On the Exploitation of a Two-Patch Metapopulation with Delayed Juvenile Recruitment and Predation

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Abstract

In this paper we discuss the application of the Lagrange multipliers method in natural resource modelling. We use the method to determine optimal harvesting strategies for a two-patch metapopulation with delayed juvenile recruitment and predation. We investigate the effects of time-delay and predation on the optimal harvesting levels of the metapopulation. We found that when the delays are the same for both subpopulations, the model in this paper suggests that we should harvest a relative source subpopulation more conservatively than the other subpopulation. However, when the delays are different, then there is a trade-off between the delays and the source/sink status of the subpopulations in determining the optimal harvesting strategies for the metapopulation.

1 Introduction

In this paper we develop a mathematical model for a predator-prey metapopulation with delayed juvenile recruitment. We consider optimal harvesting strategies in exploiting the metapopulation using the method of Lagrange multipliers. The work in this paper generalises the results of the previous authors who have developed optimal harvesting strategies for various structures of biological populations, such as [2,4,12,14]. The results in this paper might be applied as a general guidance in the practice of the exploitation of marine living organisms, in which delayed juvenile recruitment are often to occur [9]. Table 1 shows some known delay time for commercial marine populations.

In nature, a time delay for marine species may result from the need of the juveniles of a species to travel from their origin/spawning habitat to the destination habitat and also may reflect the time needed to mature before recruiting to the breeding stock [10].

Organism:	Age at maturity:
Red lip abalone	≥ 3 years
Sauces scallop	1 year
Iceland scallop	6 years
Baleen whale	≥ 5 years
Sei whale	≥ 9 years
Fin whale	± 8 years
Orange roughy	≥ 23 years
Chinook salmon	3 to 7 years
Sturgeons	10 to 20 years
Pacific ocean perch	8 to 10 years
Atka mackerel	≥ 3.6 years
Squid	≥ 270 days

Table 1: Some known delay time for commercial marine populations (Source:[11,13]).

Sometimes this time delay is longer than just ten or twenty years, as in the case of the Australia's orange roughy. This species may take several years for juveniles to reach sexual maturity. They become sexually mature after about 23 years [6]. In the next section we begin to develop a simple delayed juvenile recruitment model using couples difference equations.

2 A model for a predator-prey metapopulation with juvenile recruitment delay

Assume that there is a predator and prey population in each of two different patches, namely patch one and patch two (see Figure 1). As with the prey, let the movement of predators between the local populations be through the dispersal of juveniles. Adult predators are assumed not to migrate from one patch to another patch. Let the population size of the prey and predator on patch i at the beginning of period k be denoted by $N_{i(k)}$ and $P_{i(k)}$, respectively. The number of mature adults of the prey and predator subpopulations i in the time period $k + 1$ is the sum of adult survival from period k and recruitment from juveniles that were born γ_i periods ago for the prey and τ_i periods ago for the predator. In the absence of a predator-prey interaction, the dynamics of the prey is given by equation

$$N_{i(k+1)} = a_i N_{i(k)} + p_{ii} F_i(N_{i(k-\gamma_i)}) + p_{ji} F_j(N_{j(k-\gamma_i)}), \qquad (1)$$

where $i = 1, 2$ and $N_{i(k)}$ is the stock abundance of prey subpopulation i in generation/year k, a_i is the per generation/year adult survival of prey subpopulation i, and the function $F_i(\cdot)$ is called the recruit production function of prey subpopulation i and
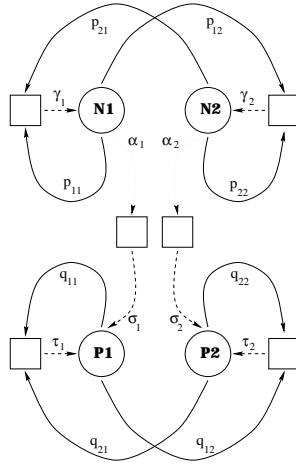
Figure 1: The figure illustrates a predator-prey metapopulation with juvenile recruitment delay. The delays for prey and predator populations are γ_i and τ_i, respectively. The boxes represent the immature stock before it joins the reproductive adults (circles). The dots with the symbol α_i indicate that the predation rate is α_i. The dashes with the symbol σ_i indicate the resulting predator's offsprings from predation σ_i periods ago.

defines the number of surviving juveniles produced γ generations/years ago that join the mature stock in generation/year $k + 1$. The growth of the predator in the absence of the prey is defined similarly, that is,

$$P_{i(k+1)} = b_i P_{i(k)} + q_{ii} G_i\big(P_{i(k-\tau_i)}\big) + q_{ji} G_j\big(P_{j(k-\tau_i)}\big), \tag{2}$$

and hence we assume that the predator has another source as a primary consumption. This delay-difference equation model is a simplification of a more detailed Leslie matrix model [3].

To include predation into the system, we use the following facts that generally food supplies may affect predator reproduction and adult survival of the predator [8]. To describe prey mortality and predator reproduction we use assumptions similar to those in [15], i.e. adult prey mortality caused by predation in period k is proportional to the number of prey and predator in that period. Predator recruitment as a result of biomass conversion from the interaction is assumed to be proportional to the number of contacts between prey and predator, in which the predator successfully kills the prey some σ_i periods ago. Mathematically the prey mortality is given by $\alpha_i N_{ik} P_{ik}$ and

predator recruitment is $\beta_i N_{ik-\sigma_i} P_{ik-\sigma_i}$, where $|\alpha_i| \geq \beta_i > 0$. With these additional assumptions, a complete model of a predator-prey metapopulation can be written as

$$
\begin{aligned}
N_{ik+1} &= p_{ii} F_i(N_{ik-\gamma_i}) + p_{ji} F_j(N_{jk-\gamma_i}) \\
&\quad + a_i N_{ik} + \alpha_i N_{ik} P_{ik},
\end{aligned}
\tag{3}
$$

$$
\begin{aligned}
P_{ik+1} &= q_{ii} G_i(P_{ik-\tau_i}) + q_{ji} G_j(P_{jk-\tau_i}) \\
&\quad + b_i P_{ik} + \beta_i N_{ik-\sigma_i} P_{ik-\sigma_i},
\end{aligned}
\tag{4}
$$

where all parameters retain the same meaning as in equations (1) and (2). Note that for the remaining of the paper we simplify the notations $N_{i(k)}$ and $P_{i(k)}$ with N_{ik} and P_{ik}. Equation (4) assumes that the delay σ_i impacts on local predator recruitment. In this case, there is a delay of σ_i time units between predation and benefit to the local predator population. If predation only aids predator's adult survival then we would expect $\sigma_i = 0$.

3 An economic aspect on the exploitation of the metapopulation

Suppose that to optimise the exploitation, the manager of the resources wants to maximise the resulting net present value, both from the predator and the prey populations. To do this, we assume that at the end of period k subpopulation i is harvested with harvest $H_{N_{ik}}$. The escapements, $S_{N_{ik}} = N_{ik} - H_{N_{ik}}$, then grow according to equations (3) and (4) to N_{ik+1}. Thus, including harvesting, equations (1) and (2) become

$$
\begin{aligned}
N_{ik+1} &= p_{ii} F_i(S_{N_{ik-\gamma_i}}) + p_{ji} F_j(S_{N_{jk-\gamma_i}}) \\
&\quad + a_i S_{N_{ik}} + \alpha_i S_{N_{ik}} S_{P_{ik}},
\end{aligned}
\tag{5}
$$

$$
\begin{aligned}
P_{ik+1} &= q_{ii} G_i(S_{P_{ik-\tau_i}}) + q_{ji} G_j(S_{P_{jk-\tau_i}}) \\
&\quad + b_i S_{P_{ik}} + \beta_i S_{N_{ik-\sigma_i}} S_{P_{ik-\sigma_i}},
\end{aligned}
\tag{6}
$$

Next, we define the net present value as

$$
PV = \sum_{k=0}^{\infty} \rho^k \sum_{i=1}^{2} \left(\Pi_{Ni}(N_{ik}, S_{N_{ik}}) + \Pi_{Pi}(P_{ik}, S_{P_{ik}}) \right).
\tag{7}
$$

We then maximise the net present value 7 over infinite time subject to equations (5) and (6), with non-negative escapement less than, or equal to, the population size. We also assume $\rho = 1/(1+\delta)$ where δ denotes a periodic discount rate and

$$
\Pi_{X_i}(X_{ik}, H_{X_{ik}}) = \int_{X_{ik}-H_{X_{ik}}}^{X_{ik}} (p_X - c_{X_i}(\xi)) d\xi,
\tag{8}
$$

$X \in \{N, P\}$.

Unlike [12], in which the authors use dynamic programming approach, in this paper we use the Lagrange multipliers to obtain optimal escapements for the prey subpopulation, $S_{N_i}^*$, and for the predator subpopulation, $S_{P_i}^*$. Appendix 1 shows that the optimal escapements satisfy the following equations:

$$
\begin{aligned}
\frac{p_N - c_{N1}(S_{N_{10}})}{\rho} = {} & (p_N - c_{N1}(N_{11}))(a_1 + p_{11}F_1'(S_{N_{10}})\rho^{\gamma_1} + \alpha_1 S_{P_{10}}) \\
& + (p_N - c_{N2}(N_{21}))p_{12}F_1'(S_{N_{10}})\rho^{\gamma_2} \\
& + (p_P - c_{P1}(P_{11}))\beta_1 S_{P_{10}}\rho^{\sigma_1},
\end{aligned}
\tag{9}
$$

$$
\begin{aligned}
\frac{p_N - c_{N2}(S_{N_{20}})}{\rho} = {} & (p_N - c_{N2}(N_{21}))(a_2 + p_{22}F_2'(S_{N_{20}})\rho^{\gamma_2} + \alpha_2 S_{P_{20}}) \\
& + (p_N - c_{N1}(N_{11}))p_{21}F_2'(S_{N_{20}})\rho^{\gamma_1} \\
& + (p_P - c_{P2}(P_{21}))\beta_2 S_{P_{20}}\rho^{\sigma_2},
\end{aligned}
\tag{10}
$$

$$
\begin{aligned}
\frac{p_P - c_{P1}(S_{P_{10}})}{\rho} = {} & (p_P - c_{P1}(P_{11}))(b_1 + q_{11}G_1'(S_{P_{10}})\rho^{\tau_1} + \beta_1 S_{N_{10}}\rho^{\sigma_1}) \\
& + (p_P - c_{P2}(P_{21}))q_{12}G_1'(S_{P_{10}})\rho^{\tau_2} \\
& + (p_N - c_{N1}(N_{11}))\alpha_1 S_{N_{10}},
\end{aligned}
\tag{11}
$$

$$
\begin{aligned}
\frac{p_P - c_{P2}(S_{P_{20}})}{\rho} = {} & (p_P - c_{P2}(P_{21}))(b_2 + q_{22}G_2'(S_{P_{20}})\rho^{\tau_2} + \beta_2 S_{N_{20}}\rho^{\sigma_2}) \\
& + (p_P - c_{P1}(P_{11}))q_{21}G_2'(S_{P_{20}})\rho^{\tau_1} \\
& + (p_N - c_{N2}(N_{21}))\alpha_2 S_{N_{20}}.
\end{aligned}
\tag{12}
$$

These equations are the general form of the optimal escapement equations for a two-patch predator-prey metapopulation with a time-delay. Note that in the absence of the delay ($\gamma_i = \sigma_i = \tau_i = 0$), we obtain optimal escapement equations given in [12]. If $\alpha_i = \beta_i = 0$, then [13] optimal escapement equation for a single-species metapopulation with time delay is obtained. On the other hand, if there is no migration between patches, $p_{ij} = q_{ij} = 0$ for $i \neq j$, and if $N_i = N_j = N$ and $P_i = P_j = P$, then the implicit optimal escapements equation for patch one is

$$
\begin{aligned}
\frac{p_N - c_N(S_{N_0}^*)}{\rho} = {} & (p_N - c_N(N_1))(F_{1N} + \rho^{\gamma_i}D_{1N}) \\
& + (p_P - c_P(P_1))(G_{1N} + \rho^{\tau_1}E_{1N}),
\end{aligned}
\tag{13}
$$

$$
\begin{aligned}
\frac{p_P - c_P(S_{P_0}^*)}{\rho} = {} & (p_N - c_N(N_1))(F_{1P} + \rho^{\gamma_i}D_{1P}) \\
& + (p_P - c_P(P_1))(G_{1P} + \rho^{\tau_1}E_{1P}),
\end{aligned}
\tag{14}
$$

where $F_{1N} = a_1 + \alpha_1 S_{P_0}^*$, $G_{1N} = \beta_1 S_{P_0}^* \rho^{\sigma_1}$, $D_{1N} = p_{11} F_1'(S_{N_0}^*)$, $E_{1N} = 0$, $F_{1P} = \alpha_1 S_{N_0}^*$, $G_{1P} = b_1 + \beta_1 S_{N_0}^* \rho^{\sigma_1}$, $D_{1P} = 0$ and $E_{1P} = q_{11} G_1'(S_{P_0}^*)$. Optimal escapements for patch two can be obtained similarly in this form. These equations are implicit optimal harvesting equations for two species derived by [2] in the presence of a time-delay in the predator numerical response such as in [15]. Finally, if both juvenile migration and predator-prey interaction are ignored, equations (40) - (43) collapse to optimal escapement equation for a single-species with time-delay as in [4]. The following section discusses further the optimal escapements and gives some interpretations of the results by comparing them with other escapements.

4   Optimal escapement properties

To facilitate interpretations of the optimal escapements, we assume that the costs of harvesting are negligible or density and subpopulation independent. Furthermore, we also assume that there are no differences between the prey and predator prices and the recruit production function for the prey is

$$F_i(N_{ik}; r_i, K_i) = r_i N_{ik} \left(1 - \frac{N_{ik}}{K_i}\right). \tag{15}$$

Similarly, recruit production function for the predator is given by $G_i(P_{ik}; s_i, L_i)$. With these assumptions, we can obtain an explicit form for the optimal escapements for the prey in each patch

$$S_{N_i}^* = \frac{A_i(q_{i1}\rho^{\tau_1} + q_{i2}\rho^{\tau_2})\frac{2s_i}{L_i} + C_i B_i}{\Delta_i}, \tag{16}$$

and the predator in each patch

$$S_{P_i}^* = \frac{B_i(p_{i1}\rho^{\gamma_1} + p_{i2}\rho^{\gamma_2})\frac{2r_i}{K_i} + C_i A_i}{\Delta_i}, \tag{17}$$

provided that $\Delta_i \neq 0$, where

$$\Delta_i = C_i^2 - (p_{i1}\rho^{\gamma_1} + p_{i2}\rho^{\gamma_2})\frac{2r_i}{K_i}(q_{i1}\rho^{\tau_1} + q_{i2}\rho^{\tau_2})\frac{2s_i}{L_i}, \tag{18}$$

$$A_i = \frac{1}{\rho} - (p_{i1}\rho^{\gamma_1} + p_{i2}\rho^{\gamma_2})r_i - a_i, \tag{19}$$

$$B_i = \frac{1}{\rho} - (q_{i1}\rho^{\tau_1} + q_{i2}\rho^{\tau_2})s_i - b_i, \tag{20}$$

and

$$C_i = \alpha_i + \beta_i \rho^{\sigma_i}. \tag{21}$$

If $\alpha_1 = \alpha_2$ or $\beta_1 = \beta_2$, we define C_i as the *discounted predator efficiency* (see [12]). It can be shown that if the following conditions (22) and (23) are satisfied,

$$A_i < 0 \text{ and } B_i < 0, \tag{22}$$

$$0 \geq C_i > max\{\frac{2B_i}{K_i}, \frac{2A_i}{L_i}\}, \tag{23}$$

then $-\Delta_i$, $S^*_{N_i}$, and $S^*_{P_i}$ are positive. The same result can be obtained if A_i, B_i, and C_i are positive. However, $C_i > 0$ is biologically unacceptable since it means the predator efficiency is more than 100% (i.e. $\frac{\beta_i}{|\alpha_i|} > 1$ or $\alpha_i + \beta_i > 0$).

In the following part we will show that if prey subpopulation one is a source subpopulation with respect to its time delay, that is, satisfying inequality

$$r_1(p_{11}\rho^{\gamma_1} + p_{12}\rho^{\gamma_2}) > r_2(p_{21}\rho^{\gamma_1} + p_{22}\rho^{\gamma_2}). \tag{24}$$

then it should be harvested more conservatively than the other subpopulation, provided the conditions (22) and (23) are both satisfied. To see this, let us assume that prey subpopulation one is a relative source, that is, $(p_{11} + p_{12})r_1 > (p_{22} + p_{21})r_2$, and also $r_{1m} > r_{2m}$ as in equation (24). All other parameters of the prey and the predator are identical for both subpopulations except delay parameters for the prey.

Let us define $a_i = a$, $b_i = b$, $C_i = C$, $R = \frac{1}{\rho} - a$, $S = \frac{1}{\rho} - b$, $r_{im} = (p_{i1}\rho^{\gamma_1} + p_{i2}\rho^{\gamma_2})r_i$ and $s_{im} = (q_{i1}\rho^{\tau_1} + q_{i2}\rho^{\tau_2})s_i$. Using these assumptions and notations, the difference between the escapement of prey in patch one to the escapement of prey in patch two is $\Delta_{S_N} = (S^*_{N_1} - S^*_{N_2})$, which can be written as

$$\Delta_{S_N} = s_{1m}\left[\frac{2}{L}C\left(C - \frac{2B}{K}\right) - \frac{4s_{1m}R}{KL}\right](r_{2m} - r_{1m})\left(\frac{1}{\Delta_1\Delta_2}\right). \tag{25}$$

Since $C > \frac{2B}{K}$ (see condition (23)), then we have $\Delta_{S_N} > 0$ if $r_{2m} < r_{1m}$, which is satisfied by inequality (24). Furthermore, since Δ_i is negative then $\Delta_{S_N} > 0$ means $S^*_{N_1} > S^*_{N_2}$. In other words, we should harvest prey subpopulation one more conservatively than prey subpopulation two if the per capita larval production of prey subpopulation one, which is discounted by its cummulative death rate is larger than the discounted per capita larval production of prey subpopulation two. If both prey subpopulations have the same delay, $\gamma_1 = \gamma_2$, then it simply restates the rule of thumb for single-species metapopulation harvesting theory [14], that the relative source prey subpopulation should be harvested more conservatively than the relative sink prey subpopulation.

Using the same method as above it can be shown that the difference between the escapement of predator in patch one to the escapement of predator in patch two is $\Delta_{S_P} = (S^*_{P_1} - S^*_{P_2})$, which can be written as

$$\Delta_{S_P} = C(r_{1m} - r_{2m})\left[C\left(\frac{2B}{K} - C\right) + \frac{4s_{1m}R}{KL}\right]\left(\frac{1}{\Delta_1\Delta_2}\right) \tag{26}$$

and has a non-positive value (since the conditions (22) and (23) are satisfied). If both prey subpopulations have the same delay, then it simply states that the predator living in the same patch with the relative source prey subpopulation should be harvested more heavily than the predator living in the other patch. This is consistent with the rule of thumb for a non-delay predator-prey metapopulation harvesting theory [12]. Furthermore, if there is no predator-prey interaction ($\alpha_i = \beta_i = 0$, and hence $C = 0$) then both predator subpopulations should be harvested equally, which is consistent with the rule of thumb in single-species metapopulation harvesting theory [14].

5   Conclusion

In this paper we have developed a mathematical model of delayed juvenile recruitment predator-prey metapopulation. Optimal escapements for the metapopulation were derived using the method of Lagrange multipliers. Results depended not only on the per capita larval production as in the non-delay model [12], but also on the delays. This means that different populations with different recruitment delays should be managed differently (see also [9]).

The results showed that when the delays are the same for both subpopulations, the model in this paper suggests that we should harvest a relative source subpopulation more conservatively than the other subpopulation. However, when the delays are different, then there is a trade-off between the delays and the source/sink status of the subpopulations in determining the optimal harvesting strategies for the metapopulation. Furthermore, we also showed that even though all predator subpopulations have the same delays, their optimal escapements might be different if the delays of their prey are different between subpopulations. This is not surprising since the dynamics of the predator is influenced by the dynamics of the prey, such as observed in many populations [1,5].

Acknowledgement

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Appendix 1

The Lagrangian for the maximisation is

$$
\begin{aligned}
\mathcal{L} \;=\; & \sum_{k=0}^{\infty} \{\rho^k [\Pi_{N_1}(N_{1k}, H_{N_{1k}}) + \Pi_{N_2}(N_{2k}, H_{N_{2k}}) \\
& + \Pi_{P_1}(P_{1k}, H_{P_{1k}}) + \Pi_{P_2}(P_{2k}, H_{P_{2k}})] \\
& - \lambda_{1k}[N_{1(k+1)} - a_1(N_{1k} - H_{N_{1k}}) - p_{11}F_1(N_{1k-\gamma_1} - H_{N_{1k-\gamma_1}}) \\
& - p_{21}F_2(N_{2k-\gamma_1} - H_{N_{2k-\gamma_1}}) - \alpha_1(N_{1k} - H_{N_{1k}})(P_{1k} - H_{P_{1k}})] \\
& - \lambda_{2k}[N_{2(k+1)} - a_2(N_{2k} - H_{N_{2k}}) - p_{12}F_1(N_{1k-\gamma_2} - H_{N_{1k-\gamma_2}}) \\
& - p_{22}F_2(N_{2k-\gamma_2} - H_{N_{2k-\gamma_2}}) - \alpha_2(N_{2k} - H_{N_{2k}})(P_{2k} - H_{P_{2k}})] \\
& - \lambda_{3k}[P_{1(k+1)} - b_1(P_{1k} - H_{P_{1k}}) - q_{11}G_1(P_{1k-\tau_1} - H_{P_{1k-\tau_1}}) \\
& - q_{21}G_2(P_{2k-\tau_1} - H_{P_{2k-\tau_1}}) \\
& - \beta_1(N_{1k-\sigma_1} - H_{N_{1k-\sigma_1}})(P_{1k-\sigma_1} - H_{P_{1k-\sigma_1}})] \\
& - \lambda_{4k}[P_{2(k+1)} - b_2(P_{2k} - H_{P_{2k}}) - q_{12}G_1(P_{1k-\tau_2} - H_{P_{1k-\tau_2}}) \\
& - q_{22}G_2(P_{2k-\tau_2} - H_{P_{2k-\tau_2}}) \\
& - \beta_2(N_{2k-\sigma_2} - H_{N_{2k-\sigma_2}})(P_{2k-\sigma_2} - H_{P_{2k-\sigma_2}})]\}.
\end{aligned}
\tag{27}
$$

To find the optimal escapements we need to solve the necessary conditions: $\frac{\partial \mathcal{L}}{\partial N_{ik}} = \frac{\partial \mathcal{L}}{\partial P_{ik}} = 0$ for $k \geq 1$ and $\frac{\partial \mathcal{L}}{\partial H_{N_{ik}}} = \frac{\partial \mathcal{L}}{\partial H_{P_{ik}}} = 0$. These conditions are equivalent to

$$
\begin{aligned}
0 \;=\; & \rho^k \frac{\partial \Pi_{N_1}}{\partial N_{1k}} - \lambda_{1(k-1)} + \lambda_{1k} a_1 + \lambda_{1k+\gamma_1} p_{11} F_1'(S_{N_{1k}}) + \lambda_{1k} \alpha_1 S_{P_{1k}} \\
& + \lambda_{2k+\gamma_2} p_{12} F_1'(S_{N_{1k}}) + \lambda_{3k+\sigma_1} \beta_1 S_{P_{1k}},
\end{aligned}
\tag{28}
$$

$$
\begin{aligned}
0 \;=\; & \rho^k \frac{\partial \Pi_{N_2}}{\partial N_{2k}} - \lambda_{2(k-1)} + \lambda_{2k} a_2 + \lambda_{2k+\gamma_2} p_{22} F_2'(S_{N_{2k}}) + \lambda_{2k} \alpha_2 S_{P_{2k}} \\
& + \lambda_{1k+\gamma_1} p_{21} F_2'(S_{N_{2k}}) + \lambda_{4k+\sigma_2} \beta_2 S_{P_{2k}},
\end{aligned}
\tag{29}
$$

$$
\begin{aligned}
0 \;=\; & \rho^k \frac{\partial \Pi_{P_1}}{\partial P_{1k}} - \lambda_{3(k-1)} + \lambda_{3k} b_1 + \lambda_{3k+\tau_1} q_{11} G_1'(S_{P_{1k}}) + \lambda_{3k+\sigma_1} \beta_1 S_{N_{1k}} \\
& + \lambda_{4k+\tau_2} q_{12} G_1'(S_{P_{1k}}) + \lambda_{1k} \alpha_1 S_{N_{1k}},
\end{aligned}
\tag{30}
$$

$$
\begin{aligned}
0 \;=\; & \rho^k \frac{\partial \Pi_{P_2}}{\partial P_{2k}} - \lambda_{4(k-1)} + \lambda_{4k} b_2 + \lambda_{4k+\tau_2} q_{22} G_2'(S_{P_{2k}}) + \lambda_{4k+\sigma_2} \beta_2 S_{N_{2k}} \\
& + \lambda_{3k+\tau_1} q_{21} G_2'(S_{P_{2k}}) + \lambda_{2k} \alpha_2 S_{N_{2k}},
\end{aligned}
\tag{31}
$$

$$
\begin{aligned}
0 \;=\; & \rho^k \frac{\partial \Pi_{N_1}}{\partial H_{N_{1k}}} - \lambda_{1k} a_1 - \lambda_{1k+\gamma_1} p_{11} F_1'(S_{N_{1k}}) - \lambda_{1k} \alpha_1 S_{P_{1k}} \\
& - \lambda_{2k+\gamma_2} p_{12} F_1'(S_{N_{1k}}) - \lambda_{3k+\sigma_1} \beta_1 S_{P_{1k}},
\end{aligned}
\tag{32}
$$

$$
\begin{aligned}
0 \;=\; & \rho^k \frac{\partial \Pi_{N_2}}{\partial H_{N_{2k}}} - \lambda_{2k} a_2 - \lambda_{2k+\gamma_2} p_{22} F_2'(S_{N_{2k}}) - \lambda_{2k} \alpha_2 S_{P_{2k}} \\
& - \lambda_{1k+\gamma_1} p_{21} F_2'(S_{N_{2k}}) - \lambda_{4k+\sigma_2} \beta_2 S_{P_{2k}},
\end{aligned}
\tag{33}
$$

$$
\begin{aligned}
0 \;=\; & \rho^k \frac{\partial \Pi_{P_1}}{\partial H_{P_{1k}}} - \lambda_{3k} b_1 - \lambda_{3k+\tau_1} q_{11} G_1'(S_{P_{1k}}) - \lambda_{3k+\sigma_1} \beta_1 S_{N_{1k}} \\
& - \lambda_{4k+\tau_2} q_{12} G_1'(S_{P_{1k}}) - \lambda_{1k} \alpha_1 S_{N_{1k}},
\end{aligned}
\tag{34}
$$

$$
\begin{aligned}
0 \;=\; & \rho^k \frac{\partial \Pi_{P_2}}{\partial H_{P_{2k}}} - \lambda_{4k} b_2 - \lambda_{4k+\tau_2} q_{22} G_2'(S_{P_{2k}}) - \lambda_{4k+\sigma_2} \beta_2 S_{N_{2k}} \\
& - \lambda_{3k+\tau_1} q_{21} G_2'(S_{P_{2k}}) - \lambda_{2k} \alpha_2 S_{N_{2k}},
\end{aligned}
\tag{35}
$$

Solving equations (28) to (35) produces

$$
\lambda_{1(k-1)} = \rho^k \left(\frac{\partial \Pi_{N_1}}{\partial N_{1k}} + \frac{\partial \Pi_{N_1}}{\partial H_{N_{1k}}} \right),
\tag{36}
$$

$$\lambda_{2(k-1)} = \rho^k \left(\frac{\partial \Pi_{N_2}}{\partial N_{2k}} + \frac{\partial \Pi_{N_2}}{\partial H_{N_{2k}}} \right), \tag{37}$$

$$\lambda_{3(k-1)} = \rho^k \left(\frac{\partial \Pi_{P_1}}{\partial P_{1k}} + \frac{\partial \Pi_{P_1}}{\partial H_{P_{1k}}} \right), \tag{38}$$

$$\lambda_{4(k-1)} = \rho^k \left(\frac{\partial \Pi_{P_2}}{\partial P_{2k}} + \frac{\partial \Pi_{P_2}}{\partial H_{P_{2k}}} \right). \tag{39}$$

Substituting λ_{1k}, λ_{2k}, λ_{3k} and λ_{4k} into equation (32) produces

$$\begin{aligned}
0 = {} & \rho^k \frac{\partial \Pi_{N_1}}{\partial H_{N_{1k}}} - a_1 \rho^{(k+1)} \left(\frac{\partial \Pi_{N_1}}{\partial N_{1k}} + \frac{\partial \Pi_{N_1}}{\partial H_{N_{1k}}} \right) \\
& - p_{11} F_1'(S_{N_{1k}}) \rho^{(k+1+\gamma_1)} \left(\frac{\partial \Pi_{N_1}}{\partial N_{1k}} + \frac{\partial \Pi_{N_1}}{\partial H_{N_{1k}}} \right) \\
& - \alpha_1 S_{P_{1k}} \rho^{(k+1)} \left(\frac{\partial \Pi_{N_1}}{\partial N_{1k}} + \frac{\partial \Pi_{N_1}}{\partial H_{N_{1k}}} \right) \\
& - p_{12} F_1'(S_{N_{1k}}) \rho^{(k+1+\gamma_2)} \left(\frac{\partial \Pi_{N_2}}{\partial N_{2k}} + \frac{\partial \Pi_{N_2}}{\partial H_{N_{2k}}} \right) \\
& - \beta_1 S_{P_{1k}} \rho^{(k+1+\sigma_1)} \left(\frac{\partial \Pi_{P_1}}{\partial P_{1k}} + \frac{\partial \Pi_{P_1}}{\partial H_{P_{1k}}} \right).
\end{aligned}$$

Divide by ρ^{k+1}, and recall that $\frac{\partial \Pi_{N_i}}{\partial H_{N_{ik}}} = p - c_N(S_{N_{i0}})$ and $\frac{\partial \Pi_{N_i}}{\partial N_{ik}} + \frac{\partial \Pi_{N_i}}{\partial H_{N_{ik}}} = p - c_N(N_{i1})$, then

$$\begin{aligned}
\frac{p_N - c_{N1}(S_{N_{10}})}{\rho} = {} & (p_N - c_{N1}(N_{11}))(a_1 + p_{11} F_1'(S_{N_{10}}) \rho^{\gamma_1} + \alpha_1 S_{P_{10}}) \\
& + (p_N - c_{N2}(N_{21})) p_{12} F_1'(S_{N_{10}}) \rho^{\gamma_2} \\
& + (p_P - c_{P1}(P_{11})) \beta_1 S_{P_{10}} \rho^{\sigma_1}. \tag{40}
\end{aligned}$$

Similarly, substituting λ_{1k}, λ_{2k}, λ_{3k} and λ_{4k} into equations (33) to (35) produces

$$\begin{aligned}
\frac{p_N - c_{N2}(S_{N_{20}})}{\rho} = {} & (p_N - c_{N2}(N_{21}))(a_2 + p_{22} F_2'(S_{N_{20}}) \rho^{\gamma_2} + \alpha_2 S_{P_{20}}) \\
& + (p_N - c_{N1}(N_{11})) p_{21} F_2'(S_{N_{20}}) \rho^{\gamma_1} \\
& + (p_P - c_{P2}(P_{21})) \beta_2 S_{P_{20}} \rho^{\sigma_2}, \tag{41}
\end{aligned}$$

$$\begin{aligned}
\frac{p_P - c_{P1}(S_{P_{10}})}{\rho} = {} & (p_P - c_{P1}(P_{11}))(b_1 + q_{11} G_1'(S_{P_{10}}) \rho^{\tau_1} + \beta_1 S_{N_{10}} \rho^{\sigma_1}) \\
& + (p_P - c_{P2}(P_{21})) q_{12} G_1'(S_{P_{10}}) \rho^{\tau_2} \\
& + (p_N - c_{N1}(N_{11})) \alpha_1 S_{N_{10}}, \tag{42}
\end{aligned}$$

$$\begin{aligned}
\frac{p_P - c_{P2}(S_{P_{20}})}{\rho} = {} & (p_P - c_{P2}(P_{21}))(b_2 + q_{22} G_2'(S_{P_{20}}) \rho^{\tau_2} + \beta_2 S_{N_{20}} \rho^{\sigma_2}) \\
& + (p_P - c_{P1}(P_{11})) q_{21} G_2'(S_{P_{20}}) \rho^{\tau_1} \\
& + (p_N - c_{N2}(N_{21})) \alpha_2 S_{N_{20}}. \tag{43}
\end{aligned}$$