Optimal Harvesting of a Prey–Predator Fishery: An Overlapping Generations Analysis

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Abstract

Maximum sustainable yield (MSY) and maximum economic yield (MEY) harvesting strategies are characterized using an overlapping generations (OLG) model of heterogeneous (prey - predator) fishery. A proper modeling of real life cycle dynamics of fish is introduced with a commonly used prey-predator interaction system of equations to create heterogeneity. Prey-predator interaction is modeled with three different functional forms: *prey dependent, predator dependent and ratio dependent.* MSY and MEY harvesting strategies with these three different forms are given under perfect and imperfect fishing selectivity and presented both numerically and graphically.

Keywords: Bioeconomics, Maximum Sustainable Yield, Maximum Economic Yield, Overlapping Generations, Prey-Predator Fishery

JEL classification codes: D04, D78, Q22

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1 Introduction

Guaranteeing the sustainability of fish population in both biological and economic terms are important and determination of the optimal harvest rates accordingly has been a controversial issue. MSY and MEY harvesting strategies have been used for management objectives of the institutions that are responsible of regulating and supervising the fishery sectors. While there are studies (Skonhoft et al., 2012; Skonhoft and Gong, 2014) that investigate fish population modeling and optimal harvesting strategies under single-type fish population, heterogeneous fish models haven't been well studied yet within this context. Since the exploitation of fishery resources is not the sole factor affecting fish population dynamics, own constraints and interactions of the ecosystem should also be considered in the determination process of optimal harvesting strategies.

In heterogeneous type modeling strategies, dynamics of the interaction between the prey and predator fish are captured by the *trophic function*[1] There are three mainstream approaches about the trophic function's arguments: prey-dependent, predator dependent and ratio-dependent. Some studies (Abrams and Ginzburg, 2000) have found the appropriate function to be *Holling Type-2* (Holling, 1959), arguing that the predator population is actually a function of the prey population and therefore the trophic function should only depend on the prey population and offers a different functional form. (Beddington, 1975) on the other hand claims the opposite and indicate that prey population is a function of predator population. Combining the two approaches, (Arditi and Ginzburg, 1989) argues that the function should not depend solely on the level of either type, but instead should have a proportional structure (ratio of prey to predator population).

In this study, all of these three different approaches (Holling, 1959; Beddington, 1975; Arditi and Ginzburg, 1989) are employed to explain the dynamics between species. The responses of both prey and predator populations have been analyzed under Maximum Sustainable Yield (MSY) and Maximum Economic Yield (MEY) harvesting strategies. Instead

[1]Throughout the study, trophic function and interaction function terms are used interchangeably.

of previous age structured fish population models, an overlapping generations model is employed and both prey and predator populations modeled in a generational accounting which models both fish species as having four different periods in their life-cycle as a new contribution to the literature. We focus on the issue of reaction of the populations to their intrinsic interaction mechanisms and propose optimal harvesting strategies for all different interaction modeling techniques. Optimal harvest rates for MSY are found using the *grid-search algorithm* method, which differs from the literature related to the characterization of MSY harvesting strategies.

The MEY problem is analyzed under both perfect fishing selectivity and imperfect fishing selectivity cases.[2] The simulations determine the optimal harvesting levels (for each type and age group) required to maximize the total biomass or economic profits in an infinite time horizon under the biological and economic constraints that determine the dynamics of prey and predator populations within optimal harvesting strategies. Outcomes of the study is expected to shed light on future research on management and quota allocation problems in fishery sector related to sustainable use of renewable resources.

The outline of this paper is as follows: In section 2, interaction of heterogeneous fish populations are introduced within the overlapping generations model. In section 3, MSY formulation is explained in detail, the solution methodology of the model is described, and the results along with the calibration parameters are presented. In section 4, the MEY problem is solved under the perfect and imperfect fishing selectivity cases with corresponding harvest rates and effort levels. Section 5 puts important aspects together to discuss on possible road maps for future studies and concludes.

[2]Perfect fishing selectivity is that each fleet do not harvests other fish species and ages, only the targeted species and age. However, imperfect fishing selectivity is that any fleet may mistakenly harvests other species and ages, not only the targeted fish species and ages.

2 OLG Fish Population Model

In order to analyze optimal harvesting strategies, life cycle behaviors of each fish population must be well demonstrated. Each population has its own dynamics and the modeling has to be done in accordance with these dynamics. In this paper, the life-cycle dynamic of a fish population is modeled with overlapping generations model, contrary to previous papers using age-structured models (Reed, 1980; Botsford, 1981; Gurtin and Murphy, 1981; Getz and Haight, 1989). Overlapping generations model can be considered as a specific type of age-structured models which allows periods in life-cycle and periods of time pass by together and at any period in time there are agents living each period of their life-cycle[3]. Moreover, each period new fish enter the ecosystem through recruitment and some leave the ecosystem at the end of their life-cycles. According to time and generation dimension, the existence of each cohort in the ecosystem can be represented by the following $m \times n$ matrix.

$$\begin{bmatrix} \vdots & \vdots & \vdots & \vdots \\ X_{s,t} & X_{s+1,t} & X_{s+2,t} & X_{s+3,t} \\ X_{s,t+1} & X_{s+1,t+1} & X_{s+2,t+1} & X_{s+3,t+1} \\ X_{s,t+2} & X_{s+1,t+2} & X_{s+2,t+2} & X_{s+3,t+2} \\ X_{s,t+3} & X_{s+1,t+3} & X_{s+2,t+3} & X_{s+3,t+3} \\ X_{s,t+4} & X_{s+1,t+4} & X_{s+2,t+4} & X_{s+3,t+4} \\ \vdots & \vdots & \vdots & \vdots \end{bmatrix}$$

Figure 1: Time and Generation Dimension in the Ecosystem

Each element of the matrix carries generation and time information; t indicates time, s indicates age. For example, the first element, $X_{s,t}$, represents the total number of X type fish at the age of s at time t.

In our setting, there are four different age-classes, i.e. in each period t, fish of ages 0, 1, 2

[3] Each period in the life-cycle of fish are referred as *age* throughout the paper although a period does not necessarily correspond to one year.

and 3 are present in the ecosystem. Fish enter the system at their age of 0 as juveniles after the recruitment process and leave it at the end of age 3. Juveniles are the fish that have not reached their adult forms yet and assumed to have no economic value due to their size and weight. Age 1 and 2 fish are the young and old matures respectively and they involve in the spawning process. Age 3 is the last period of the life-cycle of fish before the natural death. Spawning assumed to occur before the prey-predator interaction occurs and just before the exploitation period.

In order to incorporate heterogeneity in fish population, we introduce prey and predator species that are always interacting each other. Number of fish in each type is denoted by $X_{i,t}$ where i and t corresponds to age and period respectively. As stated in 1, there are two types of fish; preys, N and predators, P. However, analyzing an ecosystem in which there exists prey and predator species interacting each other can be quite tricky. It is because, you cannot simply run the algorithm separately for prey and predator populations. Instead, one has to consider the dynamic interaction between the populations. While doing so, the algorithm has to have two layers, in inner layer, each population grows in accordance with its internal dynamics. At the second layer, interaction occurs and the final population at each period is determined.

$$X_{i,t} = \{N_{i,t}, P_{i,t}\} \qquad and \qquad i = 0, 1, 2, 3 \tag{1}$$

Total number of preys and predators at any period t are the sum of population of the corresponding type of each age as stated in Equation 2.

$$X_t = \sum_{i=0}^{3} X_{i,t} \qquad \forall \;\; X. \tag{2}$$

Each year, age 1 and 2 fish join the recruitment process and spawns the juveniles of the proceeding year of its own type. Recruitment function is given in equation 3 and the same applies for both types.

$$X_{0,t+1} = Rec(t+1) = \frac{a(X_{1,t} + \beta X_{2,t})}{b + X_{1,t} + \beta X_{2,t}} \tag{3}$$

Juveniles those survived natural death and prey-predator interaction at the end of one period becomes young matures, as stated in equation 4. Young and old mature fish of each type on the other hand are faced with another exploitation type which is human activity of fishing denoted by h, given in equations 5 and 6.

$$X_{1,t} = X'_{0,t-1} s_0 \tag{4}$$

$$X_{2,t} = X'_{1,t-1} s_1 (1 - h_{1X,t-1}) \tag{5}$$

$$X_{3,t} = X'_{2,t-1} s_2 (1 - h_{2X,t-1}) \tag{6}$$

Figure 2 provides a summary of events in the life span of a fish generation for both preys and predators. Figure 2 can be helpful to visualize the life-cycle of a cohort in a timeline form.

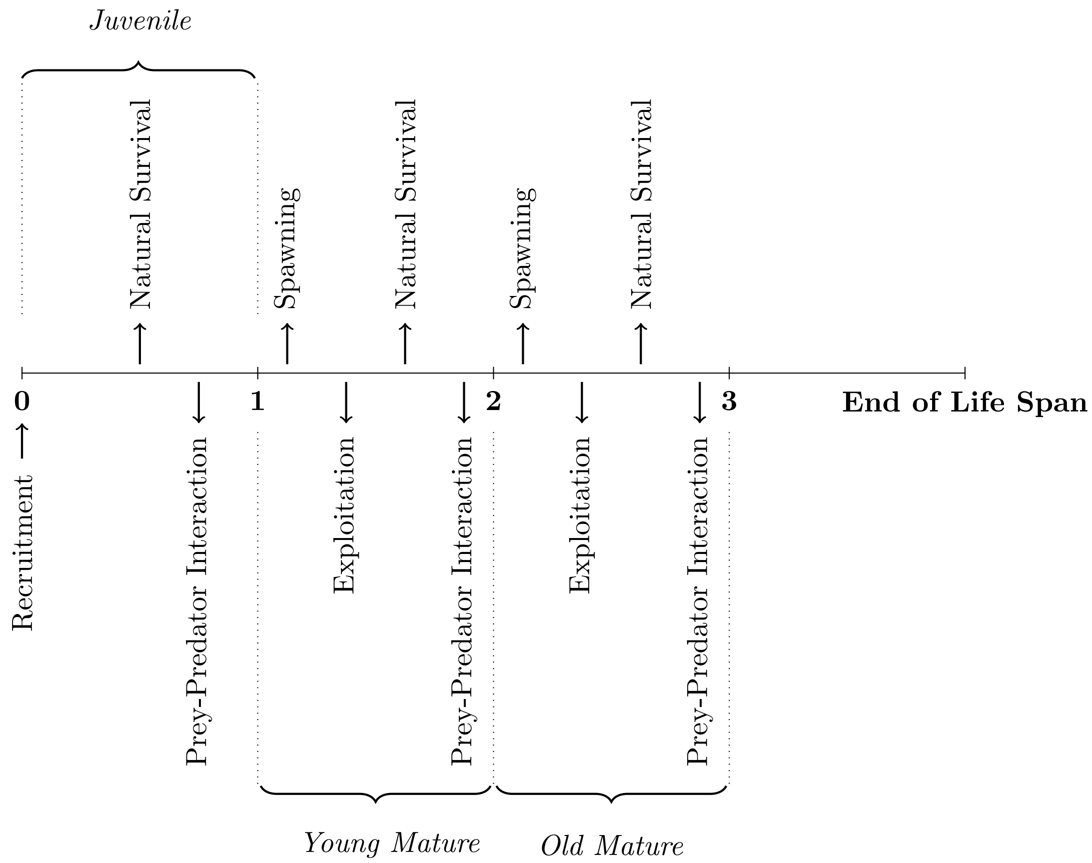


Figure 2: Life-Span of a Cohort

To model prey-predator interaction, discrete version of differential models which are frequently used in the literature is employed. In the equation system which consists of Equations 7 and 8, the same g function is named differently as *functional* and *numerical* response ((Akcakaya et al., 1995)). Also, e denotes trophic efficiency.

$$N_t^{'} = N_t - \mathbf{g}(N_t, P_t)Pt \tag{7}$$

$$P_t^{'} = e\mathbf{g}(N_t, P_t)P_t \tag{8}$$

The equation system governs the growth rates of both species. These growth rates have been distributed to the population of different generations by the age-dependent m_{Xi} parameter. As the experience increases, the chance of being advantageous from the prey-predator interaction increases, so the model is calibrated in a way that m_{Xi} increases as fish get older.

There are different formulations in the literature for the response function, g including (Okuyama and Ruyle, 2011) *Holling Type II* (prey-dependent), *Arditi-Ginzburg* (ratio-dependent), *Beddigton-DeAngelis* (predator-dependent). This study uses all three functional responses, given in the equations 9, 10 and 11.

$$\mathbf{g}(N_t, P_t) = \frac{\epsilon N/P}{1+\epsilon\omega N/P} \qquad (Arditi - Ginzburg) \tag{9}$$

$$\mathbf{g}(N_t, P_t) = \frac{\epsilon N}{1+\epsilon\omega N} \qquad (Holling\ Type\ II) \tag{10}$$

$$\mathbf{g}(N_t, P_t) = \frac{\epsilon N}{1+\gamma P+\epsilon\omega N} \qquad (Beddington - DeAngelis) \tag{11}$$

The modeling approach employed in this section provides a well-suited population dynamics system to investigate the effects of interactions between the types and exploitation on different types and age groups while also allowing for dynamics with demonstration of transition paths.

3 Maximum Sustainable Yield

In this section, the problem of maximizing the harvest rate is discussed in details, provided that the sustainability of fish populations is preserved[4]. In this environment, the optimization problem is the maximization of total harvest, 12, in an infinite time horizon under the biological constraints defined by the equations 3, 4, 5 and 6.

$$max \sum_{t}^{\infty} Y_t \tag{12}$$

[4]The model is solved by *MATLAB* program, and the code is available upon request from the authors.

In equation 12, Y_t refers to total harvested biomass at time t. Total harvested biomass is the total amount of harvested fish from all economically valuable ages.

$$Y_t = h_{N1}N_{1,t}w_{N1} + h_{N2}N_{2,t}w_{N2} + h_{P1}P_{1,t}w_{P1} + h_{P2}P_{2,t}w_{P2} \tag{13}$$

In equation (13), w_{N1} corresponds to the weight of prey young mature, while h_{N1} is the harvesting level of prey young mature. While h_{P2} represents the harvesting rate of the old mature fish in the predator species. Other species and age groups are similarly defined.

The values of the parameters and definitions are presented in detail in Table 1 [5].

[5] The scaling, fertility and shape parameters, survival rates and weights are taken from (Skonhoft et al., 2012).

Table 1: Parameters for MSY

Symbol	Definition	Value
a	Scaling parameter in recruitment function	1500 (number of fish)
β	Fertility parameter in recruitment function	1.5
b	Shape parameter in recruitment function	500 (number of fish)
s_0	Natural survival rate of juveniles from one period to another	0.6
s_1	Natural survival rate of young matures from one period to another	0.7
s_2	Natural survival rate of old matures from one period to another	0.7
w_{N0}	Weight of prey juveniles	1 (kg/fish)
w_{N1}	Weight of prey young mature	2 (kg/fish)
w_{N2}	Weight of prey old mature	3 (kg/fish)
w_{N3}	Weight of the oldest prey fish	3 (kg/fish)
w_{P0}	Weight of predator juveniles	4 (kg/fish)
w_{P1}	Weight of predator young mature	5 (kg/fish)
w_{P2}	Weight of predator old mature	6 (kg/fish)
w_{P3}	Weight of the oldest predator fish	6 (kg/fish)
m_{N0}	Percentage of population growth originated from juvenile prey	0.30
m_{N1}	Percentage of population growth originated from young mature prey	0.33
m_{N2}	Percentage of population growth originated from old mature prey	0.37
m_{P0}	Percentage of population growth originated from juvenile predator	0.30
m_{P1}	Percentage of population growth originated from young mature predator	0.33
m_{P2}	Percentage of population growth originated from old mature predator	0.37
e	Trophic efficiency	0.8
ϵ	Encounter rate	0.6
ω	Handling time	1.75
γ	Interference during foraging	0.7

In the MSY problem, choice variables are the harvest rates, h_{N1}, h_{N2}, h_{P1}, h_{P2}. Grid-search method is used to find the optimal harvest rates. With this method, harvesting rates that optimize total sustainable yield under the necessary biological constraints are sought in a 4-dimensional matrix $[0.01, 0.99]^4$. That is, for each possible $h_{X_{i,t}}$, total harvested biomass is recorded and the algorithm chooses the quartet of harvest rates corresponding to the entry with maximum value of the *Total Harvested Biomass* matrix as a solution.

As expected, algorithm chooses the harvest entire generation of old mature fish (regardless of prey or predator species). That is, the solution is the highest allowed value of 0.99 for the harvest rate ($h_{N2} = 0.99$ and $h_{P2} = 0.99$). Furthermore, a corner solution for old mature fish always maximizes the total biomass harvested, since the exploitation happens after spawning. If some old mature fish survives both types of mortality they will become age 3 in next period, and die. Thus, predicting that old mature fish will not have any economic value unless they are harvested, algorithm offers the optimal solution for the fleet as the highest possible value for h_2. The optimal catch rates for young mature fish are 0.01 for prey species and 0.99 for predator species ($h_{N1} = 0.01$ and $h_{P1} = 0.99$). The reason for the algorithm's desire to harvest the entire predator population stems from the fact that predators *negative* effect on the total biomass. In addition, the reason for algorithm's unwillingness to harvest the prey species is that the young mature prey participate to the spawning one period later, also becoming even heavier and more economically valuable. [6]

Figure 3 reveals the total biomass over time under MSY harvest strategy for three different trophic functions.

[6]However, at different calibrations the algorithm suggests harvesting rates for prey species higher than 0.01.

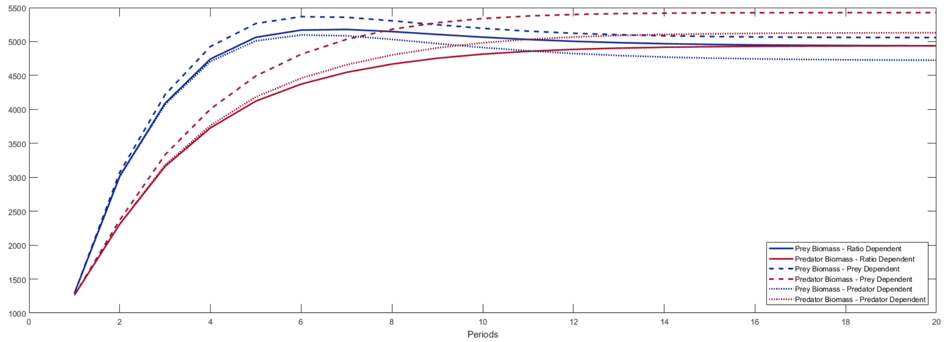


Figure 3: Biomass Over Time under MSY Harvest Strategy

As presented in Figure 3, both prey and predator populations increase and reach to a steady state level. Also the results for choice of different trophic functions give similar results and hence, in terms of biomass, choice of trophic function nearly does not matter under MSY setup.

4 Maximum Economic Yield

In this section, the maximum economic yield harvesting strategy tis analyzed. There are without loss of generality four different fleets that target young and old mature fish of prey and predator fish. Under the perfect fishing selectivity case, each fleet only harvests the targeted species and the age group while under the imperfect fishing selectivity case, in addition to targeted fish there exists by-catch harvest for all untargeted age groups and species. Model parameters are again calibrated to the values given in 1 and additional parameters required for MEY analysis are given in table 2.

Table 2: Additional Parameters for MEY

Symbol	Definition	Value
q_{iX}	Catchability coefficient of fleet iX (1/effort)	0.25
$\tilde{q}_{iX,jY}$	Catchability coefficient of fleet iX for by-catch jY fish (1/effort)	0.05
c_{iX}	Effort cost of fleet iX	0.25 (euro/effort)
p_{iX}	Price of iX Fish	1 (euro/kg)
μ	Stock effect in harvest function	0.08
η	Marginal product of fishing effort	0.20

In this problem, a social planner is assumed to maximize the total economic yield for current and all future periods for all four fleets of the representative fishing agent. That is, the problem of the social planner is to maximize the sum of profits of the fishery sector (Equation 14).

$$max \sum_t \Pi_t \tag{14}$$

Profit for a given period t i.e.; Π_t is calculated by subtracting the costs from the sum of monetary value of the harvest in the corresponding period given in equation 15.

$$max \sum_t \sum_i [p_{iX,t} h_{iX,t} - C_{iX,t}] \tag{15}$$

In equation 15, $p_{iX,t}$ stands for the price of i-aged fish X at time t, whereas $h_{iX,t}$ and $C_{iX,t}$ stand for harvest rate and cost of harvesting respectively for the same subset of fish population. Harvest rate on the other hand is a function of effort exerted for the specific type and age fish and is calculated based on the seminal work of Grafton et al. (2010) given in equation 16.

$$h_{iX,t} = q_{iX} \left(b_{iX,t}\right)^{\mu} E^{\eta}_{iX,t} \tag{16}$$

In equation 16, μ shows the sensitivity of the amount of harvest to the size of corresponding fish population, i.e, *stock effect*, η is the marginal product of fishing effort, $q_{iX,t}$ is the coefficient of catchability and lastly $b_{iX,t}$ is the biomass index defined in $b_{iX,t} \in [0,1]$ given in equation 17.

$$b_{iX,t} = \frac{X'_{i,t} w_{iX}}{\sum_i X'_{i,t} w_{iX}} \qquad\qquad i = 0,1,2,3 \tag{17}$$

Fishing cost on the other hand is represented by C_{iX} and is a linear function of fishing effort given in equation 18 where c_{iX} is the constant marginal cost of per unit effort.

$$C_{iX} = c_{iX} E_{iX,t} \tag{18}$$

Under the imperfect fishing selectivity case, $iX \in \{N1, N2, P1, P2\}$ fleet harvests not only targeted i-aged X fish, but also harvests j-aged Y fish by-catch. This situation is integrated to the model with equation 19 and unintended catchability coefficients $\tilde{q}_{iX}$ are defined as in (Skonhoft et al., 2012). Also, $\tilde{h}_{iX,t}$ denotes the unintended harvest rates at any given time t.

$$\tilde{h}_{iX,t} = \sum_{j,Y} \tilde{q}_{jY,iX} \, (b_{iX,t})^{\mu} \, E^{\eta}_{jY,t} \tag{19}$$

$$Y'_{i,t} = \{N'_{i,t}, P'_{i,t}\} \quad i \neq j \quad \textit{and} \quad Y'_{i,t} \neq X'_{i,t} \tag{20}$$

The total harvest of i-aged X fish is the sum of intended and unintended catches attained and defined in equation 21.

$$h^{total}_{iX,t} = h_{iX,t} + \tilde{h}_{iX,t} \tag{21}$$

Under the imperfect fishing selectivity case, biological constraints take the form of equations 22 and 23 since the total harvest function is altered.

$$X_{2,t} = X_{1,t-1}s_1(1 - h^{total}_{1X,t}) \tag{22}$$

$$X_{3,t} = X_{2,t-1}s_2(1 - h^{total}_{2X,t}) \tag{23}$$

The total biomass of prey and predator fish under the optimal harvesting strategy for MEY problem under perfect selectivity case is given in figure 4 for three different trophic functions.

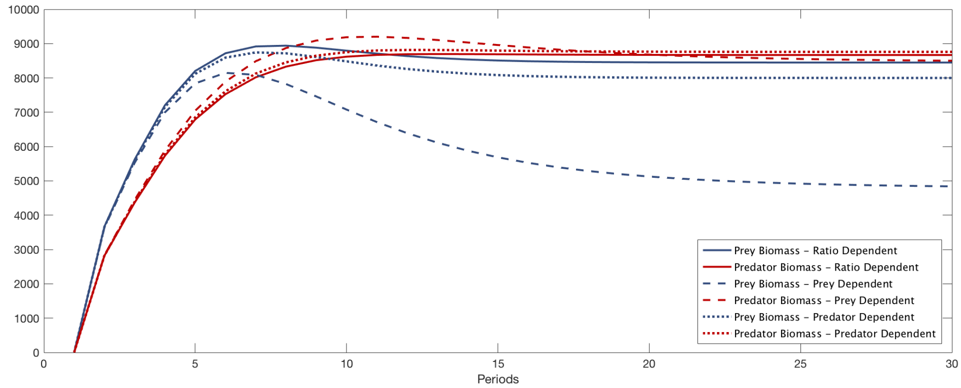


Figure 4: Biomass Over Time under MEY Harvest Strategy, Perfect Fishing Selectivity

Thus, when the MEY strategy is adopted, biomass level of both prey and predator fish increase and after 25^{th} period both populations reach the steady state level, meaning that unless a shock to the environment occurs the population will remain on this level. Another finding that can be read from the figure is that, at steady state levels, prey-dependent trophic function gives the least favorable results in terms of biomass whereas predator dependent and ratio dependent ones give higher levels and their results are very close to each other.

Under the imperfect fishing selectivity case, the biomass of prey and predator fish populations obtained with optimal harvesting strategy that are solution to MEY are given in Figure 5.

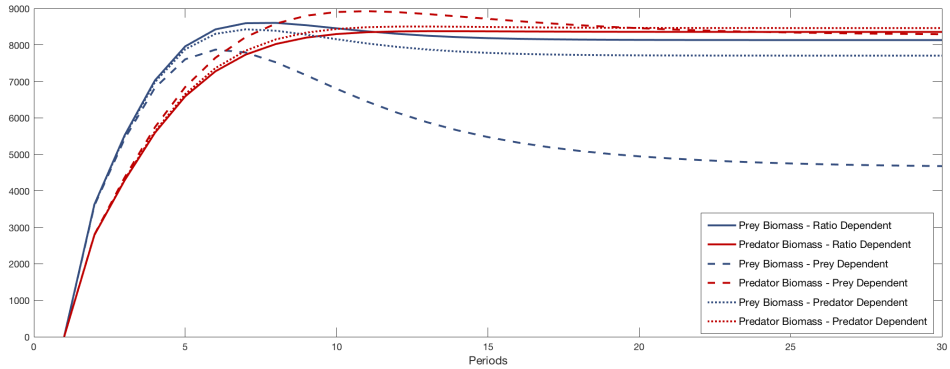
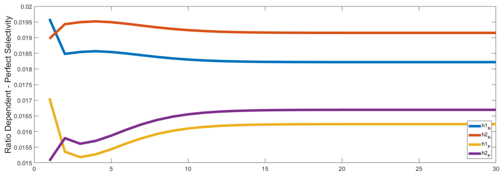


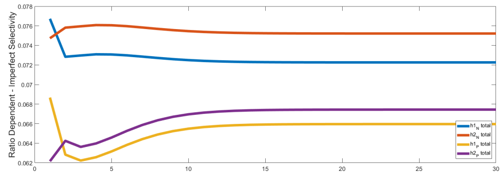
Figure 5: Biomass Over Time under MEY Harvest Strategy, Imperfect Fishing Selectivity

Similar to the prefect selectivity case, both populations increase and reach to a steady state level. Also the results for choice of different trophic functions give the similar results as in perfect selectivity case.

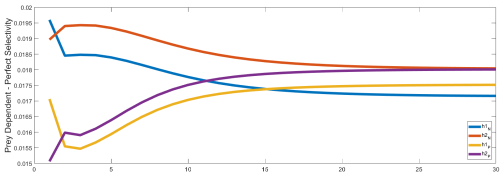
When we compare the profit levels in perfect and imperfect selectivity cases, we see that in all three functional forms, profit level increases. Moreover, another key finding here is the fact that imperfect fishing selectivity provides higher profits for the fishery sector compared to that of perfect fishing selectivity.



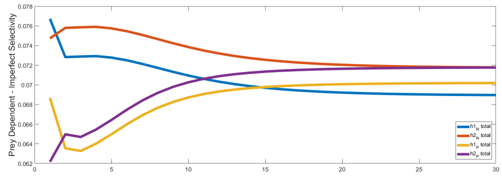
(a) Perfect Selectivity and Ratio-dependent Trophic Function



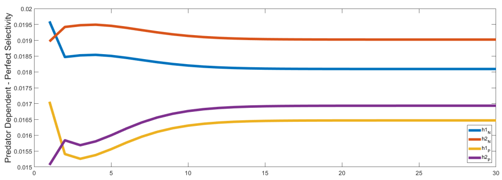
(b) Imperfect Selectivity and Ratio-dependent Trophic Function



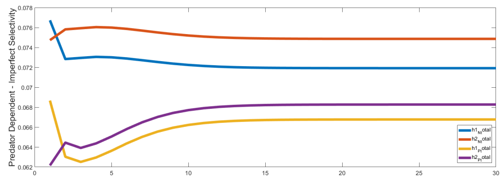
(c) Perfect Selectivity and Prey-dependent Trophic Function



(d) Imperfect Selectivity and Prey-dependent Trophic Function



(e) Perfect Selectivity and Predator-dependent Trophic Function



(f) Imperfect Selectivity and Predator-dependent Trophic Function

Figure 6: Solutions to MEY Problem: Harvest Rates for Different Fishing Selectivity Cases and Trophic Functions

In Figure 6, rows indicate the trophic function type. Namely, first row belongs to prey dependent functional form, whereas the second and third rows indicate the ratio dependent and predator dependent functional forms, respectively. Also, in each row, first column shows the perfect selectivity setup and the second column shows the imperfect selectivity setup. (e.g. second row first column - Figure 6/c - represents the harvest rate of ratio dependent functional form under perfect fishing selectivity case.)

In each graph, the color of the lines always indicate the same cohort. Blue line indicates the young mature cohort of prey species, red line shows the old mature cohort of prey species, whereas yellow and purple color shows the young mature and old mature cohorts of predator species, respectively.

Another finding from the simulations is that the steady state levels of harvest rates under different trophic functional forms. As can be seen from the Figure 6 is that, at steady state levels, prey-dependent trophic function has the lowest harvest rate, while predator dependent and ratio dependent functions behave similarly and their harvest rate levels are very close to each other. Moreover, simulations of MEY problem with imperfect fishing selectivity exhibit higher steady state for the optimal harvesting rates than perfect fishing selectivity case.

5 Conclusion

In this study, MSY and MEY harvesting strategies for heterogeneous species fishery are investigated numerically in an overlapping generations framework under both perfect and imperfect fishing selectivity cases. The study repeats the analysis for three different trophic functions commonly studied in the literature in order to capture how the choice of interaction behavior between the prey and predator types alter the simulation results and thus the optimal harvesting strategies needed to achieve MSY and MEY.

In MSY, we find that both prey and predator populations increase and reach to a steady state level. Also, comparing the functional responses, the results for choice of different trophic functions give similar results and hence, in terms of biomass, choice of trophic function nearly does not matter under MSY setup.

In MEY optimal harvest strategies under the perfect and imperfect selectivity cases, proposed strategy increases biomass of both prey and predator fish population and helps to achieve a steady state level. Furthermore, the proposed levels can be achieved with finite level of effort exerted and implementable harvest rates. The results also reveal that the choice of trophic function may not change the results in case of the predator dependent or ratio dependent functions are used; however, the results change drastically when one works with prey-dependent function. This suggests that each system should be observed and studied empirically before the simulation results directly implemented. Another key finding is that comparing the two selectivities we see that the profit levels are higher in imperfect fishing selectivity case than perfect fishing selectivity case.

Having analyzed the optimal strategies, this study can be used by calibrating the true parameters of the systems and initial population levels in achieving fishery management objectives. Since the analytical solution is not available in MEY case for this problem, avenue for future research can include the stability analyses of the population dynamics in order to see the responses of the system to external shocks. Also, one another area of research in this subject open to improvement is the response of an ecosystem to environmental shock(s).

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