Journal of Sustainability Science and Management
Volume 7 *Number* 2, December 2012: 201-206

ISSN: 1823-8556

MAXIMUM SUSTAINABLE YIELD FOR MARINE METAPOPULATION GOVERNED BY COUPLED GENERALISED LOGISTIC EQUATIONS

SUPRIATNA, A. K.

Department of Mathematics, Faculty of Mathematics and Natural Sciences, Padjadjaran University, Jatinangor 45363 West Java, Indonesia.

Corresponding author: aksupriatna@bdg.centrin.net.id / ak_supriatna@unpad.ac.id

Abstract: Many important renewable natural resources, such as commercial marine populations, are known to form metapopulations structure. They consist of several inter-connected subpopulations that live in different patches of habitat and have different biological and demographical characteristics. Managing them either as a single well-mixed population or barely as several disconnected populations is clearly inappropriate, and may lead to unsustainable utilisation of those populations. In this paper, the effect of demographic and biological parameters variability on the maximum sustainable yield for the metapopulation is discussed. The traditional maximum sustainable yield that ignores the variability of these parameters is compared with the maximum sustainable yield that considers this variability. Several insights on how to manage the populations in a sustainable manner are derived and could be used as guidance in the exploitation of precious renewable natural resources. The result of the paper shows that the magnitude of the maximum sustainable yield depends critically on the biological parameters with the respect to the corresponding spatial scale. Different places give different values of maximum sustainable yield. In general, there is a trade-off among biological parameters in different patches determining whether the stock living in one patch should be harvested more conservatively or less conservatively than the stock living in another patch.

KEYWORDS: maximum sustainable yield, harvesting theory, metapopulation

Introduction

Most commercial marine populations have some degree of spatial heterogeneity. This spatial heterogeneity means that modelling the species as one single population is not adequate. Moreover, many of these marine populations have a metapopulation structure with local populations connected by the dispersal of individuals (Prince, 1992; Secor, 2002). An approach of using metapopulation structure in harvesting theory can dramatically change the ideas on how to manage the exploited populations (Jonzen *et al.*, 2001). Numerous examples have shown that inappropriate management by neglecting this metapopulation structure may result in the collapse of the exploited populations (Frank and Leggett, 1994).

Ecologists have paid more attention to spatial heterogeneity patterns than economists have in studying exploited natural resources (Sanchirico and Wilen, 2001). Examples include scallop fishery (Hilborn and Walters, 1987), tuna fishery (Kleiber and Edwards, 1988), abalone fishery Tuck (Supriatna and Possingham, 1998; 1999), hypothetical (Supriatna *et al.,* 2002) and lingcod fishery (Martel *et al,*. 2000). Following the success of the ecologists in exploring the effects of spatial heterogeneity on natural resources exploitation, economists such as Bhat *et al.* (1996), Bulte and van Kooten (2001) and Sanchirico and Wilen (1999) begun to take into account the spatial implications of resources exploitation.

In this paper, the effect of spatial heterogeneity on the maximum sustainable yield for the metapopulation is discussed. It is assumed that the spatial heterogeneity manifestation is in the form of the variability of the demographic and biological parameters. The traditional maximum sustainable yield that ignores the variability of these parameters is compared with the maximum sustainable yield that considers this variability.

Received: 09 January2012 / Accepted: 30 July 2012

Review on One-Patch Mathematical Model

Despite the advances of harvesting theory (Kellner *et al.*, 2007; Costello *et al.*, 2008), many practical fisheries management and fisheries data analysis are still based on the maximum sustainable yield (MSY) concept, especially in the developing countries. This indicates that the study of the MSY for exploited population which take account various relevant biological and economical aspects is still worthwhile to improve the implementation of the MSY concept. Even the study on the understanding of the underlying process or the dynamics of the natural growth of the exploited population may also provide useful guidance in utilising the population (Mamat *et al.*, 2011; Salleh *et al.,* 2011).

To capture a brief explanation of the concept, let us assume that there is a natural stock of a harvested population having natural growth given by $f(N)$, with $N(t)$ (or simply N) denotes the number of individuals of the stock at time t. As an illustration, let us assume that the logistic function $f(N) = rN(1 - N/K)$ be the natural growth of the population with r and K be the intrinsic growth and the carrying capacity of the population, respectively. If there is a constant rate of harvesting h then the dynamics of the exploited population is given by $\frac{dN}{dt} = rN(1 - N/K) - h$. Steady-state condition ensures the sustainability of the stock existence, and gives the harvest as a function of stock escapement, $h = rN(1 - N/K)$. It is easy to show that, at $N^* = K/2$, the harvest is maximum with the corresponding harvest $h^* = rK/4$, which is called the MSY. Harvesting at the MSY level ensures that the stock is sustainable, while harvesting above the MSY level leads to the extinction of the stock.

In the next section, the MSY concept in a metapopulation is discussed. Hanski and Gilpin (1991) use the term metapopulation to describe a population which has a patchy spatial structure, and define is as a population of populations. A metapopulation falls between two extremes possible population structures: a well-mixed population and an unconnected collection of populations. Migration of individuals between patches is among the mechanisms connecting the subpopulations within the metapopulation (see Figure 1). The logistic growth function is also generalised by following Pella and Tomlinson (1969).

Two-Patch Mathematical Model

Assume that a metapopulation consists of two different patches, namely Patch 1 and Patch 2. Let the population in Patch 1 and Patch 2 be denoted by N_1 and N_2, with the natural growth is given by $f_1(N_1)$ and $f_2(N_2)$, respectively. If there is a constant rate of harvesting, h_1 and h_2 then the dynamics of the exploited population, respectively, is given by $\frac{dN_1}{dt} = f_1(N_1) - h_1$ and $\frac{dN_2}{dt} = f_2(N_2) - h_2$. Suppose that there is a movement of individuals between patches, with the rate proportional to the size of subpopulation 1, that is $p_{12}N_1$ for the movement from subpopulation 1 to subpopulation 2, and $p_{21}N_2$, otherwise. Taking this into account then we have a system of coupled differential equations governing the growth of the metapopulation in the following form,

$$\frac{dN_1}{dt} = f_1(N_1) - p_{12}N_1 + p_{21}N_2 - h_1 \quad (1)$$

$$\frac{dN_2}{dt} = f_2(N_2) - p_{12}N_2 + p_{21}N_1 - h_2 \quad (2)$$

Assume that $f_i(N_i)$ is given by the generalised logistic function $f_i(N_i) = r_iN_i\left(1 - \frac{N_i^\alpha}{K_i}\right)$. The exponent α can be interpreted as the intensity of the intra-specific competition within subpopulations. Figure 2 illustrates the effect of this intra-specific competition into the steady state of the population. It reveals that the higher the intra-specific competition, the lower the nontrivial steady state of the population. Sustainable harvest functions for (1) and (2) are given by

$$h_1 = r_1N_1\left(1 - \frac{N_1^\alpha}{K_1}\right) - p_{12}N_1 + p_{21}N_2 \quad (3)$$

$$h_2 = r_2N_2\left(1 - \frac{N_2^\alpha}{K_2}\right) - p_{21}N_2 + p_{12}N_1 \quad (4)$$

To find the MSY, consider the total harvest $h_{tot} = h_1 + h_2$ and look for the solution of the

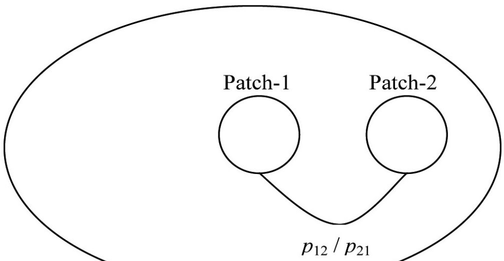


Figure 1: An illustration of a metapopulation consists of two subpopulations (subpopulation 1 in Patch 1 and subpopulation 2 in Patch 2) and is connected by the migration of individuals between the two subpopulations (p_{ij} indicates migration rate from Patch i to Patch j).

necessary conditions $\frac{\partial h_{tot}}{\partial N_1} = 0$ and $\frac{\partial h_{tot}}{\partial N_2} = 0$ to obtain the optimal escapements $N_1^* = e^{\frac{\ln(K_1/(1+\alpha))}{\alpha}}$ and $N_2^* = e^{\frac{\ln(K_2/(1+\alpha))}{\alpha}}$. It can be shown from the sufficient conditions $\frac{\partial^2 h_{tot}}{(\partial N_1)^2} < 0$ and $\frac{\partial^2 h_{tot}}{(\partial N_1)^2}\frac{\partial^2 h_{tot}}{(\partial N_2)^2} - \frac{\partial^2 h_{tot}}{\partial N_1 \partial N_2} > 0$, the total harvest h_{tot} reaches its global maximum at (N^*_1, N^*_2) as the optimal escapements. Substituting these optimal escapements into the sustainable harvest function in (3) and (4) produces the maximum sustainable yields in (5) and (6).

$$MSY_1 = r_1\left(\frac{K_1}{1+\alpha}\right)^{1/\alpha}\left(1-\left(\frac{1}{1+\alpha}\right)\right) - p_{12}\left(\frac{K_1}{1+\alpha}\right)^{1/\alpha} + p_{21}\left(\frac{K_2}{1+\alpha}\right)^{1/\alpha} \quad (5)$$

$$MSY_2 = r_2\left(\frac{K_2}{1+\alpha}\right)^{1/\alpha}\left(1-\left(\frac{1}{1+\alpha}\right)\right) - p_{21}\left(\frac{K_2}{1+\alpha}\right)^{1/\alpha} + p_{12}\left(\frac{K_1}{1+\alpha}\right)^{1/\alpha} \quad (6)$$

Clearly, the magnitude of the MSY depends critically on the biological parameters with the respect of the corresponding spatial scale. Different places give different values of MSY. It is noted that if $\Delta MSY = MSY_1 - MSY_2$ then

$$\Delta MSY = \left(\frac{1}{1+\alpha}\right)^{1/\alpha}\left[\left(\frac{\alpha}{1+\alpha}\right)\left(r_1K_1^{1/\alpha} - r_2K_2^{1/\alpha}\right) - 2\left(p_{12}K_1^{1/\alpha} - p_{21}K_2^{1/\alpha}\right)\right] \quad (7)$$

In general, there is a trade-off between biological parameters in different patches determining the sign of ΔMSY, specifically determining whether the stock in Patch 1 should be harvested more conservatively than that in Patch 2 or the opposite? For example, if the stock in Patch 1 is relatively more productive, i.e. $r_1K_1^{1/\alpha} > r_2K_2^{1/\alpha}$, and it is also relatively more important, i.e. $p_{12}K_1^{1/\alpha} < p_{21}K_2^{1/\alpha}$,

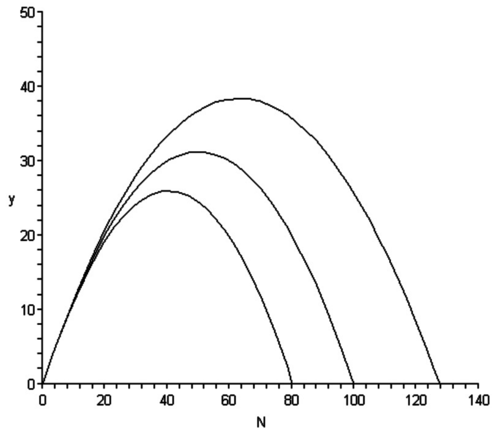


Figure 2: Examples of generalised logistic growth function with various values of the intra-specific competition intensities (α). The horizontal axis denotes the population density and the vertical axis denotes the production function at a specified density. We use $K = 100$, $r = 1.25$ and $\alpha = 0.95, 1.00, 1.05$ with the resulting non-trivial steady state ($e^{\ln(K)/\alpha}$) is $N^* = 127.4, 100, 80.3$, respectively. It shows that the higher the intra-specific competition the lower the nontrivial steady state of the population.

then the stock in Patch 1 should be harvested more heavily than that in Patch 2 since $MSY_1 > MSY_2$, and vice-versa.

To gain more insight, some special cases are explored, such as completely homogeneous subpopulations, a symmetrical migration, and a one-way migration. Equations (5) and (6) show that in the case of completely homogeneous subpopulations, in which $K_1 = K_2 = K$ and $r_1 = r_2 = r$ then the MSY difference between patches is given by

$$\Delta MSY = 2(p_{21} - p_{12})\left(\frac{K}{1+\alpha}\right)^{1/\alpha}. \quad (8)$$

This means that if there is more individuals migrate from Patch 2 to Patch 1 then Patch 2 should be harvested more conservatively than Patch 1. One-way migration follows this rule since it is a more special case in which either p_{12} or p_{21} is zero. This indicates that ignoring the presence of migration may over-harvest one subpopulation (which acts as a source subpopulation with a greater migration rate) while also may under-harvest the other subpopulations (which acts as a sink subpopulations with a smaller migration rate). A more prudent management in harvesting a biological stock certainly should take into account the presence of migration.

In the case of symmetrical migration, in which $p_{12} = p_{21}$, with $K_1 = K_2 = K$ then the MSY difference between patches is given by

$$\Delta MSY = \left(\frac{K}{1+\alpha}\right)^{1/\alpha}\left(\frac{1}{1+\alpha}-1\right)(r_2 - r_1). \quad (9)$$

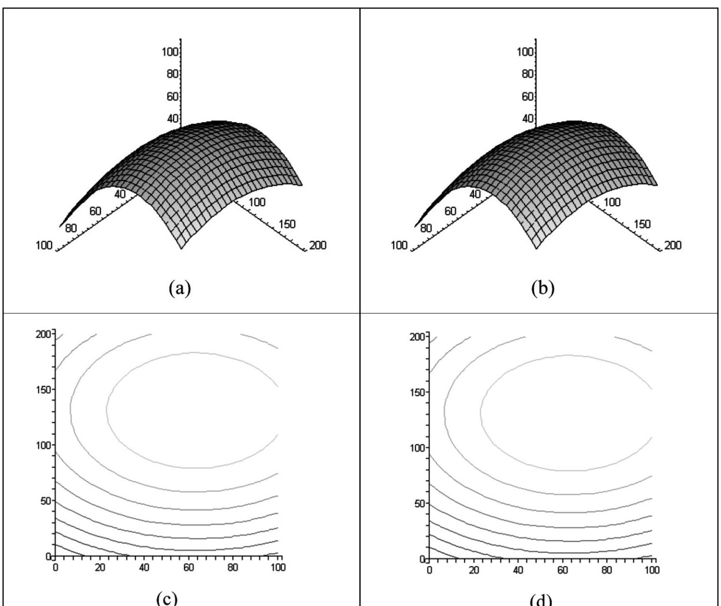
Since $1/(1+\alpha)-1$ is always negative, then the equations states that a more productive subpopulation (a subpopulation with a greater intrinsic growth rate r) should be harvested relatively more heavily than the less productive subpopulation, which is intuitive and easy to understood. In the other case, when the system has a symmetrical migration, i.e. $p_{12} = p_{21} = p$ (where $0 \le p \le 1$), but with $r_1 = r_2 = r$ then the MSY difference between patches is given by

$$\Delta MSY = \left(\frac{\alpha}{1+\alpha} r - 2p\right)\left(\left(\frac{K_1}{1+\alpha}\right)^{1/\alpha} - \left(\frac{K_2}{1+\alpha}\right)^{1/\alpha}\right). \quad (10)$$

The formula reveals that for a small migration rate such as $p < \frac{\alpha}{1+\alpha}\frac{r}{2}$ then the subpopulation with a higher carrying capacity should be harvested more heavier than that with a lower carrying capacity, but when the migration rates are big enough such that $p > \frac{\alpha}{1+\alpha}\frac{r}{2}$ then the rule is the opposite. In a more special case, when there is no migration at all, then the subpopulations with a lower carrying capacity should be protected more than that with a higher carrying capacity. The following numerical examples in Figures 3, 4, and 5 illustrate the results above.

Conclusion

A mathematical model for a spatially heterogeneous population was developed via a metapopulation framework. It is assumed that the population is patchily distributed and connected by the dispersal of individuals between its subpopulations. The formula for the maximum sustainable yield (MSY) for each patch was presented and some rules of thumb on how to harvest the metapopulation were found for some special cases. The formula shows that the magnitude of the MSY depends critically on the biological parameters with respect to the



Migration: $p_{12} = 0.1$, $p_{21} = 0.25$	Migration: $p_{12} = 0.01$, $p_{21} = 0.025$
Escapement: $N_1 = 63$, $N_2 = 130$	Escapement: $N_1 = 63$, $N_2 = 130$
Harvest: $MSY_1 = 57.1$, $MSY_2 = 53.3$	Harvest: $MSY_1 = 30.7$, $MSY_2 = 79.7$

Figure 3: Maximum harvests and the corresponding escapements for different migration rates. In (a) and (b) the horizontal axis denote the population density/ escapement for each patch and the vertical axis denotes the MSY for a pair of escapements. Figures (c) and (d) are the contour plots of (a) and (b) respectively. In the left figure the migration parameters are p_{12}= 0.1 and p_{21}= 0.25 while in the right figure the migration parameters are p_{12}= 0.01 and p_{21}= 0.025. Both figure use the same carrying capacities and intrinsic growth rates, i.e. K_1= 100, K_2= 200, r_1= 1, r_2= 1.25 and α = 0.95.

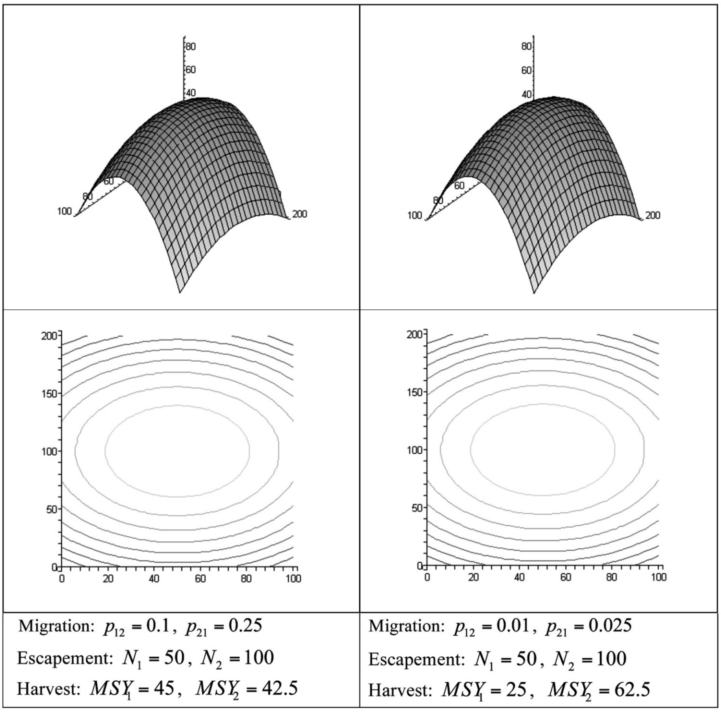


Figure 4: Maximum harvests and the corresponding escapements for different migration rates. In the left figure the migration parameters are p_{12}= 0.1 and p_{21}= 0.25 while in the right figure the migration parameters are p_{12}= 0.01 and p_{21}= 0.025. Both figures use the same carrying capacities and intrinsic growth rates, i.e. K_1= 100, K_2= 200, r_1= 1, r_2= 1.25 and α = 1. See the caption of Figure 3 for the explanation of the axis.

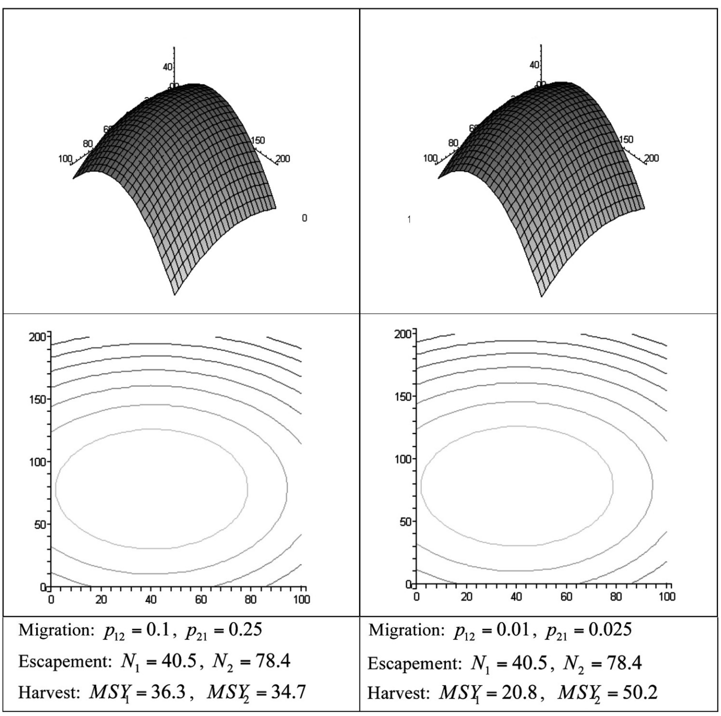


Figure 5: Maximum harvests and the corresponding escapements for different migration rates. In the left figure the migration parameters are p_{12}= 0.1 and p_{21}= 0.25 while in the right figure the migration parameters are p_{12}= 0.01 and p_{21}= 0.025. Both figures use the same carrying capacities and intrinsic growth rates, i.e. K_1= 100, K_2= 200, r_1= 1, r_2= 1.25 and α = 1.05. See the caption of Figure 3 for the explanation of the axis.

corresponding spatial scale. Different places give different values of MSY. In general, there is a trade-off between biological parameters in different patches. It uncovers the sign of the difference of the MSY values between patches, specifically determining whether the stock living in one patch should be harvested more conservatively than that living in the other patch or the opposite. The rules of thumb may give assistance in determining a prudent spatial regulation for fisheries activities. Further research can be done by investigating the effect of the existence of a metapopulation on the maximum sustainable yields compared to the MSY computed if the metapopulation system is incorrectly considered, either as two unconnected populations or as a single well-mixed population, and its consequences on various aspects of the exploitation, e.g. stock abundance, conservation, and management.

Acknowledgements

The author would like to thank two anonymous referees for their suggestions in improving the paper. The work presented in this paper is funded by the Indonesian government through Penelitian Sentralisasi Hibah Kompetensi 2012.

References

Bhat, M. G., R. G. Huffaker, & S. M. Lenhart. (1996). Controlling transboundary wildlife damage: modeling under alternative management scenarios. *Ecol. Model.* 92: 215-224.

Bulte, E. H., & G. C. van Kooten. (1999). Metapopulation dynamics and stochastic bioeconomic modeling. *Ecol. Econ.* 30: 293-299.

Costello, C., S. D. Gaines, & J. Lynham. (2008). Can catch shares prevent fisheries collapse? *Science*. 321: 1678 – 1681.

Frank, K. T., & W. C. Leggett. (1994). Fisheries ecology in the context of ecological and evolutionary theory. *Annu. Rev. Ecol. Syst.* 25: 401–422.

Hanski, I., & M. Gilpin. (1991). Metapopulation dynamics: brief history and conceptual domain. *Biol. J. Linnean Soc.* 42: 3-16.

Hilborn, R., & C. J. Walters. (1987). A general model for simulation of stock and fleet dynamics in spatially heterogeneous fisheries. *Can. J. Fish. Aqut. Sci.* 44: 1366-1369.

Jonzen, N., P. Lundberg, & A. Gardmark. (2001). Harvesting spatially distributed populations. *Wildl. Biol.* 7: 197-203.

Kellner, J. B., I. Tetreault, S. D. Gaines, & R. M. Nisbet. (2007). Fishing the line near marine reserves in single and multispecies. *Ecol. Appl.* 17:1039-1054.

Kleiber, P. & E. Edwards. (1988). A model of tuna vessel and dolphin school movement in the eastern tropical Pacific ocean: Technical description of model. SWFC Admin. Dept. LJ-88-28. 28.

Mamat, M., M. S. W. Sunaryo, Z. Salleh, & M. F. Ahmad. (2011). Numerical simulation dynamical model of three-species food chain with Lotka-Volterra linear functional response. *J. Sustain. Sci. Manage*. 6: 44-50.

Martell, S. J. D., C. J. Walters, & S. Wallace. (2000). The use of marine protected areas for conservation of lingcod (*Ophiodon elongatus*). *Bull. Mar. Sci.* 66: 729-745.

Pella J. J., & P. K. Tomlinson. (1969). A generalized stock production model. *Bull. Inter-Amer. Trop. Tuna Comm.* 13: 419-496.

Prince, J. D. (1992). Using a spatial model to explore the dynamics of an exploited stock of the abalone *Haliotis rubra*. In: Shepherd, S.A. *et al*. (Eds), *Abalone of the World: Biology, Fisheries and Culture*. Fishing News Books, Cambridge Scientific Publication, Cambridge. 305–317.

Salleh, Z., M. S. W. Sunaryo, M. Mamat, & N. Maizura. (2011). The dynamics of a three-species food chain interaction model with Michaelis-Menten type functional response. *J. Sustain. Sci. Manage*. 6: 215-223.

Sanchirico, J. N., & J. E. Wilen. (1999). Bioeconomics of spatial exploitation in a patchy environment. *J. Environ. Econ. Manag.* 37: 129-150.

Sanchirico, J. N., & J. E. Wilen. (2001). Dynamics of spatial exploitation: a metapopulation approach. *Natur. Res. Model.* 14: 391-418.

Secor, D. H. (2002). Is Atlantic Bluefin tuna a metapopulation? *Col.Vol.Sci.Pap. ICCAT.* 54: 390-399.

Supriatna, A. K. & H. P. Possingham. (1998). Optimal harvesting for a predator-prey metapopulation. *Bull. Math. Biol.* 60: 49-65.

Supriatna, A. K., & H. P. Possingham. (1999). Harvesting a two-patch predator-prey metapopulation. *Natur. Res. Model.* 12: 481-498.

Supriatna, A. K., G. N. Tuck, & H. P. Possingham. (2002). On the exploitation of a two-patch metapopulations with delayed juvenile recruitment and predation. *J. Indones. Math. Soc.* 8: 139-150.