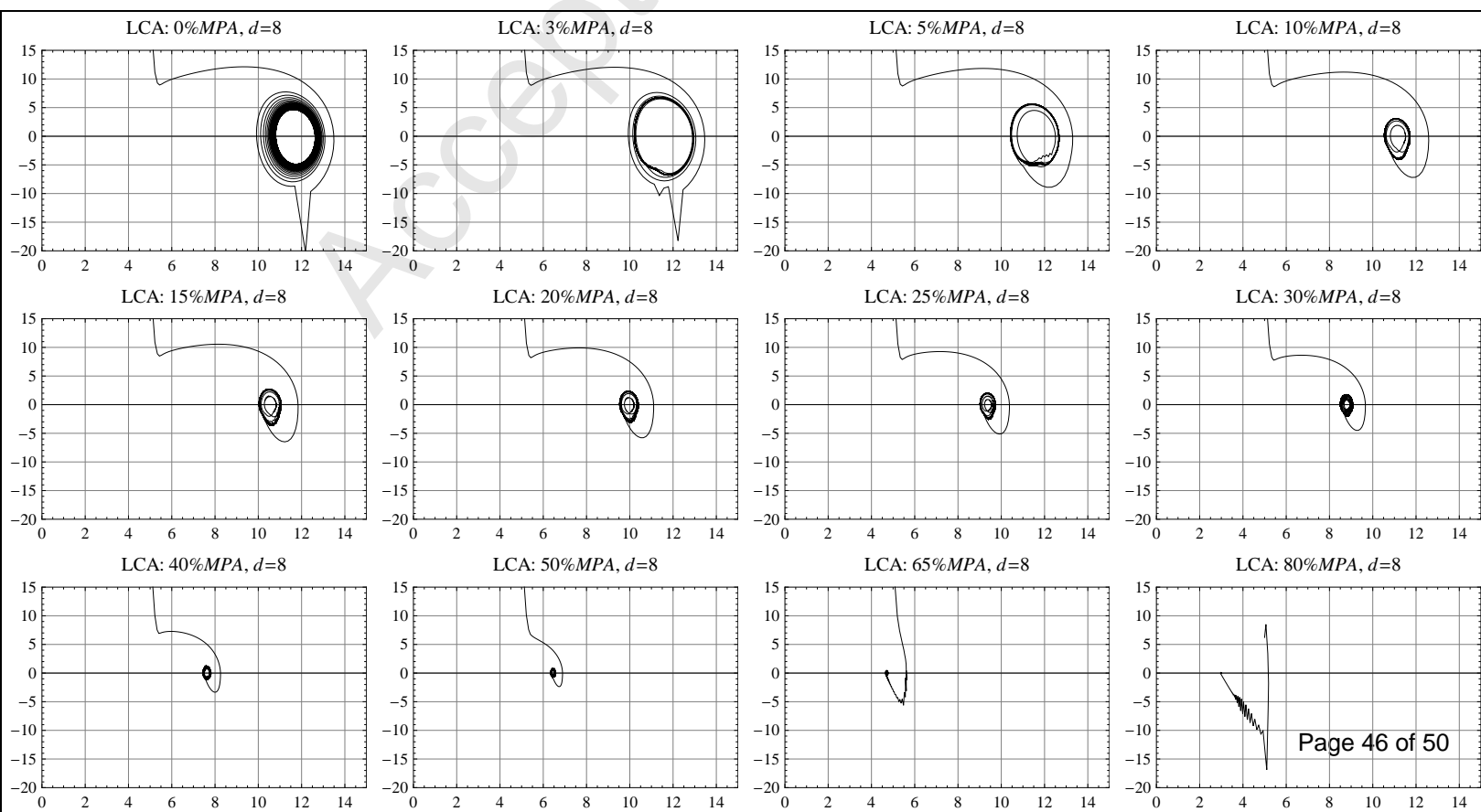
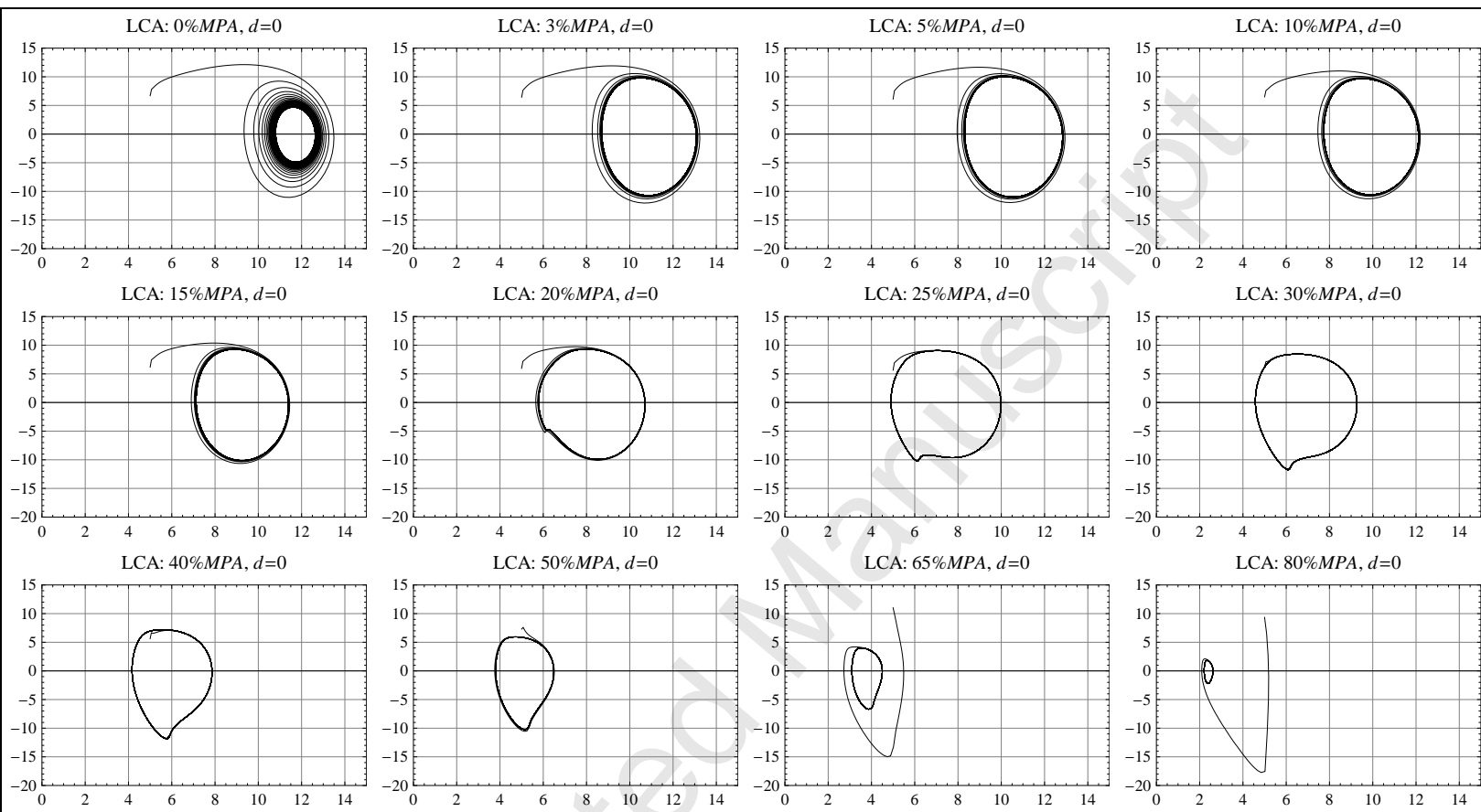


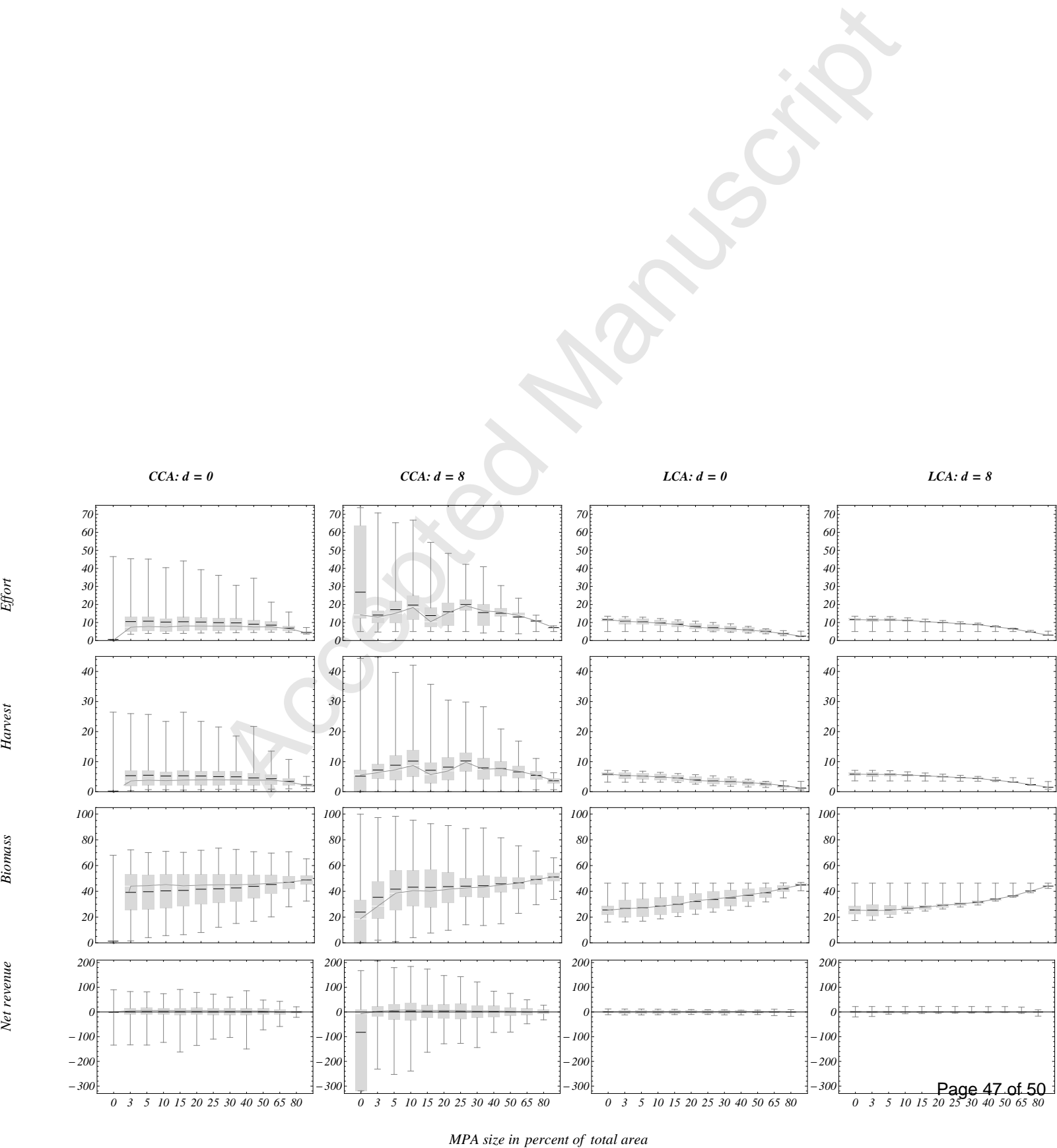




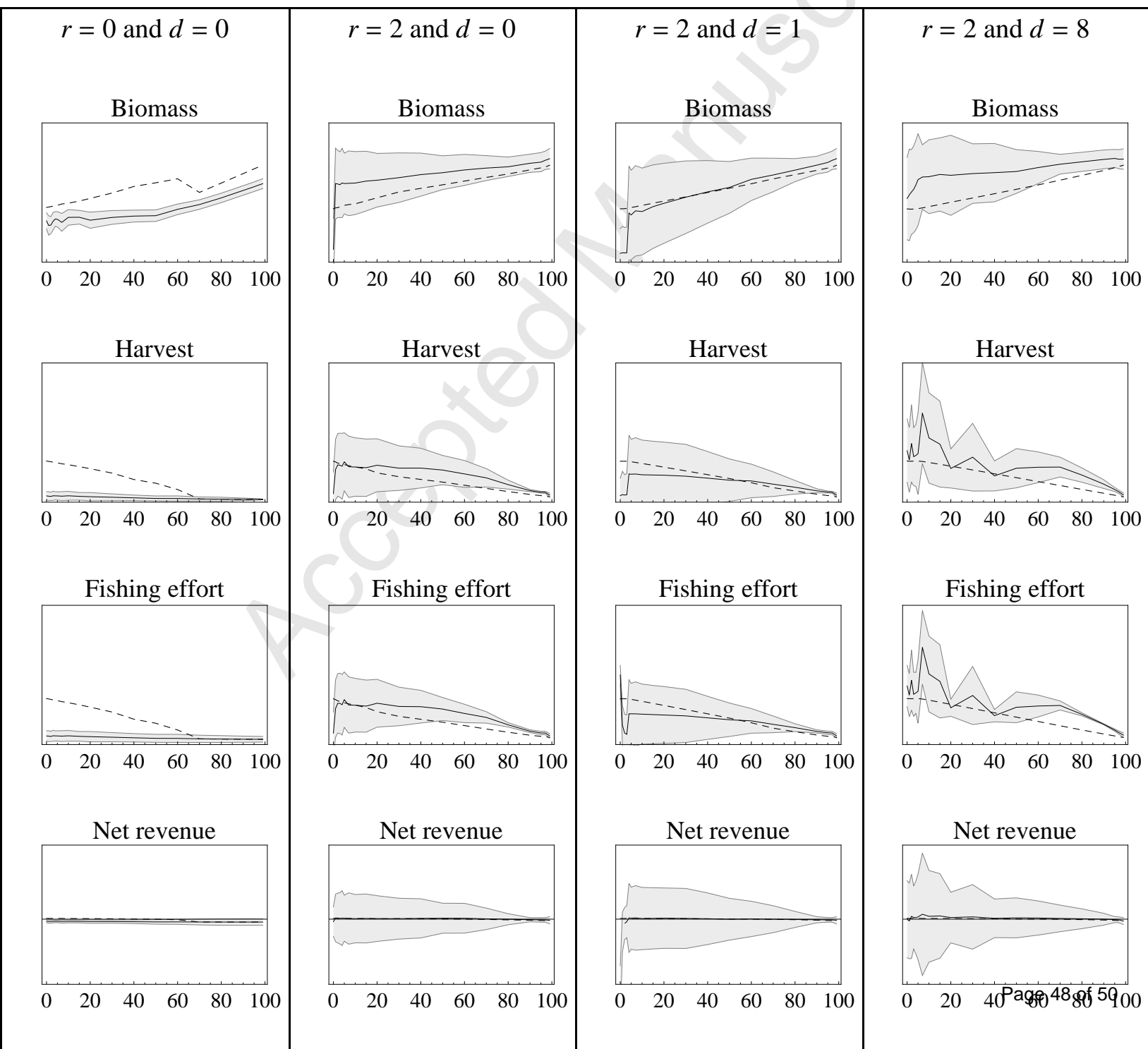


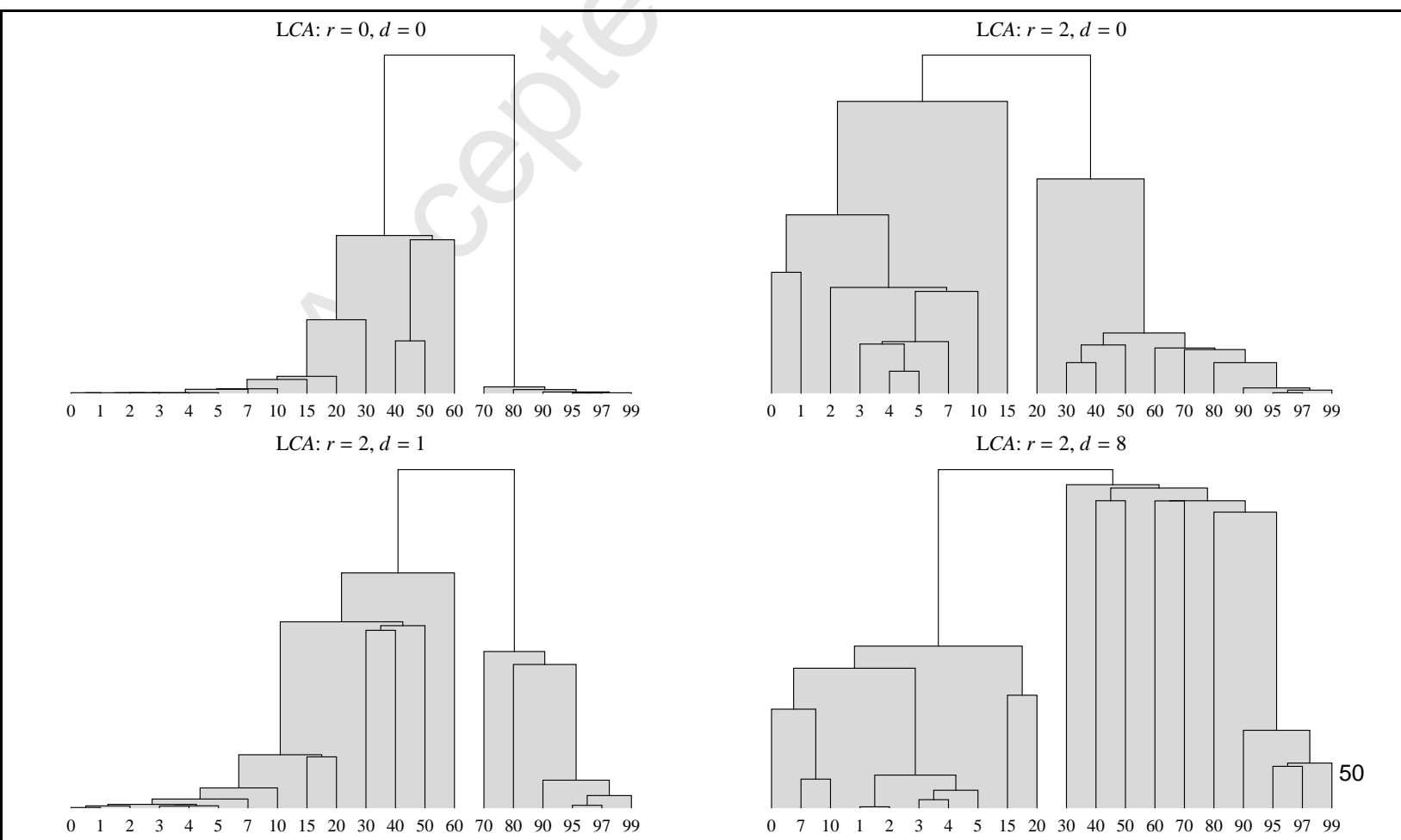
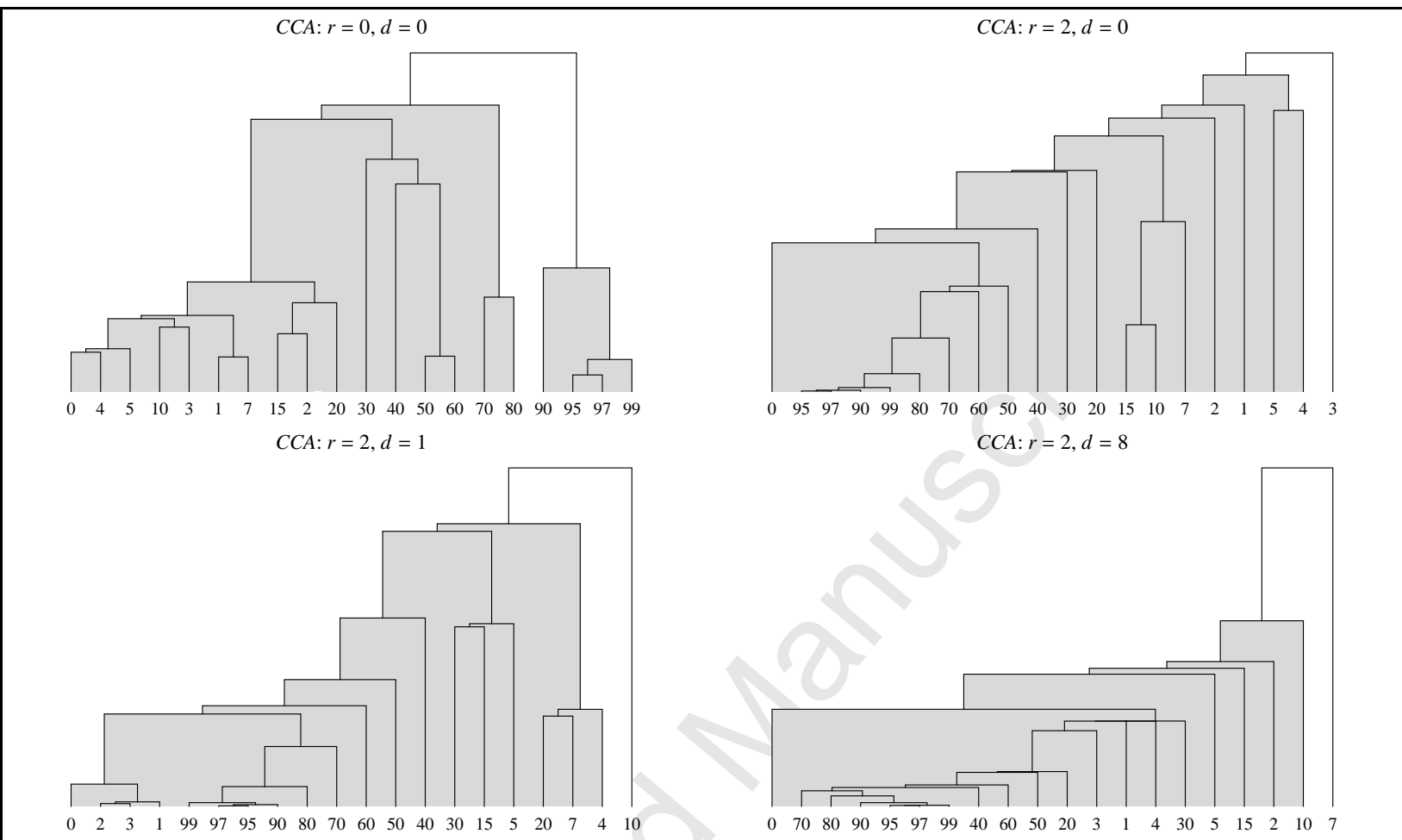










*Stock biomass*

## Net revenue

