Fisheries Management Under Cyclical Population Demands

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Almost all fishery models assume time-invariant parameter values of the underlying biological growth function except for an i.i.d. error term. We examine the economic implications of cyclical growth parameters in both single and multi-species models, which are frequently observed in many real-world fisheries. Neither optimal harvest rates nor optimal escapement (remaining fish stock after fishing) remain constant as current models would predict. The amplitude of the optimal escapement is increasing in the amplitude of the biological growth function. Moreover, the optimal harvest rate lags the cycle of the biological growth function, i.e., the highest harvest rate is observed after biological conditions have started to decline and the optimal escapement level has already decreased. This is in sharp contrast to current policies which are in phase with biological conditions and hence imply an increase/decrease in harvest quotas when the biological system is improving/deteriorating. In our model, harvest closures are only optimal during time periods when growth parameters are improving most rapidly. We show that once the periodicity of the biological growth function is incorporated, many of the traditional policy prescriptions reverse.
Reports of two recent high level commissions, one sponsored by a major foundation (Pew Oceans Commission 2003) and one by the government (U.S. Oceans Commission 2004), suggest that serious problems exist with respect to the management of fisheries. Many fisheries are clearly overfished and in serious decline. Conventional wisdom is that political considerations have prevented rational management of fisheries by allowing overfishing, failing to curtail increases in fishing capacity, and not taking steps to prevent ecosystem damage by fishing selective species or size classes.\footnote{These findings contrast sharply with those of the earlier 1969 Stratton Commission, the country’s first oceans commission. It viewed the sea a vast resource and much of that report addresses how to expand the extraction of resources from the sea (U.S. Commission on Marine Science, Engineering and Resources 1969).} While international fisheries are a classical example of an open-access resource, the extension of exclusive fishing zones out to 200 miles around countries in the mid 1970s appropriated large parts of fisheries to individual nations. It is estimated that more than 90% of all fish reside within this 200-mile zone as coastal regions offer a more ample food supply for fish (Bjorndal and Munro 1998). There is an extensive literature on how countries can best to manage their costal zone fisheries. A standard result from economic optimization is an constant escapement rule, where regulators have a time-invariant target stock and increase/decrease harvest quotas to meet this target stock.

However, many of the classical optimal policy prescriptions reverse or no longer hold once we introduce cyclical growth parameters found in many real-world fisheries. This paper develops the economic and management implications of fluctuating environmental conditions which have distinct time series properties. This varies sharply from the existing literature that usually assumes parameters to be stable. For example, Reed (1979), Clark and Kirkwood (1986), Weitzman (2002), and Sethi et al. (2005) make one or more aspects of fish growth, quantity harvested, or stock level stochastic, but the random component in those models are i.i.d. and do not have any time series properties. In the simplest sense, the bio-economic model that dominates fisheries management has a stable set of parameters of the underlying fishing model and results in \textit{time-invariant} management objectives.\footnote{There might be disturbances to the system through random shocks, but the policy rule remains time-}
We put forth there is no time-invariant solution that either maximizes biological yield or economic rent. The predictable cyclic-pattern of environmental conditions suggests that a time-invariant harvest quantity will not only result in a suboptimal economic outcome, but also doesn’t achieve the highest average harvest quantity.

There are several recent papers that motivated us to pursue our approach. First, reconstructions of historical fish stocks suggest that those fish stocks were considerably larger than at present and considerably larger than the "carrying capacity" or maximum stock size estimated by current models of fish populations (Jackson et al. 2001). Accordingly, the maximum stock size is not constant over time. Second, there are well-known cycles that influence environmental conditions: the El Nino Southern Oscillation (ENSO) phenomena is of moderate duration on the order of several years, but its impact has varied substantially across longer time periods depending upon whether the El Nino was followed by the opposite La Nina cycle. Over somewhat longer time periods, there are distinct regimes with respect to salinity. Other cycles such as the Pacific Decadal Oscillation are on the order of fifty years. This cycle is now thought (Chavez et al. 2003) to have influenced the large scale reduction in the sardine population off the coast of California made famous in Steinbeck’s novel Cannery Row with a commensurate increase in anchovies and back then sardines.

Where data exist, many fish stocks are observed to exhibit substantial temporal variation. Such variation is often in the form of oscillations between high and low stock levels even though there may be minimal or constant fishing effort. In the biological literature on fisheries, variability in environmental conditions is usually given as the underlying cause but there is surprisingly little incorporation of such conditions in the modeling done for fisheries management purposes (Clark 1985, Rothschild 1986, Hilborn and Walters 1992). Of course, overfishing and adverse environmental conditions may occur together. For example, though still controversial, there is some indication that the Peruvian anchoveta collapsed because...
high fishing efforts overlapped with environmental events that resulted in low growth rates (Ludwig et al. 1993).

The rest of this paper is devoted to laying out a simple model this is consistent with the set of stylized facts put forth and examining its implications for fisheries management more thoroughly. In a first step we focus on the implications of a time-varying growth rate and carrying capacity for a single species. We start with a model where harvest cost are independent of the fish stock to illustrate our main conclusions in Section 1. Previous papers assuming a stationary growth function result in a constant escapement-rule, where negative shocks to the systems and declining fish stocks imply harvest closures. Quiet to the contrary, our model suggests a time-varying escapement and harvest rule, where the periodicity of the latter lags the former, i.e., optimal harvest rates peak after the optimal escapement already started to decline. This has strong policy implications as almost all other model support a policy that increases harvest quotas if and only if fish abundance is increasing. In sharp contrast, periodic fluctuations in the growth rate imply that it is best to close a fishery during times when the non-stationary biological growth parameters are improving most rapidly, and hence the return from not fishing is highest. The same reasoning still holds when we introduce stock-dependent cost in Section 2. Section 3 compares the optimal harvest policy under cyclical fluctuations to traditional models of maximum sustainable yield and constant escapement rules, as well as adaptive rules where fishing quotas are repeatedly revised or set to a constant fraction of the fish stock. We show that a policy that derives the maximum sustainable harvest quota using the average growth rate will lead to overfishing and a crashing fish stocks, as will an adaptive policies that utilizes a limited time-series of past data. Both policies are currently used by regulators to determine harvest quotas.

Fluctuating growth rates are one key aspect of moving towards an ecosystem based management system. The other is the interaction between species. In Section 4, we look at cyclically varying growth rates in the context of a predator-prey system with one predator
species and two prey species. Small fluctuations in growth parameters in one species can lead to sizable fluctuations in optimal harvest policies of all species due to the interplay of the species. Finally, Section 5 concludes.

1 A motivating example

This section introduces cyclical fluctuations to a simple logistic single-species model with stock-independent harvest cost. The purpose of this section is to give an intuition for similar results we obtain in later sections.

Before launching into our model assumptions, one might wonder whether real world fisheries exhibit time-varying growth parameters. First, a plot of sea surface temperatures in the Pacific Ocean exhibits strong cyclical components over time and there is a large literature in biology suggesting that fish stocks are influenced by temperature. Moreover, the classical book on fish stock assessment by Hilborn and Walters (1992, p. 52) shows that the recruitment of Pacific halibut between 1945 and 1985 appear to follow predictable synodal cycles. Such fluctuations in recruitment will result in varying fish densities and hence fluctuating values of fishing licenses along the lines of Stefanou and Wilen (1992). Finally, Chavez et al. (2003) link the fluctuations in sardine and anchovies cycles to fluctuations in the Pacific Decadal Oscillation.

A paper with some resemblance to ours is Walters and Parma (1996), which also examines systematic fluctuations in growth rates. However, the focus of their paper is primarily on the resulting biological system. The authors introduce an elaborate system of density-dependent and density-independent mortality rates, but the objective is to maximize total catch over a finite period. Our paper uses a more simplistic biological model but, in later parts, emphasizes stock-dependent harvest cost as well as discounting to derive implications for the economic optimum, i.e., the harvest strategy that maximizes net benefits from harvest.
The unique feature of our setup is that there are predictable cycles in the biological growth process. This differs from almost all economic approaches to renewable resources that assume i.i.d. error terms (Pindyck 1984). More specifically, consider a fish species with stock \( F(t) \) at time \( t \) that follows a logistics growth function \( \dot{F}(t) = \left[ \alpha_0(t) + \alpha_1(t)F(t) \right] F(t) \) where \( \alpha_0 > 0, \alpha_1(t) < 0 \). Note that the intrinsic growth rate \( \alpha_0(t) \) can be time-varying, and hence so is the carrying capacity \( \frac{-\alpha_0(t)}{\alpha_1(t)} \). Assume that fisheries management maximizes the present value of future harvests \( h(t) \).

As a first-step assume that there are constant marginal stock-independent harvesting cost \( \omega \). Using a discount rate \( \delta(t) \) the optimization problem becomes

\[
\max_{h(t)} \int_0^\infty e^{-\int_0^s \delta(s)ds} \left[ p - \omega \right] h(t) dt \quad \text{s.t.} \quad \dot{F}(t) = \left[ \alpha_0(t) + \alpha_1(t)F(t) \right] F(t) - h(t)
\]

It is well-known that the optimal policy requires a target stock \( F^* \) where the tangent to the growth function equals the interest rate. The intuition is quite simple: a fishermen faces the choice of either harvesting now and putting the proceeds in the bank to earn interest \( \delta(t) \), or delaying harvest by some time to obtain some additional biological growth as given by the slope of the growth function. Since the slope of a logistic growth function is decreasing in the
stock size, the biological growth exceeds the economic opportunity cost of earning interest rate \( \delta(t) \) to the left of the stock level \( F^* \), and is lower than the economic opportunity cost \( \delta(t) \) to the right of it.

**Proposition 1** The optimal harvest policy \( h(t) \) is to keep the optimal stock size of the fish species at \( F^*(t) = \frac{\alpha_0(t) - \delta(t)}{-2\alpha_1(t)} \)

The derivation is given in the appendix. Note the complete symmetry between fluctuations in the growth rate \( \alpha_0(t) \) and the interest rate \( \delta(t) \), as only the difference between the two determines the optimal stock size. Hence, business cycle models with cyclical interest rates will have analogous effects on the optimal harvest policy. In this paper we focus on cyclical biological growth parameters, but a similar story could be told for a stable time-invariant biological system when there are fluctuations in the interest rate.

In the remainder we fix \( \delta \) and \( \alpha_1 \) but let \( \alpha_0(t) \) be a synodal function. We assume that \( \alpha_0(t) > \delta \) for all \( t \), i.e., we rule out a border solution where it is best to wipe out the entire fish species. Changing intrinsic growth rates translate into changing carrying capacities as well as changing optimal stock levels \( F^* \) as shown in Figure 1. Varying intrinsic growth rates \( \alpha_0(t) \) imply a periodic carrying capacity \( \frac{\alpha_0(t)}{-\alpha_1} \) as well as a periodic optimal fish stock \( \frac{\alpha_0(t) - \delta}{-2\alpha_1} \), ranging from \( F_{\text{min}}^* \) under the lowest intrinsic growth rate to \( F_{\text{max}}^* \) under the highest intrinsic growth rate. The optimal harvest policy is simply the difference between the growth rate and the desired change in the optimal fish stock, i.e., \( \frac{\alpha_0(t)^2 - \delta^2 - 2\alpha_0(t)}{-4\alpha_1} \) (for a case where there are no harvest closures, i.e., the above fraction is never negative).

Intuitively, if the system is at \( F_{\text{max}}^* \), and the intrinsic growth rate \( \alpha_0 \) starts to decline, the slope of the growth function at \( F_{\text{max}}^* \) becomes smaller than the interest rate, suggesting that the return of keeping an extra fish in the ocean is less than the opportunity cost of earning interest \( \delta \). Hence one should reallocate funds to the investment opportunity with the larger return, i.e., decrease the fish stock, thereby raising its return until it equals the
Figure 1: Oscillating Intrinsic Growth Rate with Stock-independent Harvest Cost

Notes: The graph displays the time-varying growth function and optimal stock levels \( F^* \) fluctuating between \( F^*_{min} \) and \( F^*_{max} \). The parameter values are \( \alpha_0 = \alpha_{01} + \alpha_{02} \sin \left( \frac{2\pi t}{T} \right) \), \( \alpha_1 = -0.15 \), \( \delta = 0.025 \).

opportunity cost again. The opposite is true as well: if the system is at \( F^*_{min} \) and the intrinsic growth rate \( \alpha_0(t) \) starts to rise again, the slope of the growth function at \( F^*_{min} \) becomes larger than the interest rate, suggesting that the additional return of keeping an extra fish in the ocean exceeds the opportunity cost of putting the proceeds from harvesting fish and earning interest. Hence one should "invest" into the fish stock, i.e., shift resources into the fishery up to the point where its return equals the market return again.

There is one asymmetry in the model: one can draw down the fish stock instantaneously to any arbitrary nonnegative amount and place the proceeds from selling the fish into into a bank account, but the opposite is not true: the natural growth rate places an upper bound on the increase in the fish stock as negative harvest rates are infeasible. Hence, if the natural growth rate of the fish population does not diminish the return on fishing enough to decrease it to \( \delta \), it is best to close the fishery to harvest.

The intuition for a harvest closure are very similar to the standard case of a stationary growth function: the manager has to ensure that the slope of the growth function equals the interest rate. In the traditional model, if a random shock decreases the fish stock below its
optimal level, it is best to prohibit harvesting. Similarly, positive shocks to the fish stock warrant increased harvest rates to draw down the fish stock to the point where the slope of the growth function equals the opportunity cost of earning interest $\delta$. This bang-bang solution is driven by the linearity of the value function for two investment opportunities: (i) fisheries and (ii) the opportunity cost of earning interest $\delta$. Arbitrage requires that the returns of the two are equal.

The difference in our model is that we aren’t examining shocks to the fish stock but rather introduce a cyclical growth function that is changing with time. Traditionally, increasing fish stocks imply that the return on fishing is below the interest rate (due to the concavity of the growth function). In our model, increasing fish stocks signal that the growth rate itself is increasing and hence the returns on fishing efforts exceed the interest rate. The system is entering a period with the most rapid biological growth and it might pay to close the fishery. In our case of predictable fluctuations, harvesting is prohibited not because the fish species experienced a negative shock, but because is entering a positive recovery phase with exceptionally good growth rates and hence the return on not harvesting is particularly large. Hence harvest closures only happen during upswings, i.e., when growth conditions improve! This has important policy implications, as we frequently hear fishery lobbyists call for increased quotas when fish stocks are increasing, yet this might be the time to actually lower the quotas.

In the remainder of this paper we use the following specification of the time-varying synodal intrinsic growth rate: $\alpha_0(t) = \alpha_{01} + \alpha_{02} \sin \left( \frac{2\pi(t+\alpha_{03})}{\alpha_{04}} \right)$, i.e, $\alpha_{01}$ is the average intrinsic growth rate, $\alpha_{02}$ the amplitude of the cyclical fluctuations, $\alpha_{03}$ an offset that allows the start of the cycle to be shifted in time, and $\alpha_{04}$ the periodicity. As mentioned above, the harvest rate becomes zero when the growth rate $[\alpha_0(t) + \alpha_1 F^*(t)] F^*(t)$ is less than the growth in the optimal stock level $\dot{F}^*(t) = \frac{\alpha_0'(t)}{-2\alpha_1}$, i.e., the change in the optimal stock size outpaces the natural growth rate. The following proposition establishes that there exists a
minimum amplitude for which harvest closures become optimal and how it relates to the average intrinsic growth rate and periodicity.

**Proposition 2** The minimum amplitude $\alpha_{02}$ for which there is a harvest closure in the cyclic single-species model is increasing in the intrinsic growth rate $\alpha_{01}$ and periodicity $\alpha_{04}$, and decreasing in the interest rate $\delta$.

The proof is given in the appendix. Intuitively, a larger periodicity implies that the desired change in fish stock happens fairly smoothly and can be sustained by natural growth. If on the other hand the optimal fish stock changes very rapidly, the desired increase may not be achieved by natural fish growth and it is optimal to set the harvest rate to zero. Accordingly, if the amplitude is too large (and the optimal fish stock hence has a larger amplitude as well), the desired changes in fish stock can not be sustained. In the extreme, once the amplitude $\alpha_{02}$ approaches the difference between the average growth rate $\alpha_{01}$ and the interest rate $\delta$, the minimum optimal fish stock approaches zero, at which point the fish growth approaches zero as well. Once the biological parameters improve again, the desired fish stock increases, but this increase can not be sustained because the natural growth is too low. The results for a particular set of parameter assumptions are shown in Figure 2.

Note that the fish stock $F$ can drop below the optimal stock level $F^*$. One might wonder whether a zero harvest rate and a stock level below the desired stock level $F^*$ can be optimal. Wouldn’t it be preferable to reduce the harvest rate at an earlier time when it is still positive to avoid the predictable harvest closure? Again, the harvest closure occurs not because the fish stock is in a "bad" condition but because the growth rate at the current stock size is increasing sufficiently fast. Reducing harvest at an earlier point hence would imply a sacrifice in a bad state (when the growth rate is even lower) in order to increase harvesting in a better state (a time period when the growth rate is larger). This can not be optimal, as investing in an asset should not occur during periods of low growth but during periods of high growth.
Figure 2: Oscillating Intrinsic Growth Rate with Stock-independent Harvest Cost

Notes: The graph displays the minimum amplitude that implies a harvest closure as a function of mean intrinsic growth rate $\alpha_{01}$ and periodicity $\alpha_{04}$. The parameter values are $\alpha_0 = 0.15 + 0.075 \sin \left( \frac{2\pi t}{50} \right)$, $\alpha_1 = -0.15$, $\delta = 0.025$.

Proposition 3 The optimal fish stock $F^*(t)$ is in phase with the biological growth parameter $\alpha_0(t)$, but the optimal harvest rate lags behind it.

The proof is given in the appendix. The result that the fish stock is in phase with the biological growth parameters is immediately evident from the solution of the optimal fish stock $F^*(t) = \frac{\alpha_0(t) - \delta(t)}{2\alpha_1}$ in Proposition 1. The intuition behind why the optimal harvest rate lags behind the optimal fish stock is as follows: the optimal harvest rate is the difference between the growth rate and the change in the optimal stock level. The time derivative of the former is zero at the same time the biological growth parameters peak, however the time derivative of the latter includes the change of the change in the biological growth parameters, which is negative when the synodal growth parameters is largest (as the sin curve is concave on $[0, \pi]$ and positive when the synodal growth parameters is smallest (as the sin curve is convex on $[\pi, 2\pi]$). In other words, the change in the change of the optimal stock level incorporates that one is switching from a period of increasing optimal fish stocks to a period of decreasing fish stocks (or visa versa) and hence gives an extra incentive (disincentive) to fish as the stock will decrease (increase).
This result has important policy implications as it is contrary to results from standard models which all increase harvest quotas when the fish stock is increasing and vice versa. Once we introduce cycle growth rates, there is no longer a monotone relationship between the harvest rate and fish stock.

2 Stock-dependent Harvest Cost - Single Species

The previous section introduced the case of stock-independent harvest cost to motivate why the harvest rate is out of phase with the biological growth function and why harvest closures will occur during periods of increasing growth rates. We will now show that both results hold for the case of stock-dependent harvest cost as well. Authors as far back as Scott (1955) have recognized that if fishing cost depend on the fish stock, there might be an incentive to cut back fishing today for lowered fishing costs tomorrow. In the remainder of this section we rely on the standard modelling framework where harvest \( h(t) \) is a linear function of effort \( e(t) \) and stock size \( F(t) \), i.e., \( h(t) = \theta e(t) F(t) \).\(^5\) Furthermore, there is a constant marginal cost of effort \( \omega \) as well as constant fish price \( p \). The regulator is maximizing the discounted value of future profits with discount rate \( \delta \), i.e., the problem becomes

\[
\max_{h(t)} \int_0^\infty e^{-\delta t} \left[ ph(t) - \omega \frac{h(t)}{\theta F(t)} \right] dt \quad \text{s.t.} \quad \dot{F}(t) = [\alpha_0(t) + \alpha_1 F(t)] F(t) - h(t)
\]

The optimal solution requires that the stock of the fish species is kept at \( F^* \), which is itself a cyclical function of \( \alpha_0 \).

**Proposition 4** The optimal harvest policy \( h(t) \) is to keep the optimal stock size of the fish species at \( F^*(t) = \frac{\theta p [\alpha_0(t) - \delta] - \alpha_1 \omega}{-4 \alpha_1 \theta p} + \sqrt{\left( \frac{\theta p [\alpha_0(t) - \delta] - \alpha_1 \omega}{-4 \alpha_1 \theta p} \right)^2 + \frac{\delta \omega}{-2 \alpha_1 \theta p}} \).\(^5\)The model assumes that the amount of fish caught per unit of effort is proportional to the fish stock.
The derivation is given in the appendix. The formula in Proposition 4 is the solution for the dynamic optimum implied by \( g'(F^*) + \frac{\omega g(F^*)}{F^*(\delta p F^* - \omega)} = \delta \) where \( g(F) = [\alpha_0(t) + \alpha_1 F(t)] F(t) \) is the logistic growth function. It differs from the solution in the standard static framework of the previous subsection where the slope of the logistic growth function equals the interest rate, \( g'(F^*) = \delta \). In the static setting the equilibrium is determined where the marginal growth rate equals the discount rate, i.e., the point where the return on holding natural resources is equivalent to the market return. The dynamic optimum incorporates the fact that a change in current harvest also influences the profit margin in the future, as harvesting cost are inversely proportional to the stock size. This effect is captured in the term \( \omega g(F^*) F^*(\theta p F^* - \omega) \).

The solution for the case of stock-independent harvest cost in Proposition 1 is just a special case of Proposition 4 where \( \omega = 0 \). Standard comparative static results for the case of stock-dependent harvest cost are given in the following proposition with the derivation provided in the appendix.

**Proposition 5** The optimal stock level is increasing in the growth parameters \( \alpha_0 \) and cost of effort \( \omega \), while it is decreasing in the growth parameter \( -\alpha_1 \), effort factor \( \theta \) and price of fish \( p \).

The comparative static results are given in the appendix, and we focus on the intuition behind these results: a larger intrinsic growth rate \( \alpha_0 \) implies larger biological growth which is more conducive to support larger fish stocks. On the other hand, \( -\alpha_1 > 0 \) measures the crowding out effect of the fish species, which implies that a smaller fish stock can be supported. A larger price of fish implies that the tradeoff of fishing now or keeping a higher stock to lower future fishing cost is further tilted towards fishing now. Higher harvest cost \( \omega \) implies that it is optimal to keep a larger fish stock to lower future harvest cost. As \( \omega \) approaches zero, the solution converges to the one with stock-independent cost. Hence the optimal fish stock is always higher for the case of stock-dependent harvest cost. Finally, an
increase in $\theta$, the efficiency factor on fishing effort is equivalent to a decrease in the cost of fishing $\omega$ and hence decreases the optimal fish stock.

Since the intrinsic growth function $\alpha_0$ is fluctuating, so is the desired optimal stock level $F^*(t)$ and the harvest rate $h(t)$. The following proposition establishes that the optimal harvest policy always lags behind the phase of the biological growth function, i.e., the harvest rate peaks once the biological growth function already started to decline, and bottoms once the biological growth function already started to increase.

**Proposition 6** The optimal fish stock $F^*(t)$ is in phase with the cyclical biological growth function, while the harvest policy $h(t)$ lags behind the phase of the biological growth function.

The proof is given in the appendix. The intuition behind this result is as follows: The optimal stock level $F^*(t)$ is in phase with the cyclical biological growth function, i.e., it peaks at the same time. The optimal harvest rate is the difference between the growth rate and the change in the optimal stock level. The change in the harvest rate therefore depends on the change in the change of the optimal stock level, which includes the second derivative of the optimal growth function. If the synodal growth function peaks, this second derivative is negative, and hence the desired harvest rate is still increasing. In other words, once the growth function peaks, the regulator realizes that the investment opportunity of leaving fish in the sea becomes less profitable in the future, and hence it is optimal to decrease the desired stock level or further increase the harvest rate. The same logic holds when the growth function is at its minimum, the regulator realizes that the system is now entering the phase with the highest return, and hence it pays to keep more fish in the sea and hence further decrease harvest.

This result is important as many real-world fishing policies are based on the observed fish stock, and once this fish stock increases, fishermen are quick in pointing out the harvest quotas should be increased. On the other hand, once fish stocks decrease environmentalists
call for a reduction in harvest quotas. Both statements would be misleading in the case of cyclical population dynamics as harvest policies and biological growth rates are out of phase. The next section contrasts the optimal policy from traditional fishing policies with the help of simulations. While we have shown formally in the last two sections that the optimal policy will differ, one might wonder how large the welfare losses are from using one of the suboptimal policies.

3 Simulation of Various Harvest Policies

We can now use the analytical results of the previous section to simulate economic rents and fish stocks under the optimal harvest rule and compare it to various fishing policies underlying fishing regulation. The most common one is an overall harvest quota imposed by the government. Most of these quotas are time-invariant and follow the concept of a maximum sustainable yield, i.e., the largest constant harvest quota that can be achieved forever. Quotas are often grandfathered based on historic catches, but once allocated, vessel operators are sometimes allowed to trade them with the idea that less efficient vessel operators will sell their quotas to more efficient operators. As has been discussed in the previous section, such a policy will deviate from an optimal harvest policy that is time-variant.

Economists have advocated a constant escapement policy in the past, where the expected fish stock at the end of a period is held constant. The advantage of a constant escapement policy over one with constant harvest quotas is that the latter deals better with random shocks to the system as it gives rise to a bang-bang solution, where increases in fish stock will immediately be offset by increases in harvest quotas, and declining fish stock will lead to harvest closures.

Other policies we consider are a quota policy that is based on the average growth rate and an adaptive policy where the harvest quota is periodically updated. In many cases,
regulators deliberately rely only on a limited historic record of fish stocks with the idea that it is more representative of the current fishery system. It should be immediately clear that such a policy will give an inaccurate assessment in a cyclical population model with a sufficient long periodicity, as too large (small) harvest quotas are set when the system is entering the low (high) phase.

Finally, we simulate how well a regulator could estimate the periodicity from past observations. There is an initial period where it is difficult to distinguish random shocks from cyclical movements, but within a few years the regulator may be able to get a reasonably precise estimates of the system.

In the remainder, the optimal harvest rule will be such that \( \dot{F}(t) - h(t) \) keeps \( F(t) \) at \( F^*(t) \) if possible, otherwise \( h(t) \) will be zero. We assume that the unit price of effort is \( \omega = 2 \), the multiplicative factor on effort is \( \theta = 1 \), the price of fish is \( p = 225 \), the discount rate \( \delta = 0.025 \), and the growth parameters are \( \alpha_0 = 0.15 + 0.075 \sin\left( \frac{2\pi t}{50} \right) ; \alpha_1 = -0.15 \), i.e., the carrying capacity is on average one.\(^6\) The system is started in a state without human intervention, and we evaluate both the economically optimal policy as well as the traditional policies for each of the 50 starting points in the assumed 50-year periodicity.

**Maximum Sustainable Yield**

One of the most widely used concepts in fishery regulations is that of a maximum sustainable yield, i.e., the highest average harvest rate that can be sustained forever. Figure 3 displays the time-invariant maximum sustainable yield in black as well as optimal harvest policy in grey. The starting value in the figure is set to equal the fish stock without human intervention.

Note that the harvest rate under the optimal policy fluctuates significantly over time and sometimes even equals zero. A harvest moratorium occurs during time periods when the

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\(^6\)Both the average growth parameters and the economic parameters are taken from Perman et al. (2003), a standard graduate natural resource economics text. The periodicity of 50 years is taken out of Taylor (2004), who looks at longterm climate change and salmon populations.
Notes: The left panel displays harvest rates, while the right panel shows resulting fish stocks. The black line uses the maximum sustainable time-invariant harvest rate, while the grey line uses the optimal policy. The parameter values are $\omega = 2, \theta = 1, p = 225, \delta = 0.025, a_0 = 0.15 + 0.075 \sin \left( \frac{2\pi t}{50} \right), a_1 = -0.15$.

Biological growth parameters rapidly improve, which is in sharp contrast to current policies that tend to increase harvest quotas as soon as the observed fish stocks start to improve. The reason for the harvest closure is that the return on not fishing is highest and hence the target stock $F^*$ increases faster than what can be sustained by natural fish growth.

The optimal time-varying harvest rule results in substantially larger discounted net benefits. Under the optimal harvest rate, the average discounted stream of profits equals 493, ranging from 423 under the least favorable of the 50 possible starting conditions to 573 under the most favorable starting condition.

The maximum sustainable harvest rate, by definition, is time-invariant. The highest sustainable rate in our system is 0.0317, which is lower than the mean harvest rate under the optimal harvest policy, which is 0.0417. It should be noted that the maximum sustainable yield in a standard stationary model is at least as high as the economically optimal harvest rate, as future harvest is traded for current harvest which is discounted at a lower rate. However, under the cyclical model this fact is no longer true. By forcing the harvest rate to
be time-invariant, the constant harvest rate is limited by the phase of lower growth. Also, the maximum sustainable yield is lower than the one attainable under the average growth rate, which is \( \frac{\alpha_2}{4\alpha_1} = 0.0375 \).

A time-invariant harvest quota together with fluctuating growth parameters imply that the fish stock is fluctuating over time as well as shown in the right graph of Figure 3. Note how the stock level under the constant harvest quota is out of phase with the optimal stock level, where the former lags the latter, which is in phase with the biological growth function.

### Constant Escapement Policy

The economic optimum in the standard stable fisheries model implies a constant escapement policy that keeps the expected stock level at the end of a period at a constant level, i.e., the number of fish that ”escape” (are not fished) is held constant. The result holds even in the presence of random shocks.

In the following we examine how well such a constant escapement policy fares in light of cyclical population dynamics. We use the same cyclical changes in the growth function as before, yet assume the regulator relies on the average growth rate when designing its regulation. Figure 4 displays the resulting harvest rate and fish stock under such a scenario where the regulator incorrectly assumes that there is a stable time-invariant logistic growth function with \( \alpha_0 = 0.15 \). The harvest policy now peaks in phase with the biological growth parameters, yet, as shown in previous sections, the optimal harvest policy lags behind, i.e., peaks later, as shown in the left graph of Figure 4. While the maximum sustainable yield by definition holds the harvest quota unchanged, the constant escapement policy fixes the stock size, even though the latter should fluctuate under the optimum. The biggest problem is that the harvest rate is too low during good, i.e., highly productive, times. Using a time-invariant escapement rule results in an average net benefit (over the 50 possible starting conditions) of 451, which is inferior to the optimal time-variant policy of 493.
Figure 4: Constant Escapement Rule under Oscillating Growth Rates

Notes: The left panel displays harvest rates, while the right panel shows resulting fish stocks. The black line uses a constant escapement rule, while the grey line uses the optimal policy. The parameter values are the same as in Figure 4.

Weitzman (2002) shows that landing fees are preferable to harvest quotas in a stochastic setting with i.i.d. error terms as they generate the same solution as the constant escapement rule. However, under cyclical population dynamics, the landing fees would have to be cyclical as well as the optimal escapement fluctuates. While many previous studies allowed for random shocks in the system, the large majority assumed that the logistic growth function is time-invariant or stationary. Similar to an error correction model in macroeconomics, the optimal harvest rate is not a stationary function but varies with the underlying growth parameters.\footnote{Alternatively to modeling a time-variant process one could use time as a state variable itself. See for example Costello et al. (2001).}

Regulation Based on the Average Growth Rate

Most regulation prefer quotas over fees or constant escapement rules as they are easier to implement and give fishermen certainty about the allowable catch in the next period. In the following we therefore consider two policies that use the average intrinsic growth rate for the
Notes: The left panels display the harvest rate, while the right panels show the resulting fish stock. The top row uses the optimal catch under the average growth rate. In the bottom row a constant fraction of the stock is harvested. The fraction is set to equal the ratio of the optimal harvest to fish stock under the average growth rate. The optimal policy is added in grey. The parameter values are the same as in Figure 3.

design of harvest quotas.

Results for the case where the regulator sets the fishing quota equal to the growth rate at the optimal stock under the average growth function are shown in the top row of Figure 5. There are some interesting policy implications: First, the stock level diminishes to the open-access level, as the average harvest rate is too high.\(^8\) This is in line with the argument by

\(^8\)It is of course possible to have case where the periodic fluctuations are large enough to lead to short-term recoveries where the fishing quota becomes binding again.
Roughgarden and Smith (1996) that the optimal harvest level is not ecological sustainable, i.e., once the stock falls below it, continued use of the same harvest rate will further diminish the stock and harvest rate. Their recommendation was to keep the stock above the level associated with the maximum sustainable yield. Second, the harvesting rate will sometimes be lower than the fishing quota, i.e., the quota is not binding. Once the stock size drops to the open-access equilibrium, further fishing becomes unprofitable.9

While a constant harvest rate is not ecological sustainable, setting the catch equal to a constant fraction of the stock size is sustainable as deteriorating conditions result in lower harvest rates. The results of such a policy are displayed in the second row of Figure 5 as a black line. The optimal harvest policy is included as a grey line for reference. The constant fraction of the stock that is harvested is the ratio of the optimal catch to the stock size under the average growth function. This policy partially simulates a system of fluctuating harvest rates, as periodic fluctuations in growth parameters translate into fluctuating stock sizes and harvest rates. However, these fluctuations are of lower magnitude and out of phase compared to the optimum policy.

These findings strongly suggest that fishing quotas may need to be time-varying, and potentially by a large amount, if there are cyclical dynamics in the underlying fishery biology. This is in line with the recommendation of the Pew Oceans Commission (2003, p.111) which recommends ecosystem based management of fish species and requires that ”Managers should evaluate the life history and habitat requirements of species to determine the appropriate types of area management tools to employ, including spatial and temporal closures, spawning closures, habitat protection areas, bycatch reduction areas, and marine reserves.”

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9 We have assumed a constant price of fish. There is a critical stock level where further fishing results in negative returns (the catch per unit of effort is low enough).
Adaptive Policy

In this section we allow for an adaptive policy where the regulator realizes that the underlying system is changing and hence repeatedly updates his or her estimate for the growth parameters. The motivation of such a policy is that many U.S. regulations require periodic review of harvest quotas. Specifically, we consider the case of a regulator who re-estimates the logistic growth function every five years using data on fish stocks and harvest from the previous two decades. The regulator again assumes that the carrying capacity is fixed, and only estimates the instantaneous growth function from the discretized version

\[ h_t + F_{t+1} - F_t = \alpha_0 [1 - F_t] F_t + \epsilon_t. \]

We include an error term in this subsection as the regulator is estimating a model from observed data.

We simulate a stochastic system using a standard Wiener process \( W(t) \) with

\[ dF(t) = [\alpha_0 + \alpha_1 F(t)] F(t) + \sigma F(t) dW(t) \]

and aggregate the observations on a yearly basis. The logistic growth parameter \( \alpha_0 \) is estimated from the 20-year history preceding each policy re-evaluation. In case the current stock of fish is above the optimal stock level, the harvest rate is set equal to the growth rate at the optimal stock level. In case the stock of fish is below the optimal stock level, the fishery is closed until it has reached the optimal stock level again, upon which the harvest rate is set to equal the growth rate at the optimal stock level. The resulting harvest rates and stock levels under both the optimal policy and the one using lagged values is displayed in Figure 6. We switch the periodicity from 50 to 49 years to avoid it being a multiple of the reauthorization process of 5 years.

Note how the lagged policy repeatedly sets the fishing quota too high when growth rates are declining. Hence, these fishing quotas turn out to be too high during periods of slow growth rates and result in serious overfishing. The fish species is saved from complete extinction as fishing efforts are stopped as soon as the population reaches the open access equilibrium and further fishing becomes unprofitable.\(^{10}\) Once the regulation is re-evaluated,

\(^{10}\)We purposefully pick a low marginal cost of effort in comparison to the price of fish. This seems
Notes: The left panel displays the harvest rate, while the right panel shows the resulting fish stock. The black line uses a lagged policy where the regulator is assumed to estimate the instantaneous growth rate $\alpha_0$ using the 20-year history preceding each policy reauthorization (which occurs every five years); and sets the harvest quota equal to the growth rate at the optimal stock level for the next five years in case the stock level is above the optimum stock level, and closes the fishery otherwise. The grey line displays the optimal harvest rate (averaged over each year). The parameter values are $\omega = 0.5, \theta = 1, p = 500, \delta = 0.025, \alpha_0 = 0.5 + 0.1 \sin \left( \frac{2\pi t}{49} \right), \alpha_1 = -0.5, \sigma = 0.03$

the fishery has to be closed until the stock has recovered.

The repeated over-fishing, closure, and re-opening leads to significantly lower average net benefits. The problem becomes only worse if we assume that private companies invest into more capital-intensive boats with lower marginal cost during good periods, which in turn yield a lower open-access equilibrium $\frac{\omega}{\theta p}$ during times of decreasing biological growth parameters when the lagged government quotas are too high. Recall that the lower stock level in the right graph of Figure 6 equals the open-access case where it is no longer profitable to fish. Once the marginal cost are very low, there is a real danger that the fish species will not recover, especially if there were to be a minimum sustainable level below which the appropriate as the largest share of cost are usually fixed cost, especially for the highly capitalized modern fleet that captures the largest fraction of fish. One might even argue that subsidies result in zero marginal cost, under which the species would crash.
species can not recover.

Estimating Periodic Growth Parameters

So far we always compared the optimal policy to suboptimal time-invariant or lagged policies. Recognizing the inferiority of the time-invariant policies, we simulate how well a regulator could estimate the periodicity using non-linear least squares. Using a system with a random component, we start with a ten-year history of the system and then re-estimate the growth parameters in each year to predict the optimal policy stock level in the next period.

Note that fluctuations in the stock level are necessary to identify the system. If a government policy of constant escapement were successful in keeping the fish stock at a constant level, it would be impossible to identify the constant part of $\alpha_0$ and $\alpha_1$ as $F$ is a constant. In a sense, the regulator can learn from mistakes. If parameters are estimated incorrectly,

![Figure 7: Estimating the Periodicity of the Growth Parameter](image)

Notes: The above graphs display the standard deviations of the estimated model parameters under the periodically fluctuating growth equation. Note that longer histories reduce the uncertainty and result in lower standard deviations, though initially, there might be large swings, even though the simulated error component is rather small. The parameter values are $\omega = 0.5, \theta = 1, p = 500, \delta = 0.025, \alpha_0 = 0.5 + 0.1 \sin \left( \frac{2\pi t}{50} \right), \alpha_1 = -0.5, \sigma = 0.01$
the harvest quota would be set incorrectly and result in deviations of the stock size away from the constant stock size $F^*$, which in turn helps to identify the system in future periods.

Figure 7 displays the coefficient of variation of repeatedly estimating the model parameters using non-linear least squares.\textsuperscript{11} Not surprisingly, these parameters are estimated more and more precisely as the history of a fish species increases. However, a relatively small error component combined with a relatively small time history can lead to estimates that are far away from the true parameter.

4 Stock-dependent Harvest Cost - Multiple Species

In the following we extend the analysis to include several species to highlight the importance of inter-species dynamics. Even when there are limited fluctuations in the biological growth function for a subset of the species, interspecies dynamics can lead to large fluctuations of the harvest rate for other species as well. Hence interspecies dynamics coupled with fluctuating biological growth parameters only amplifies the results of previous sections that the optimal fish stock/harvest quotas should be time-varying. Moreover, looking at one species at a time can give a misleading picture.

The general setup of a three-species fish system with fish stocks $F_1(t), F_2(t),$ and $F_3(t)$ can be expressed using $\log(\dot{F}_i(t)) = \frac{\dot{F}_i(t)}{F_i(t)}$

$$
\begin{bmatrix}
\log(\dot{F}_1(t)) \\
\log(\dot{F}_2(t)) \\
\log(\dot{F}_3(t))
\end{bmatrix} =
\begin{bmatrix}
\alpha_{10} \\
\alpha_{20} \\
\alpha_{30}
\end{bmatrix}
+ 
\begin{bmatrix}
\alpha_{11} & \alpha_{12} & \alpha_{13} \\
\alpha_{21} & \alpha_{22} & \alpha_{23} \\
\alpha_{31} & \alpha_{32} & \alpha_{33}
\end{bmatrix}
\begin{bmatrix}
F_1(t) \\
F_2(t) \\
F_3(t)
\end{bmatrix}
$$

In the following we assume that the matrix $A$ has full rank and is hence invertible.\textsuperscript{12} The

\textsuperscript{11}We restrict both periodicity and offset of $\alpha_0$ to be integer-valued. The coefficient of variation is the standard deviation of the estimate divided by the true mean.

\textsuperscript{12}In another paper we examine the effect of fishing co-integrated species where the matrix $A$ has less than rank three. If two species are co-integrated, there is no stable maximum sustainable harvest of one the co-integrated species, as fishing one species alone will lead it to be replaced by the other co-integrated species.
steady-state stocks without human interventions are hence given to be:

\[
\begin{bmatrix} \hat{F}_1(t), \hat{F}_2(t), \hat{F}_3(t) \end{bmatrix}' = -A^{-1}b
\]

Let the two prey species be \( F_1(t) \) and \( F_2(t) \), and the predator species be \( F_3(t) \). We use a revised Lotka-Volterra predator-prey system that allows for a reduction in the growth rate once the combined prey population gets too large and available food supplies diminish. (Lotka 1925, Volterra 1931). We assume that \( \alpha_{i0} > 0, \alpha_{ij} < 0 \), for \( i \in \{0, 1\}; j \in \{1, 2, 3\} \), i.e., there is an intrinsic growth rate for prey fish, which gets reduced by the number of fish in all species. On the other hand, \( \alpha_{30} = 0, \alpha_{31} > 0, \alpha_{32} > 0, \alpha_{33} < 0 \), i.e., the predator fish feeds exclusively on the two prey fish, the stock of which increase the growth rate of the predator fish. There is again crowding out by the own species.

The multi-species system can be compared to the single-species model in the previous section. The fish stocks of other species act as shifters to the intrinsic growth rate, e.g., for fish species 1, the analogous term to \( \alpha_0 \) in the single-species model now becomes \( \alpha_{10}(t) + \alpha_{12}F_2(t) + \alpha_{13}F_3(t) \), while \( \alpha_1 \) is now labeled \( \alpha_{11} \). Accordingly, the carrying capacity for species 1 is \( K_1 = \frac{\alpha_{10}(t) + \alpha_{12}F_2(t) + \alpha_{13}F_3(t)}{-\alpha_{11}} \), which can not only fluctuate due to the possibly time-varying parameter \( \alpha_{10} \), but also through varying population sizes of the other fish species. Even for the predator fish (species 3) which exclusively feeds of the prey fish (and hence \( \alpha_{30} = 0 \)), the carrying capacity will become time-varying if the stock of the two prey fish fluctuate over time as \( K_3 = \frac{\alpha_{31}F_1(t) + \alpha_{32}F_2(t)}{-\alpha_{33}} \). Similarly, even if the food fish would not directly interact (\( \alpha_{12} = \alpha_{21} = 0 \)), fluctuations in biological growth parameter of one food fish would still impact the other food fish through common links with the predator fish (species 3). Once fish species are allowed to interact, fluctuations in the growth parameter of one species can translate directly or indirectly into fluctuations of other species.

Similar to the previous section, we abstract from uncertainty. Assume that fisheries
management maximizes the present value of future harvests $h_i(t), \ i = 1, 2, 3.$ In the following we rely on the standard modelling framework where harvest $h_i(t)$ is a linear function of effort $e_i(t)$ and stock size $F_i(t)$, i.e., $h_i(t) = \theta_i e_i(t) F_i(t).$ Furthermore, there is a constant marginal cost of effort $\omega$ as well as constant fish price $p_i$. The regulator is maximizing the discounted value of future profits with discount rate $\delta$, i.e., the problem becomes

$$\max_{h_i(t)} \int_0^\infty e^{-\delta t} \left[ p_1 h_1(t) - \omega \frac{h_1(t)}{\theta_1 F_1(t)} + p_2 h_2(t) - \omega \frac{h_2(t)}{\theta_2 F_2(t)} + p_3 h_3(t) - \omega \frac{h_3(t)}{\theta_3 F_3(t)} \right] dt$$

s.t. \begin{align*}
\dot{F}_1(t) &= [\alpha_{10} + \alpha_{11} F_1(t) + \alpha_{12} F_2(t) + \alpha_{13} F_3(t)] F_1(t) - h_1(t) \\
\dot{F}_2(t) &= [\alpha_{20} + \alpha_{21} F_1(t) + \alpha_{22} F_2(t) + \alpha_{23} F_3(t)] F_2(t) - h_2(t) \\
\dot{F}_3(t) &= [\alpha_{30} + \alpha_{31} F_1(t) + \alpha_{32} F_2(t) + \alpha_{33} F_3(t)] F_3(t) - h_3(t)
\end{align*}

The derivation is similar to the single-species case in the previous section and given in the appendix.

**Proposition 7** The optimal stock level in the multi-species system is given by

$$-2\alpha_{11} p_1 \theta_1 F_1^2 + \left[ \theta_1 p_1 [\delta - \alpha_{10}] + \omega \left( \alpha_{11} + \alpha_{21} \frac{\theta_1}{\theta_2} + \alpha_{31} \frac{\theta_1}{\theta_3} \right) - \theta_1 \left[ \alpha_{12} + \alpha_{21} \frac{\theta_1}{\theta_2} + \alpha_{31} \frac{\theta_1}{\theta_3} \right] F_2 - \theta_1 \left[ \alpha_{13} + \alpha_{31} \frac{\theta_1}{\theta_3} \right] F_3 \right] F_1 - \delta \omega = 0$$

$$-2\alpha_{22} p_2 \theta_2 F_2^2 + \left[ \theta_2 p_2 [\delta - \alpha_{20}] + \omega \left( \alpha_{22} + \alpha_{12} \frac{\theta_2}{\theta_1} + \alpha_{32} \frac{\theta_2}{\theta_3} \right) - \theta_2 \left[ \alpha_{21} + \alpha_{12} \frac{\theta_2}{\theta_1} + \alpha_{32} \frac{\theta_2}{\theta_3} \right] F_1 - \theta_2 \left[ \alpha_{23} + \alpha_{32} \frac{\theta_2}{\theta_3} \right] F_3 \right] F_2 - \delta \omega = 0$$

$$-2\alpha_{33} p_3 \theta_3 F_3^2 + \left[ \theta_3 p_3 [\delta - \alpha_{30}] + \omega \left( \alpha_{33} + \alpha_{23} \frac{\theta_3}{\theta_2} + \alpha_{13} \frac{\theta_3}{\theta_1} \right) - \theta_3 \left[ \alpha_{32} + \alpha_{23} \frac{\theta_3}{\theta_2} + \alpha_{13} \frac{\theta_3}{\theta_1} \right] F_2 - \theta_3 \left[ \alpha_{31} + \alpha_{13} \frac{\theta_3}{\theta_1} \right] F_1 \right] F_3 - \delta \omega = 0$$

The idea is analogous to the single species case with logistic growth function $g(F) = \left[ \alpha_0(t) + \alpha_1 F(t) \right] F(t)$ where $g'(F^*) = \frac{\omega g(F^*)}{F^*(\eta F^* - \omega)} = \delta,$ except that the stock size $F_j, j \neq i$ of the fish populations different from species $i$ shifts the intrinsic growth rate $\alpha_0(t)$.

In the following we let the growth rates of the two prey fish oscillate by 5%. The parameters are as follows: $\dot{F}_1 = [0.8 + 0.04 \sin \left( \frac{2\pi t}{50} \right) - 0.025 F_1 - 0.025 F_2 - 0.004 F_3] F_1$ for food species $1$ and $\dot{F}_2 = [1 + 0.05 \sin \left( \frac{2\pi t}{10} \right) - 0.0125 F_1 - 0.0375 F_2 - 0.005 F_3] F_2$ for food species $2$ as well as $\dot{F}_3 = [0.003 F_1 + 0.004 F_2 - 0.003 F_3] F_3$ for the predator species. Furthermore, let $\theta_1 = \theta_2 = \theta_3 = 1,$ $\omega = 50,$ and $p_1 = p_2 = 100, p_3 = 500$, i.e., the predator fish is more
Notes: The left graph displays the optimal harvest rate while the right graph shows the resulting stock size. The intrinsic growth rates of the two prey fish oscillate according to $\alpha_{10} = 0.8 + 0.04 \sin \left( \frac{2\pi t}{50} \right)$, $\alpha_{20} = 1 + 0.05 \sin \left( \frac{2\pi t}{10} \right)$. The economic parameters are $\theta_1 = \theta_2 = \theta_3 = 1$, $\omega = 50$, and $p_1 = p_2 = 100, p_3 = 500$. The discounted value of the harvest from the three species are 11713, 17855, and 4687, respectively.

The optimal harvest quantities and resulting stock fish stocks are displayed in Figure 8. There are several noteworthy features. First, even though the two prey species have growth rates that oscillate with different periodicities of 10 and 50 years, each species oscillates with a combination of the two due to the interlinkage between species. Second, the unique stable equilibrium without human intervention under the average growth rates are $[6.67, 20.00, 33.33]$, yet the optimal stock level of the predator species is significantly lower. The reason for this effect is that the predator species has a negative effect on the prey species, while the prey species on the other hand have a positive effect on the growth rate of the predator. In the economic equilibrium, the stock of the latter is reduced. This effect becomes less pronounced, the larger the profit margin of the predator species. Third, even though the growth rates fluctuate by a relative small $\pm 5\%$, the optimal harvest rate fluctuates between 0.049 and 0.43, almost a nine-fold difference. This reinforces our main conclusions from the
single-species model: even modest fluctuation can lead to strong time-varying harvest rates due to inter-species dynamics.

5 Conclusions

Traditional fisheries model assume time-invariant biological growth parameters with possibly i.i.d error terms, yet there is ample evidence that these growth parameters vary periodically. We examine the implications of cyclical population dynamics on optimal fishing policies and show that they drive a further wedge between optimal economic policies and the biological concept of maximum sustainable yield underlying many regulations. Economists have long argued for fishing quotas or constant escapement rules to cope with the open-access problem, yet most regulations are still based on the concept of maximum sustainable yield (MSY), i.e., the highest time-invariant harvest rate that can be sustained forever. In the standard model of the fishery, the harvest rate maximizing economic rents is identical to MSY for a zero discount rate and stock-independent harvest cost. While a non-zero discount rate and stock-dependent harvest cost drive the economist’s recommendation away from the biologist’s MSY, these factors work in opposite directions. However, once the growth rate is allowed to vary periodically, so do optimal fish stock and harvest rate. The optimal economic policy diverges from the biological concept of maximum sustainable yield, which by definition is time-invariant, even in the presence of a zero discount rate and stock-independent harvest cost.

We show that the optimal harvest rate is out of phase with the biological growth parameters. This has strong policy implications as the optimal policy is no longer directly related to the observed fish stock. Fishermen are quick to argue for higher quotas as soon fish stocks are

\[\text{The economically optimal stock size is increasing in the former and decreasing in the latter. Because these two factors work in opposite directions, the stock level associated with MSY can still be a good approximation to the stock level which maximizes the economic rent associated with the resources.}\]
increasing, for the same reason that environmentalists advocate harvest reductions once fish stocks decline. Neither argument is accurate in the presence of cyclical population dynamics. Contrary to conventional wisdom, harvest closures occur during times when biological growth parameters are improving most rapidly as the return to not fishing is largest. Once we introduce inter-species dependence, modest fluctuations in the growth parameter in one species can lead to very large fluctuations in species that feed of it. Standard fishing policies of a maximum sustainable yield based on the average growth functions, or adaptive policies that periodically adjust the optimal harvest quota could lead to repeated collapses in the fish stock as the resulting harvest quotas will ruin the fish stock during consecutive years with low biological growth.

Our results can be seen as developing some of the economic implications of the ecosystem approach to management that has been recommended by the Pew Oceans Commission (2003) and many biologists which calls for considering environmental conditions and links between species. We do this by considering the simple case where biological growth varies in a smooth, cyclical, and highly predictable way for both a single species and interlinked species. The results of standard economic model of the fishery, which imbeds a time invariant growth rate, are surprisingly non-robust to this change.

There are two ways to expand upon our work. First, one could take our cyclical growth rate and make it a function of various environmental factors like temperature and salinity. This will introduce considerable complexity, particularly as one moves to the multi-species case, and the key issue is likely to be how predictable is the growth rate and at what time horizon. Still, the main result that the optimal harvest policy is time-variant and out-of-phase with the biological growth parameters should remain. Second, we have largely abstracted from the entry and exit decision into fisheries that has received considerable attention from economists (e.g., Berck and Perloff (1984)). How the dynamics of this process work in the face of time varying growth rate is an open question and one with strong implications for
current generation of regulatory instruments proposed by economists including limited entry programs (Walker et al. 1990), individual transferable quotas (Newell et al. 2005) and landing fees (Weitzman 2002) because of the issues posed for the connection between fishing capacity and fish stocks (Kirkley et al. 2002).
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6 Appendix: Proofs

Proof of Proposition 1 The optimal harvest policy \( h(t) \) is to keep the optimal stock size of the fish species at \( F^*(t) = \frac{\alpha_0(t) - \delta(t)}{-2\alpha_1(t)} \).

Proof: The current-value Hamiltonian becomes

\[
H = [p - \omega]h(t) + \mu(t) \{[\alpha_0(t) + \alpha_1(t)F(t)] F(t) - h(t)\}
\]

\[
= [p - \omega - \mu(t)] h(t) + \mu(t) [\alpha_0(t) + \alpha_1(t)F(t)] F(t)
\]

Note that the Hamiltonian is a linear function in the harvest rate \( h(t) \). If the multiplicative term on the harvest rate is different from zero, one would either set the harvest rate to zero or infinite. The necessary conditions for \( h(t) \) hence imply that

\[
h(t) = \begin{cases} 
0, & \text{if } p - \omega - \mu(t) < 0 \\
\infty, & \text{if } p - \omega - \mu(t) > 0 \\
\text{see below}, & \text{if } p - \omega - \mu(t) = 0
\end{cases}
\]

In the following consider first the case where \( p - \omega - \mu(t) = 0 \), which implies that \( \mu(t) = \bar{\mu} \). Differentiating the Hamiltonian with respect to the state variable \( F(t) \) gives

\[
H_F = \mu(t) [\alpha_0(t) + 2\alpha_1(t)F(t)] = \delta(t)\mu(t) - \dot{\mu}(t)
\]

Since \( \bar{\mu} > 0 \) (a larger fish stock can always be fished down instantaneously for a profit) we know that \( \alpha_0(t) + 2\alpha_1(t)F(t) - \delta(t) = 0 \), and hence \( F^*(t) = \frac{\alpha_0(t) - \delta(t)}{-2\alpha_1(t)} \).

Now consider the two border cases: Decreasing the fish stock increases the shadow value due to the assumed concave logistic growth function, and hence letting \( \mu(t) \) fall below \( \bar{\mu} \) can never be optimal in this deterministic model as one should increase fishing efforts. The converse is however not true: While one can instantly draw down the fish stock as much as desired, one cannot increase it an arbitrary speed as harvest is non-negative and fish growth is limited. So if \( \mu(t) \) rises above \( \bar{\mu} \), it becomes optimal to set the harvest rate to zero.

Proof of Proposition 2 The minimum amplitude \( \alpha_{02} \) for which there is a harvest closure in the cyclic single-species model is increasing in the intrinsic growth rate \( \alpha_{01} \) and periodicity \( \alpha_{04} \), and decreasing in the interest rate \( \delta \).

Proof: The change in the optimal stock level is \( \dot{F}^*(t) = \frac{\alpha_0(t)}{-2\alpha_1(t)} \). The growth rate at the optimal stock \( F^* \) is \( g(F^*(t)) = \frac{\alpha_0(t) + \alpha_1(t)F^*(t)}{F^*(t)} = \frac{\alpha_0(t)^2 - \delta^2}{-2\alpha_1(t)} \). If the former exceeds the latter, i.e., if the required increase in the stock level can not be sustained by natural growth, the
harvest rate will become zero, i.e.,

\[ \alpha_0(t)^2 - \delta^2 \leq 2\alpha'_0(t) \quad \Leftrightarrow \quad \alpha_0(t)^2 - \delta^2 - 2\alpha'_0(t) \leq 0 \]

The first order condition for minimizing \( \alpha_0(t)^2 - \delta^2 - 2\alpha'_0(t) \) gives \( 2\alpha_0(t)\alpha'_0(t) - 2\alpha''_0(t) = 0 \). Using \( \alpha_0(t) = \alpha_{01} + \alpha_{02} \sin \left( \frac{2\pi(t+\alpha_{04})}{\alpha_{04}} \right) \) we have for the solution \( \alpha_0(t) = \frac{\alpha_0'(t)}{\alpha_0(t)} = -\frac{2\pi}{\alpha_{04}} \tan(x) \), where \( x = \frac{2\pi(t+\alpha_{04})}{\alpha_{04}} \). Since \( \alpha_0(t) > 0 \) the shape of \( -\tan(x) \) implies that there are two possible solutions, \( x_1^* \in \left(-\frac{\pi}{2}, 0\right) \) and \( x_2^* \in \left(\frac{\pi}{2}, \pi\right) \).

Using \( \sin(x_1^*) < 0, \cos(x_1^*) > 0 \) and \( \sin(x_2^*) > 0, \cos(x_2^*) < 0 \) we hence know that \( x_1^* \) is a minimum and \( x_2^* \) is a maximum. In the remainder we hence limit the analysis to \( x^* = x_1^* \in \left(-\frac{\pi}{2}, 0\right) \). Totally differentiating \( \alpha_{01} + \alpha_{02}\sin(x^*) + \frac{2\pi}{\alpha_{04}} \tan(x^*) = 0 \) we get

\[
\{1\} \; d\alpha_{01} + \{\sin(x^*)\} \; d\alpha_{02} - \left\{ \frac{2\pi}{\alpha_{04}} \tan(x^*) \right\} d\alpha_{04} + \left\{ \alpha_{02} \cos(x^*) + \frac{2\pi}{\alpha_{04}} \cos(x^*)^2 \right\} dx^* = 0
\]

The derivatives of \( x^* \) with respect to the parameters of the synodal growth function are (recall that \( x^* \in \left(\frac{\pi}{2}, 0\right) \)):

\[
\frac{dx^*}{d\alpha_{01}} = -\frac{1}{\alpha_{02} \cos(x^*) + \frac{2\pi}{\alpha_{04}} \cos(x^*)^2} < 0
\]

\[
\frac{dx^*}{d\alpha_{02}} = -\sin(x^*) > 0
\]

\[
\frac{dx^*}{d\alpha_{04}} = \frac{\frac{2\pi}{\alpha_{04}} \tan(x^*)}{\alpha_{02} \cos(x^*) + \frac{2\pi}{\alpha_{04}} \cos(x^*)^2} < 0
\]

Call the minimum amplitude were the harvest rate becomes zero as \( \bar{\alpha}_{02} \). Hence we have

\[
M = \left[ \alpha_{01} + \bar{\alpha}_{02} \sin(x^*) \right]^2 - \delta^2 - \frac{4\pi\bar{\alpha}_{02}}{\alpha_{04}} \cos(x^*) = 0
\]

We have

\[
\frac{dM}{d\alpha_{02}} = 2 \left[ \alpha_{01} + \bar{\alpha}_{02} \sin(x^*) \right] \left[ \sin(x^*) + \bar{\alpha}_{02} \cos(x^*) \frac{dx^*}{d\alpha_{02}} \right] - \frac{4\pi}{\alpha_{04}} \cos(x^*) + \frac{4\pi\bar{\alpha}_{02}}{\alpha_{04}} \sin(x^*) \frac{dx^*}{d\alpha_{02}}
\]

\[
= 4\pi \sin(x^*) \left[ \alpha_{01} + \bar{\alpha}_{02} \sin(x^*) \right] - \frac{4\pi}{\alpha_{04}} \cos(x^*) - \frac{4\pi\bar{\alpha}_{02}}{\alpha_{04}} \sin(x^*)^2 < 0
\]

\[
\frac{dM}{d\alpha_{01}} = 2 \left[ \alpha_{01} + \bar{\alpha}_{02} \sin(x^*) \right] \left[ 1 + \bar{\alpha}_{02} \cos(x^*) \frac{dx^*}{d\alpha_{01}} \right] + \frac{4\pi\bar{\alpha}_{02}}{\alpha_{04}} \sin(x^*) \frac{dx^*}{d\alpha_{01}}
\]

\[
= \frac{4\pi \left[ \alpha_{01} + \bar{\alpha}_{02} \sin(x^*) \right]}{\alpha_{02} \alpha_{04} \cos(x^*)^3 + 2\pi} - \frac{4\pi\bar{\alpha}_{02}}{\alpha_{04} \left[ \alpha_{02} \cos(x^*) + \frac{2\pi}{\alpha_{04}} \cos(x^*)^2 \right]} > 0
\]

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Finally, using $\alpha_0(t) + \alpha_2(t)\sin(x^*) + \frac{2\pi}{\alpha_4(t)}\tan(x^*) = 0$ we get

$$\frac{dM}{d\alpha_0} = 2 \left[ \alpha_0(t) + \alpha_2(t)\sin(x^*) \right] \frac{\alpha_2(t)\cos(x^*)}{\alpha_0} \frac{dx^*}{d\alpha_0} + \frac{4\pi\alpha_2(t)}{\alpha_0} \cos(x^*) + \frac{4\pi\alpha_2(t)}{\alpha_0} \sin(x^*) \frac{dx^*}{d\alpha_0}$$

$$= -\frac{4\pi\alpha_2(t)}{\alpha_0} \cos(x^*) > 0$$

$$\frac{dM}{d\delta} = -2\delta < 0$$

And hence $M$ is increasing in both $\alpha_0$ and $\alpha_4$, yet decreasing in $\alpha_2$ and $\delta$.

**Proof of Proposition 3** The optimal fish stock $F^*(t)$ is in phase with the biological growth parameter $\alpha_0(t)$, but the optimal harvest rate lags behind it.

Proof: First, the optimal fish stock is $F^*(t) = \frac{\alpha_0(t) - \delta(t)}{-2\alpha_1}$ by Proposition 1 and hence the optimal fish stock is in phase with $\alpha_0(t)$.

Second, the harvest rate is given by the difference between the growth rate and the change in desired stock level, i.e.,

$$h(t) = \max \left\{ \frac{\alpha_0(t)^2 - \delta^2 - 2\alpha_0'(t)}{4\alpha_1}, 0 \right\}$$

In case the harvest rate is nonzero, we have

$$h'(t) = \frac{2\alpha_0(t)\alpha_0'(t) - 2\alpha_0''(t)}{-4\alpha_1}$$

When the biological growth function is at its maximum we have $\alpha_0'(t) = 0$ and $\alpha_0''(t) < 0$ and hence the harvest rate is still increasing. When the biological growth function is at its minimum we have $\alpha_0'(t) = 0$ and $\alpha_0''(t) > 0$ and hence the harvest rate is still increasing.

In case the harvest rate becomes zero, Proposition 2 has shown that the harvest rate becomes zero on $(\alpha_0(t) - \pi_2, \alpha_0(t))$, while the biological growth function is at its lowest at $\alpha_0(t) - \frac{\pi_2}{2}$.

**Proof of Proposition 4** The optimal harvest policy $h(t)$ is to keep the optimal stock size of the fish species at $F^*(t) = \frac{\theta p\alpha_0(t) - \delta - \alpha_1 \omega}{-4\alpha_1 \theta p} + \sqrt{\left( \frac{\theta p\alpha_0(t) - \delta - \alpha_1 \omega}{-4\alpha_1 \theta p} \right)^2 + \frac{\delta_\omega}{-2\alpha_1 \theta p}}$.
Proof: The current-value Hamiltonian becomes

\[ H = ph(t) - \omega \frac{h(t)}{\theta F(t)} + \mu(t) \{[\alpha_0(t) + \alpha_1 F(t)] F(t) - h(t)\} \]

\[ = \left[ p - \frac{\omega}{\theta F(t)} - \mu(t) \right] h(t) + \mu(t) [\alpha_0(t) + \alpha_1 F(t)] F(t) \]

The necessary conditions for \( h(t) \) imply that

\[ h(t) = \begin{cases} 0, & \text{if } p - \frac{\omega}{\theta F(t)} - \mu(t) < 0 \\ h_{\text{max}}, & \text{if } p - \frac{\omega}{\theta F(t)} - \mu(t) > 0 \\ \text{see below}, & \text{if } p - \frac{\omega}{\theta F(t)} - \mu(t) = 0 \end{cases} \]

Hence there are two border conditions. In the following consider the case where \( p - \frac{\omega}{\theta F(t)} - \mu = 0 \), which implies that

\[ \dot{\mu}(t) = \frac{\omega}{\theta F(t)^2} \dot{F}(t) \]

Differentiating the Hamiltonian with respect to the state variable \( F(t) \) gives

\[ H_F = \frac{\omega h(t)}{\theta F(t)^2} + \mu(t) [\alpha_0(t) + 2\alpha_1 F(t)] = \delta \mu(t) - \dot{\mu}(t) \]

Using the expression for \( \mu(t) \) and \( \dot{\mu}(t) \) we get

\[ \frac{\omega h(t)}{\theta F(t)^2} + \dot{\mu}(t) = \mu(t) [\delta - \alpha_0(t) - 2\alpha_1 F(t)] \]

\[ \Leftrightarrow \omega \frac{\dot{F}(t) + h(t)}{\theta F(t)^2} = \frac{\theta p F(t) - \omega}{\theta F(t)} [\delta - \alpha_0(t) - 2\alpha_1 F(t)] \]

\[ \Leftrightarrow \omega \left[ \frac{[\alpha_0(t) + \alpha_1 F(t)] F(t) - h(t) + h(t)}{F(t)} \right] = [\theta p F(t) - \omega] [\delta - \alpha_0(t) - 2\alpha_1 F(t)] \]

\[ \Leftrightarrow \omega \alpha_0(t) + \omega \alpha_1 F(t) = \theta p F(t) [\delta - \alpha_0(t)] - 2\alpha_1 \theta p F(t)^2 - \omega \delta + \omega \alpha_0(t) + 2\alpha_1 \omega F(t) \]

\[ \Leftrightarrow -2\alpha_1 \theta p F(t)^2 + [\theta p [\delta - \alpha_0(t)] + \alpha_1 \omega] F(t) - \omega \delta = 0 \]

The only positive solution to this quadratic formula is (Note that \( \alpha_1 < 0 \))

\[ F^*(t) = \frac{\theta p [\alpha_0(t) - \delta] - \alpha_1 \omega}{-4\alpha_1 \theta p > 0} + \sqrt{\left( \frac{\theta p [\alpha_0(t) - \delta] - \alpha_1 \omega}{-4\alpha_1 \theta p > 0} \right)^2 + \frac{\delta \omega}{-2\alpha_1 \theta p > 0}} \]
Proof of Proposition 5 The optimal stock level is increasing in the growth parameters $\alpha_0$ and cost of effort $\omega$, while it is decreasing in the growth parameter $-\alpha_1$, effort factor $\theta$ and price of fish $p$.

Proof: We assume that the instantaneous growth rate $\alpha_0(t) > \delta \forall t$, and hence $\alpha_0(t) - \delta > 0$. The optimal stock level is given by:

$$F^*(t) = \frac{\theta p [\alpha_0(t) - \delta] - \alpha_1 \omega}{-4\alpha_1 \theta p} + \sqrt{\left(\frac{\theta p [\alpha_0(t) - \delta] - \alpha_1 \omega}{-4\alpha_1 \theta p}\right)^2 + \frac{\delta \omega}{-2\alpha_1 \theta p}}$$

$$= \frac{\alpha_0 - \delta}{-4\alpha_1} + \frac{\omega}{4\theta p} + \sqrt{\left(\frac{\alpha_0 - \delta}{-4\alpha_1} + \frac{\omega}{4\theta p}\right)^2 + \frac{\delta \omega}{-2\alpha_1 \theta p}}$$

Hence we have (recall that $\alpha_1 < 0$)

$$\frac{\partial F^*(t)}{\partial \alpha_0} = \frac{1}{-4\alpha_1} \left[ 1 + \frac{\frac{\alpha_0 - \delta}{-4\alpha_1} + \frac{\omega}{4\theta p}}{\sqrt{\left(\frac{\alpha_0 - \delta}{-4\alpha_1} + \frac{\omega}{4\theta p}\right)^2 + \frac{\delta \omega}{-2\alpha_1 \theta p}}} \right] > 0$$

$$\frac{\partial F^*(t)}{\partial \alpha_1} = \frac{\alpha_0 - \delta}{4\alpha_1^2} \left[ 1 + \frac{\frac{\alpha_0 - \delta}{-4\alpha_1} + \frac{\omega}{4\theta p} + \frac{\delta}{-\alpha_1}}{\sqrt{\left(\frac{\alpha_0 - \delta}{-4\alpha_1} + \frac{\omega}{4\theta p}\right)^2 + \frac{\delta \omega}{-2\alpha_1 \theta p}}} \right] > 0$$

$$\frac{\partial F^*(t)}{\partial \omega} = \frac{1}{4\theta p} \left[ 1 + \frac{\frac{\alpha_0 - \delta}{-4\alpha_1} + \frac{\omega}{4\theta p} + \frac{\delta}{-\alpha_1}}{\sqrt{\left(\frac{\alpha_0 - \delta}{-4\alpha_1} + \frac{\omega}{4\theta p}\right)^2 + \frac{\delta \omega}{-2\alpha_1 \theta p}}} \right] > 0$$

$$\frac{\partial F^*(t)}{\partial \theta} = -\frac{\omega}{4\theta^2 p} \left[ 1 + \frac{\frac{\alpha_0 - \delta}{-4\alpha_1} + \frac{\omega}{4\theta p} + \frac{\delta}{-\alpha_1}}{\sqrt{\left(\frac{\alpha_0 - \delta}{-4\alpha_1} + \frac{\omega}{4\theta p}\right)^2 + \frac{\delta \omega}{-2\alpha_1 \theta p}}} \right] < 0$$

$$\frac{\partial F^*(t)}{\partial p} = -\frac{\omega}{4\theta p^2} \left[ 1 + \frac{\frac{\alpha_0 - \delta}{-4\alpha_1} + \frac{\omega}{4\theta p} - \frac{\delta}{\alpha_1}}{\sqrt{\left(\frac{\alpha_0 - \delta}{-4\alpha_1} + \frac{\omega}{4\theta p}\right)^2 + \frac{\delta \omega}{-2\alpha_1 \theta p}}} \right] < 0$$
Proof of Proposition 6 The optimal fish stock \( F^*(t) \) is in phase with the cyclical biological growth function, while the harvest policy \( h(t) \) lags behind the phase of the biological growth function.

The desired stock level is

\[
F^*(t) = \frac{\theta_p [\delta - \alpha_0(t)] + \alpha_1 \omega}{4 \alpha_1 \theta_p} + \sqrt{\left( \frac{\theta_p [\delta - \alpha_0(t)] + \alpha_1 \omega}{4 \alpha_1 \theta_p} \right)^2 - \frac{\delta \omega}{2 \alpha_1 \theta_p}}
\]

which is in phase with \( \alpha_0(t) \), and hence the optimal stock level fluctuates in phase with the biological growth function. Furthermore, we have

\[
\frac{dF^*(t)}{dt} = \frac{-\alpha'_0(t)}{4 \alpha_1} \left[ 1 + \frac{\theta_p [\delta - \alpha_0(t)] + \alpha_1 \omega}{4 \alpha_1 \theta_p} \right] \left[ 1 + \sqrt{1 - \frac{8 \alpha_1 \theta_p \delta \omega}{\theta_p [\delta - \alpha_0(t)] + \alpha_1 \omega}} \right] - \frac{\alpha'_0(t)^2}{4 \alpha_1} \left[ 1 - \frac{2 \theta_p^2 \delta \omega}{\theta_p [\delta - \alpha_0(t)] + \alpha_1 \omega} \right]
\]

And hence the desired stock level \( F^*(t) \) peaks at the same time as the cyclical biological growth function as \( \frac{dF^*(t)}{dt} = 0 \) if and only if \( \alpha'_0(t) = 0 \).

The optimal non-zero harvest rate (when the system is not in a corner solution due to the non-negativity of the harvest rate) is

\[
h(t) = g(F^*(t)) - \frac{dF^*(t)}{dt} = [\alpha_0(t) + \alpha_1 F^*(t)] F^*(t) - \frac{dF^*(t)}{dt}
\]

and hence

\[
h'(t) = \alpha'_0(t) F^*(t) + [\alpha_0(t) + 2 \alpha_1 F^*(t)] \frac{dF^*(t)}{dt} - \frac{d^2 F^*(t)}{dt^2}
\]

If the biological growth function peaks we have \( \alpha'(t) = \frac{dF^*(t)}{dt} = 0 \) and hence \( h'(t) = -\frac{d^2 F^*(t)}{dt^2} > 0 \), i.e., the optimal harvest rate is still increasing.

On the other hand, if the biological growth rate is at its minimum, we again have \( \alpha'(t) = \frac{dF^*(t)}{dt} = 0 \), but the sinus function is now in the convex portion and \( h'(t) = -\frac{d^2 F^*(t)}{dt^2} < 0 \), i.e., the optimal harvest rate is still decreasing (assuming it is not a corner solution at zero to begin with).
Proof of Proposition 7 The optimal stock level in the multi-species system is given by

\[-2\alpha_{13}p_3 \tilde{\theta}_3 F_3^2 + \left[ \theta_1 p_1 (\delta - \alpha_{i0}) + \omega \left[ \frac{\alpha_1 + \alpha_2 \tilde{\theta}_1}{\theta_1} + \frac{\alpha_3 \tilde{\theta}_3}{\theta_3} \right] - \frac{\delta_1}{\theta_1} \right] F_1 - \delta \omega = 0\]

\[-2\alpha_{22}p_2 \tilde{\theta}_2 F_2^2 + \left[ \theta_2 p_2 (\delta - \alpha_{i0}) + \omega \left[ \frac{\alpha_2 + \alpha_3 \tilde{\theta}_1}{\theta_1} + \frac{\alpha_3 \tilde{\theta}_3}{\theta_3} \right] - \frac{\delta_2}{\theta_2} \right] F_2 - \delta \omega = 0\]

\[-2\alpha_{33}p_3 \tilde{\theta}_3 F_3^2 + \left[ \theta_3 p_3 (\delta - \alpha_{i0}) + \omega \left[ \frac{\alpha_3 + \alpha_1 \tilde{\theta}_1}{\theta_1} + \frac{\alpha_1 \tilde{\theta}_1}{\theta_2} \right] - \frac{\delta_3}{\theta_3} \right] F_3 - \delta \omega = 0\]

The Hamiltonian for the multi-species model is

\[H = \sum_{i=1}^{3} \left( p_i h_i(t) - \frac{\omega}{\theta_i} h_i(t) \right) + \mu_i(t) \left\{ [\alpha_{i0} + \alpha_{i1} F_1(t) + \alpha_{i2} F_2(t) + \alpha_{i3} F_3(t)] F_i(t) - h_i(t) \right\} \]

\[= \sum_{i=1}^{3} \left[ p_i - \frac{\omega}{\theta_i} F_i(t) - \mu_i(t) \right] h_i(t) + \mu_i(t) [\alpha_{i0} + \alpha_{i1} F_1(t) + \alpha_{i2} F_2(t) + \alpha_{i3} F_3(t)] F_i(t) \]

The necessary conditions for \( h_i(t) \) implies that

\[h_i(t) = \begin{cases} 0, & \text{if } p_i - \frac{\omega}{\theta_i} F_i(t) - \mu_i(t) < 0 \\ h_{i,max}, & \text{if } p_i - \frac{\omega}{\theta_i} F_i(t) - \mu_i(t) > 0 \\ \text{see below}, & \text{if } p_i - \frac{\omega}{\theta_i} F_i(t) - \mu_i(t) = 0 \end{cases} \]

Hence there are two border conditions. In the following consider the case where \( p_i - \frac{\omega}{\theta_i} F_i(t) - \mu_i(t) = 0 \), which implies that \( \dot{\mu}_i(t) = \frac{\omega}{\theta_i F_i(t)} \).

Differentiating the Hamiltonian with respect to the state variables \( F_i(t) \) gives

\[H_1 = \frac{\omega h_1(t)}{\theta_1 F_1(t)^2} + \mu_1(t) [\alpha_{i0} + 2\alpha_{i1} F_1(t) + \alpha_{i2} F_2(t) + \alpha_{i3} F_3(t)] + \alpha_{i1} \mu_2(t) F_2(t) + \alpha_{i3} \mu_3(t) F_3(t) \]

\[= \delta \mu_1(t) - \dot{\mu}_1(t) \]

\[H_2 = \frac{\omega h_2(t)}{\theta_2 F_2(t)^2} + \mu_2(t) [\alpha_{i0} + \alpha_{i1} F_1(t) + 2\alpha_{i2} F_2(t) + \alpha_{i3} F_3(t)] + \alpha_{i2} \mu_1(t) F_1(t) + \alpha_{i3} \mu_3(t) F_3(t) \]

\[= \delta \mu_2(t) - \dot{\mu}_2(t) \]

\[H_3 = \frac{\omega h_3(t)}{\theta_3 F_3(t)^2} + \mu_3(t) [\alpha_{i0} + \alpha_{i1} F_1(t) + \alpha_{i2} F_2(t) + 2\alpha_{i3} F_3(t)] + \alpha_{i3} \mu_1(t) F_1(t) + \alpha_{i2} \mu_2(t) F_2(t) \]

\[= \delta \mu_3(t) - \dot{\mu}_3(t) \]

Substituting the expression for \( \mu_i(t) \) and \( \dot{\mu}_i(t) \) in the first equation

\[\delta \frac{p_1 \theta_1 F_1 - \omega}{\theta_1 F_1^2} - \frac{\omega}{\theta_1 F_1^2} \dot{F}_1 = \frac{\omega h_1(t)}{\theta_1 F_1^2} + \frac{p_1 \theta_1 F_1 - \omega}{\theta_1 F_1^2} [\alpha_{i0} + 2\alpha_{i1} F_1 + \alpha_{i2} F_2 + \alpha_{i3} F_3] \]

\[+ \alpha_{i2} \frac{p_2 \theta_2 F_2 - \omega}{\theta_2 F_2} F_2 + \alpha_{i3} \frac{p_3 \theta_3 F_3 - \omega}{\theta_3 F_3} F_3 \]
Which yields after multiplying through by $\theta_1 F_1$

$$\delta [p_1 \theta_1 F_1 - \omega] = \omega \left( \frac{\dot{F}_1 + h_1(t)}{F_1} + [p_1 \theta_1 F_1 - \omega] \left[ \alpha_{10} + 2\alpha_{11} F_1 + \alpha_{12} F_2 + \alpha_{13} F_3 \right] \right)$$

$$+ \alpha_{21} \frac{\theta_1}{\theta_2} [p_2 \theta_2 F_2 - \omega] F_1 + \alpha_{31} \frac{\theta_1}{\theta_3} [p_3 \theta_3 F_3 - \omega] F_1$$

Using the definition of $\dot{F}_1$

$$\delta [p_1 \theta_1 F_1 - \omega] = \omega \left[ \frac{\alpha_{10} + \alpha_{11} F_1 + \alpha_{12} F_2 + \alpha_{13} F_3}{F_1} + [p_1 \theta_1 F_1 - \omega] \left[ \alpha_{10} + 2\alpha_{11} F_1 + \alpha_{12} F_2 + \alpha_{13} F_3 \right] \right]$$

$$+ \alpha_{21} \frac{\theta_1}{\theta_2} [p_2 \theta_2 F_2 - \omega] F_1 + \alpha_{31} \frac{\theta_1}{\theta_3} [p_3 \theta_3 F_3 - \omega] F_1$$

$$= p_1 \theta_1 F_1 [\alpha_{10} + 2\alpha_{11} F_1 + \alpha_{12} F_2 + \alpha_{13} F_3] - \omega \alpha_{11} F_1 + \alpha_{21} \frac{\theta_1}{\theta_2} [p_2 \theta_2 F_2 - \omega] F_1$$

$$+ \alpha_{31} \frac{\theta_1}{\theta_3} [p_3 \theta_3 F_3 - \omega] F_1$$

Which implies that

$$0 = -2\alpha_{11} p_1 \theta_1 F_1^2 + \left( \theta_1 p_1 [\delta - \alpha_{10}] + \omega \left[ \alpha_{11} + \alpha_{21} \frac{\theta_1}{\theta_2} + \alpha_{31} \frac{\theta_1}{\theta_3} \right] \right) F_1 - \delta\omega$$

$$- \theta_1 \left[ \alpha_{12} p_1 + \alpha_{21} p_2 \right] F_1 F_2 - \theta_1 \left[ \alpha_{13} p_1 + \alpha_{31} p_3 \right] F_1 F_3$$

Similar transformations for $H_2$ and $H_3$ give

$$0 = -2\alpha_{22} p_2 \theta_2 F_2^2 + \left( \theta_2 p_2 [\delta - \alpha_{20}] + \omega \left[ \alpha_{22} + \alpha_{12} \frac{\theta_2}{\theta_1} + \alpha_{32} \frac{\theta_2}{\theta_3} \right] \right) F_2 - \delta\omega$$

$$- \theta_2 \left[ \alpha_{21} p_1 + \alpha_{12} p_2 \right] F_1 F_2 - \theta_2 \left[ \alpha_{23} p_2 + \alpha_{32} p_3 \right] F_2 F_3$$

$$0 = -2\alpha_{33} p_3 \theta_3 F_3^2 + \left( \theta_3 p_3 [\delta - \alpha_{30}] + \omega \left[ \alpha_{33} + \alpha_{23} \frac{\theta_3}{\theta_2} + \alpha_{13} \frac{\theta_3}{\theta_1} \right] \right) F_3 - \delta\omega$$

$$- \theta_3 \left[ \alpha_{32} p_2 + \alpha_{23} p_3 \right] F_2 F_3 - \theta_3 \left[ \alpha_{31} p_3 + \alpha_{13} p_1 \right] F_1 F_3$$

The last three equation specify the three unknown $F_1, F_2, F_3$. 

\[ \square \]