An Application of the Z-Transform in Extracting the Density Regulation from the Periodic Output of an Age-Structured Population Model

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Abstract- The application of the Z-transform, a manipulation tool from the discrete signal processing (DSP) toolbox, on an ecological model was motivated by the mathematical similarities between an age-structured fish population model with a non linear density regulation and a linear time invariant (LTI) control system. Both models include a switching mechanism in regulating stock/signal throughput in accordance with a given density limitation/set value and both models can be expressed in terms of a negative feedback loop difference equations (Getz & Haight, 1989; Åström & Murray, 2008). In the fish model, the switching mechanism is a density regulated stock-recruitment (SR) function which models the strategies implemented by the population in keeping the vulnerable egg-larvae-juvenile densities within an environmental limitation thereof (Subbey et al., 2014). A switching mechanism is also present in control engineering, for example, in the mechanism associated with cruise control in cars which keeps traveling speed close to a chosen set value amidst varying weather and road conditions (Antsaklis and Gao, 2005). In both cases, the choosing of the control action and the tuning of its parameters requires careful consideration to avoid failures such as incorrectly timed switching actions in a control plant (see Kuphaldt (2019)) and errors in estimating total allowable catch (TAC) in the fishing industry (see Borlestan et al. (2015), Skagen et al. (2013) and Taboada and R. Anadn (2016)). The Z-transform has proven itself useful in tuning LTI control models for a desired control action (see Orfanidis, (2010) and Smith, (1999)) and it is on this account that its application was extended to the ecological model in pursuit of a more efficient way of estimating SR parameters to simulate an already existing output. It was however found that it could not be used for parameter tuning but rather for the extraction of the SR component hidden in the output together with components resulting from the age structure itself. Such an extraction can greatly assist in the mathematical identification of the SR, reducing the complexity of its choosing as there are many different types used in the fishing industry such as the classic Beverton-Holt model, the Ricker model and Shepherd model (Myers, 2001; Iles, 1994; Shepherd, 1982). It can also be used to monitor changes in the SR over time which can indicate the presence of strategy evolution (Apaloo et al., 2009; Brännström et al., 2013). In 1998 Schoombie and Getz investigated the latter by subjecting the Shepherd SR to strategy optimization with regards to a parameter associated with population interventions in regulating recruitment throughput and it is because of this versatility that the Shepherd SR is chosen for the intended extraction. In true control style, Simulink, a graphic environment for designing control simulations, is used to visualize the production of the output as well as the extraction of the SR from it. This paper showcases the versatility of the Z transform and the possibilities and unexpected finds when applied to similar systems designed to regulate signals or, in this case, recruitment densities.

Keywords- Age-structure, Stock-recruitment, Z-transform, Shepherd function, Simulink

I. INTRODUCTION

In control engineering, a subfield of DSP, a controller or regulator measures the error between a deterministic system’s output $y$ and a given set value $K$ upon which it relays a correction response $x$ back to the system for the assembly of the next output with value closer to the desired set value $[1, 8]$. This behavior is similar to that of an SR mechanism at the recruitment level of an age-structured marine fish population. The SR, indicated as $\psi$, weighs the parental stock biomass $y$ against its
environmental limitation \( K \) upon which the throughput of the implicated egg-larvae-juvenile population to the recruitment population \( x \) is adjusted before being propagated through the age-structure for the assembly of the next generation of parental stock [17]. In both models the output is relayed back to the system, a process referred to as negative feedback which aims to stabilize processes by lessening the difference between a measured variable and its desired value [13].

Determining a suitable control action (cause) in a control model is based on a desired outcome (effect), for example, a simple bang-bang control is chosen to switch very basic water heaters on/off when temperatures are lower/higher than the set value. Another example is proportional integral (PI) control which can be found in cruise control where the controller output \( x \) adjusts the throttle in proportion to the magnitude of the error measured between the set value \( K \) and the current speed \( y \). From Kuphaltdt (2019) and Aström and Murray (2008) a very basic definition of control is

\[
x = w(K - y) + r
\]

Here \( w \) is the proportional gain affecting the intensity of the correction action and \( r \) is the bias or constant response when the error \( K - y \) is zero. The parameter \( w \) can be tuned to suit a variety of applications.

In the ecological model on the other hand, the SR (cause) is chosen to simulate existing data tendencies (effect) and is not chosen with intent as is the case in the control model [25]. The Ricker SR function (developed in 1954 for fisheries), for example, models a dome shaped relationship (observed for sockeye salmon) where a rapid increase in \( x \) was observed at low densities of \( y \), reaching a maximum or saturation at a \( y \approx K \) after which there was a fast decline in \( x \) [19, 20]. The 2 parameter (referring to \( r \) and \( K \)) Ricker model shares characteristics with bang-bang control and is expressed as

\[
x = \psi_r y
\]

where \( \psi_r = e^{r(1 - \frac{y}{K})} \)

In the above, \( e^r \) is the intrinsic growth rate which is the maximum growth rate this population can experience when \( y \) densities are very low and is measured in recruits per unit biomass. In a study conducted by Borlestad et al (2015) on an alga population it was found that the population studied adapted their density regulation when resources were limited. The cause of the observed effect was matched to the theta-Ricker model

\[
\psi_{TR} = e^{r(1 - \left(\frac{y}{K}\right)^w)}
\]

which has a third parameter \( w \) allowing increased shape fitting flexibility (tuning) in matching the variation in density curves in the different control groups. To include more diversity in fisheries, Shepherd (1982) developed an \( S \) or sigmoid shaped SR model (North Sea herring) showing a slow increase in \( x \) at low densities of \( y \), becoming more rapid as \( y \) increases, reaching saturation at \( y \approx K \) after which \( x \) remains saturation bound either asymptotically or oscillatory. This model also contains \( w \) which models a variety of egg-larvae-juvenile saturation responses which can be ascribed to changes in endogenous processes (a change in drift route, predation, cannibalism, competition for resources) and give rise to the observed variations (see Canales et al (2020), Hutchings (2013), Myers (2001) and Subbey et al (2014) for extensive discussions). It is on this account that Schoenbie and Getz (1998) in the non age-structured model perceived \( w \) in the Shepherd SR as an evolving strategy. It was envisioned that a population, through small mutations in endogenous processes, will evolve to a \( w \)-density pattern securing invasion immunity from more such adaptations/mutations. Such an optimal strategy was termed evolutionary stable (ESS) and represented an evolutionary halt in the ability to better occupy a resource capped space [3, 6]. The Shepherd SR function shares characteristics with PI control and is expressed as the three parameter model

\[
x = \frac{r}{1 + \left(\frac{y}{K}\right)^w}
\]

where \( \psi_s = \frac{r}{1 + \left(\frac{y}{K}\right)^w} \)

Here \( r \) represents the intrinsic growth rate. The model with \( w = 1 \) is the classic 2 parameter Beverton-Holt model introduced in the context of fisheries in 1957 by Beverton and Holt.

A typical demonstration of model fitting using recorded scientific data can be found in Taboada and R. Anadn (2016) where abundance estimates for European anchovy for the period 1987 to 2011 as logged in ICES (2012) was used to populate an age-structured model. Parameters were estimated under a Bayesian framework for a variety of nonlinear, age-structured population models, each containing a combination of mechanisms including self regulation and harvesting hypothesized to be responsible for the observed population outcome. In this model, the 3 parameter DerisoSchmunte SR was matched to the data and is defined as

\[
\psi_{DS} = r \left(1 + \frac{y}{K}\right)^w
\]

The case \( w = -1 \) is again the classic Beverton-Holt model. Each model was initiated with randomly selected initial values and parameter estimates and involved multiple iterations until one could be identified as true to documented data within an acceptable margin of error. It is at this point noteworthy that the output data, which contains information/frequencies induced by both the SR and the age-structure, is not directly used, only matched. The inclusion of additional flexibility in an SR increases its application range but it adds to the already complicated logistics of fitting parameters to other endogenous processes included in the model construction [23]. If the existing data can be used to reverse engineer the SR, it would alleviate some of the logistics but this will only
II. Model construction

Borrowing from Getz and Haight (1989), the age-structured population model with \( m \) distinct age groups is constructed with the SR at time \( n-1 \) placed at the recruitment level, acting as a density regulated survival rate of the stock \( y(n-1) \) (eggs spawned from all the individual adult age groups \( y_k(n-1), k = 1, \ldots, m \)). The survivors of the density regulation, also referred to as the recruitment population \( x(n-1) = \psi(n-1)y(n-1) \), are then further exposed to a non density regulated survival rate \( s_k \) before being propagated to the first adult (spawning) age group \( y_i \) at time \( n \) which is modeled as

\[
y_i(n) = s_i x(n-1)
\]

(2)

The remaining \( m-1 \) age groups are generated from (2) in a linear fashion by assuming constant survival rates \( s = \{s_k\}, k = 0, \ldots, m-1 \) where \( s_k \) models the transition from age group \( k \) to \( k+1 \) as

\[
y_k(n) = s_{k-1} y_{k-1}(n-1) \quad k = 2, \ldots, m
\]

(3)

The next generation of stock \( y(n) \) is then compiled from the spawning contribution from each of the individual \( y_k \) as

\[
y(n) = \sum_{k=1}^{m} b_k y_k(n)
\]

(4)

where \( b = \{b_k\}, k = 1, \ldots, m \) are constant stock replacement rates.

Recursions of (3), ending in (2), lead to expressing each adult age group \( y_k \) in terms of the recruitment population it generated from as

\[
y_k(n) = \left( \prod_{i=0}^{k-1} s_i \right) x(n-k) \quad k = 1, \ldots, m
\]

(5)

Combining (4) and (5), the next generation of stock \( y(n) \) is expressed in terms of previous recruitment generations as

\[
y(n) = \sum_{k=1}^{m} A_k x(n-k)
\]

(6)

with \( A_k = b_k \left( \prod_{i=0}^{k-1} s_i \right) \quad k = 1, \ldots, m \)

As all entries of the age-structure defining parameters \( A = \{A_k\} \) are constant, the relationship between stock and recruitment in (6) is linear as well as time invariant (LTI) making it mathematically suitable for the application of the Z-transform [18]. In a control system, the coefficients of \( x(n) \) represent the independent gain or input imposed on the natural feedback system (from sensors placed at strategic positions in the model) defined by the coefficients of the output \( y(n) \) and, for physically realizable control systems, the latter amount of coefficients should be in the majority as degenerative negative feedback from the output improves stability and reduces the effects of the gain, also known as BIBO stability (bounded input - bounded output) [13, 25]. In the ecological model (6) however, the coefficient of \( y(n) \) is in the minority. Conforming to a physically realizable control model, the roles of \( x(n) \) and \( y(n) \) in (6) must therefore be switched, an action not supported in the ecological space but can be realized in the Z-space through the application of the Z-transform.

III. From Ecology to Signal Processing

The materials required in generating a population output to serve as the input of the intended extraction formula is an age-structured model (6) with a known SR and age-specific survival and replacement rates (hypothetical parameters will be chosen). The methodology is to recurse the population model over several time units until a periodic equilibrium population output is achieved. The Z transform, a discrete-time equivalent of the Laplace transform, will be used to convert the age-structured cause and effect model into an effect and cause model in the Z-domain. The Z-domain is suited to the algebraic manipulation of the expression which consists largely of partial fraction decomposition, after which the inverse Z-transform will reveal the effect and cause model in the ecological domain, enabling the extraction of the SR [18, 25]. The extraction formula will then be applied to the periodic equilibrium outputs of three hypothetical models, extracting the SR in each case. The extractions will be compared to the true SR from which the accuracy of the formula can be determined. Setting the stage (and suited to a Simulink demonstration), the following two-age-group population model is chosen:

| Model number | I |
|--------------|---|
| age groups   | \( m = 2 \) |
| initial stock densities | \( y(0) = 0.2, y(1) = 0.2 \) |
| age group parameters | \( \hat{A} = [0.4 \ 0.56] \) |
| equation (6) | \( y(n) = 0.4 x(n-1) + 0.56 x(n-2) \) |
| SR relationship | \( \psi(n) = \frac{r}{1 + \left( \frac{x(n)}{K} \right)^w} \) |
| intrinsic growth rate | \( r = 1.75 \) |
| scaled density limitation | \( K = 1 \) |
| intensity parameter | \( w = 8.6178 \) |

The Simulink diagram for model I is captured in subsystem B of Fig.1. The initial conditions \( y(0) \) and \( y(1) \) serve as initiators of the feedback loop after which the output \( y(n) \) will sustain the system. The shaded block in this diagram is subsystem A with detailed diagram shown in Fig.2. Starting the time clock at \( n = 2 \), subsystem A crafts the SR output \( x(n-2) = x(0) \) and \( x(n-1) = x(1) \) from \( y(0) \) and \( y(1) \) which is then exported to subsystem B where the delay blocks \( z^{-2} \) and \( z^{-1} \) keep them in time order \( z^{-2} : x(0) \) and \( z^{-1} : x(1) \). They
are then amplified through the triangular gain blocks to amplitudes \(A_1 = 0.4\) and \(A_2 = 0.56\) respectively and added through the summation block to produce \(y(2)\) after which \(y(2)\) flows back (negative feedback) into subsystem A for the calculation of \(x(2)\) and the process repeats. The \(\psi(n)\) and \(y(n)\) output of subsystem B can be viewed in Fig.3. After several recursions, the stock output of model I reaches the period 3 equilibrium:

\[
\bar{y} = [0.7520\ 1.1229\ 0.8903]
\]

A. The Z-transform properties

There is an abundance of literature on the properties and uses of the Z-transform in DSP. The next two subsections will however be grounded in the versions of Orfanidis (2010) and Smith (1999).

For an infinite real or complex input signal \(x(n) = \{\ldots, x(-1), x(0), x(1), \ldots\}\), the Z-transform is defined as the infinite summation

\[
Z\{x(n)\} = \sum_{k=-\infty}^{\infty} x(k)z^{-k}
= \ldots + x(-1)z + x(0) + x(1)z^{-1} + \ldots
= X(z)
\]

The properties and definitions of the Z-transform required in the derivation of the extraction formula are:

1) The inverse Z-transform is the operation \(Z^{-1}\) where

\[
Z^{-1}\{X(z)\} = Z^{-1}\{Z\{x(n)\}\} = x(n)
\]

2) The Z-transform is termed causal if the summation range is limited to \(k \geq 0\) and anti-causal if the range is limited to \(k < 0\).

3) The function \(u(n)\) is the unit function where \(u(n) = 1, n \geq 0\) and \(u(n) = 0, n < 0\).

4) The region of convergence (ROC) is the region in the complex z-plain for which the Z-transform summation converges. As a series, the ROC comprises all \(z\) such that \(|z| > 0\), but in cases where the infinite series can be expressed in closed form, the ROC is the z-domain defined by this process. The closed forms used in this derivation are

- The causal case \(Z\{x(n)\} = p^n u(n)\) defined for \(|p| < 1\)

\[
Z\{p^n u(n)\} = 1 + pz^{-1} + (pz^{-1})^2 + \ldots
= \frac{1}{1 - pz^{-1}}
\]

or \(\frac{z}{z - p}\)

provided that \(|pz^{-1}| < 1\) or rather \(|z| > |p|\) which defines the ROC in this case.

- The anti-causal case defined for \(x(n) = -p^n u(-n - 1)\) defined for \(|p| > 1\)

\[
Z\{-p^n u(-n - 1)\} = -p^{-1}z - (p^{-1}z)^2 - \ldots
= \frac{1}{1 - pz^{-1}}
\]

or \(\frac{z}{z - p}\)

provided that \(|p^{-1}z| < 1\) defining the ROC as \(|z| < |p|\). The ROC ensures a unique transform allocation as the closed forms above are otherwise the same.

5) BIBO stability (the consequence of negative feedback in both the control model and ecological model) requires absolute convergence in the real space which is why, when transforming \(\frac{x}{z-p}\) back in both the control model and ecological model requires absolute convergence in the real space, \(p \neq 1, p < 1\) is interpreted as having a causal response,

\[
Z^{-1}\left[\frac{z}{z-p}\right] = p^n u(n) \quad \text{if} \quad |p| < 1 \quad (7)
\]

and \(p > 1\) as having an anti-causal response,

\[
Z^{-1}\left[\frac{z}{z-p}\right] = -p^n u(-n - 1) \quad \text{if} \quad |p| > 1 \quad (8)
\]

In the context of (7) and (8), \(p\) is referred to as a pole.

6) The shift theorems required are

\[
Z\{x(n-k)\} = z^{-k}X(z)
\]

\[
Z\{x(n+k)\} = z^kX(z) - \sum_{i=0}^{k-1} z^{k-i}x(i) \quad (9)
\]

where the \(x(i), i = 0, \ldots, k-1\) are the initial values of \(x(n)\). For the ecological model (6), \(x(i), i = 0, \ldots, k-1\) represent the initial densities of the recruitment population which is assumed to be negligible in comparison to the eventual output and can therefore be omitted from (9) reducing this expression to

\[
Z\{x(n+k)\} = z^kX(z) \quad (10)
\]

B. The effect and cause transfer function

The application of the Z-transform and its properties to (6) will result in a mathematical equation suited to an effect and cause view compatible with BIBO stability as well as the extraction of \(\psi\). The steps are:

1) Apply the causal Z-transform and shift theorems to (6):

\[
Z\{y(n)\} = \sum_{k=1}^{m} A_kZ\{x(n-k)\}
\]

\[
Y(z) = \sum_{k=1}^{m} A_k z^{-k}X(z)
= \left(\sum_{k=1}^{m} A_k \frac{z^{-k}}{z^m}\right)X(z)
= G(z)X(z), \quad (11)
\]
Subsystem B models the recursion equation of model I with \( m = 2, r = 1.75, w = 8.618, A_1 = 0.4 \) and \( A_2 = 0.56 \). Subsystem A crafts the corresponding recruitment population \( x(n) \) from the stock feedback \( y(n) \). Subsystem B’s output is the next generation of stock \( y(n) \) and relays the true representation of \( \psi(n) \) from its construction in subsystem A.

Subsystem A crafts the recruitment population \( x(n) \) from the feedback stock \( y(n) \) and the density regulation \( \psi(n) \). Subsystem A’s output, \( x(n) \) and \( \psi(n) \), is subsystem B’s input.

The Simulink scope representation of subsystem B’s output, comparing the density output \( y(n) \) and the true \( \psi(n) \) as a function of time \( n \).

\[
G(z) = \sum_{k=1}^{m} A_k z^{m-k} \]

is the transfer function supporting the cause and effect action in the Z-space. The effect and cause version will require presenting \( X(z) \) in (11) as the subject of the equation:

\[
X(z) = \frac{1}{G(z)} Y(z)
\]
\[ G^{-1}(z) = \sum_{k=1}^{m} z^{m-k} A_k \]  
(13)

2) If \( A_1 \) is the first non-zero term in \( \tilde{A} \), the \( m - 1 \) degree polynomial in the denominator of (13) can be expressed in terms of its \( m - 1 \) poles \( p_k \) as

\[ G^{-1}(z) = \frac{z^m}{A_1 \prod_{k=1}^{m-1} (z - p_k)} = \frac{z^m}{A_1 \left( \prod_{k=1}^{m-1} (z - p_k) \right)} \]  
(14)

When there is more than one pole, the ROC is defined as follows:

- in the causal case, as the region \( P \) defined by the pole with maximum magnitude \( |z| > |p_{\text{max}}| \) and

- in the anti-causal case, as the region \( Q \) defined by the pole with minimum magnitude \( |z| < |p_{\text{min}}| \).

- in the mixed case, it is defined as the region defined by the doughnut shaped intercept \( P \cap Q \).

The unit circle is always included in the ROC.

3) Continuing from (14), partial fractions is applied to

\[ \prod_{k=1}^{m-1} (z - p_k) \]

resulting in \( m - 1 \) individual terms

\[ G^{-1}(z) = \sum_{k=1}^{m-1} \frac{D_k}{z - p_k} \]  
(15)

where \( D_k, k = 1, \ldots, m - 1 \) are the partial fraction constants.

In preparation of taking the inverse Z-transform using (7) and (8), \( z^m \) is expressed as \( z^{m-1}z \) leading to

\[ G^{-1}(z) = \frac{z^{m-1}}{A_1} \sum_{k=1}^{m-1} \frac{D_k}{z - p_k} \]  
(16)

In realizing BIBO stability, these terms will transform back to the physical space as either \( p_k^n u(n) \) or \( -p_k^{-n} u(-n - 1) \) depending on the magnitudes of \( p_k \).

C. Extracting \( \psi \) from the output

In demonstrating the extraction of \( \psi \) from (6), a hypothetical model with \( m \) age groups, period \( T = 3 \) output and \( A_1 \neq 0 \) will be assumed. The extraction formula in terms of a general period \( T \) and in terms of the first non zero entry \( A_u \) of \( \tilde{A} \) will be formulated thereafter. The steps are:

1) Return to (12) and use expression (15) for \( G^{-1} \)

\[ A_1z^{-m+1}X(z) = \sum_{k=1}^{m-1} \frac{D_k}{z - p_k} Y(z) \]

where \( D_k = \frac{1}{\prod_{i \neq k} (p_k - p_i)} \) \( k = 1, \ldots, m - 1 \ m > 2 \)

For models with \( m = 2 \), no partial fractions are required and \( D_1 = 1 \).

2) Separate the causal (C) poles from the anti-causal (AC) poles in the above summation by labeling \( |p_k| > 1, k = 1, \ldots v \) and \( |p_k| < 1, k = v + 1, \ldots m - 1 \) which results in the two summations

\[ A_1z^{-m+1}X(z) = AC + C \]

\[ AC = \left( \sum_{k=1}^{v} D_k \frac{z}{z - p_k} \right) Y(z) \]

\[ C = \left( \sum_{k=v+1}^{m-1} D_k \frac{z}{z - p_k} \right) Y(z) \]  
(17)

3) Expanding \( AC \) according to (8),

\[ AC = \sum_{k=1}^{v} D_k \frac{z}{z - p_k} Y(z) \]

\[ = -\sum_{k=1}^{v} D_k \left( p_k^{-1}z + p_k^{-2}z^2 + \ldots \right) Y(z) \]

\[ = -\sum_{k=1}^{v} D_k \left( p_k^{-1}zY(z) + p_k^{-2}z^2Y(z) + \ldots \right) \]

Taking the inverse Z-transform of \( AC \) and applying the shift theorems (10),

\[ Z^{-1}\{AC\} \]

\[ = -\sum_{k=1}^{v} D_k \left( p_k^{-1}y(n+1) + p_k^{-2}y(n+2) + \ldots \right) \]  
(18)

A period 3 equilibrium of (17) will reduce the right hand side to three terms,

\[ Z^{-1}\{AC\} \]

\[ = -\sum_{k=1}^{v} D_k \left( B_1y(n+1) + B_2y(n+2) + B_3y(n+3) \right) \]

where

\[ B_1 = p_k^{-1} \left( 1 + p_k^{-3} + p_k^{-6} + \ldots \right) \]

\[ = p_k^{-1} \frac{1}{1 - p_k^{-3}} \]

\[ = \frac{p_k^2}{1 - p_k} \]
Similarly,

\[ B_2 = -\frac{p_k}{1 - p_k^3} \quad \text{and} \quad B_3 = -\frac{1}{1 - p_k^3} \]

4) Expanding \( C \) according to (7),

\[
C = \sum_{k=v+1}^{m-1} D_k \frac{z}{z-p_k} Y(z)
\]

\[ = \sum_{k=v+1}^{m-1} D_k \left(1 + p_k z^{-1} + p_k^2 z^{-2} + \ldots\right) Y(z)
\]

\[ = \sum_{k=v+1}^{m-1} D_k \left( Y(z) + p_k z^{-1} Y(z) + p_k^2 z^{-2} Y(z) + \ldots\right)
\]

Taking the inverse Z-transform and enforcing a period 3 equilibrium,

\[ Z^{-1}\{C\} = \sum_{k=v+1}^{m-1} D_k (y(n) + p_k y(n-1) + p_k^2 y(n-2) + \ldots)
\]

\[ = \sum_{k=v+1}^{m-1} D_k (B_4 y(n) + B_5 y(n-1) + B_6 y(n-2))
\]

(19)

where

\[ B_4 = \left(1 + p_k^3 + p_k^6 + \ldots\right)
\]

\[ = \frac{1}{1 - p_k^3}
\]

Similarly,

\[ B_5 = \frac{p_k}{1 - p_k^3} \quad \text{and} \quad B_6 = \frac{p_k^2}{1 - p_k^3}
\]

5) The inverse Z-transform of the left hand side of (16) is

\[ Z^{-1}\{A_1 z^{-m+1} X(z)\} = A_1 x(n - m + 1) \]

6) The inverse Z-transform of (16) is then

\[ A_1 x(n - m + 1) = \sum_{k=1}^{v} D_k \frac{p_k^3 y(n+1) + p_k y(n+2) + y(n+3)}{1 - p_k^3} + \]

\[ + \sum_{k=v+1}^{m-1} D_k \left(y(n) + p_k y(n-1) + p_k^2 y(n-2)\right)
\]

Enforcing \( T = 3 \), \( y(n+3) = y(n), y(n+1) = y(n+2) \) and \( y(n-1) = y(n+1) \) leading to

\[ A_1 x(n - m + 1) = \sum_{k=1}^{v} D_k \frac{p_k^3 y(n+1) + p_k^2 y(n+2) + y(n+3)}{1 - p_k^3} + \]

\[ + \sum_{k=v+1}^{m-1} D_k \left(y(n+3) + p_k y(n+2) + p_k^2 y(n+1)\right)
\]

As the expressions inside the two summations are the same irrelevant of the magnitude of \( p \), they can be combined into a single summation,

\[ A_1 x(n - m + 1) = \sum_{k=1}^{m-a} D_k \frac{\psi(n+3) + p_k y(n+2) + p_k^2 y(n+1)}{1 - p_k^3}
\]

\[ = \sum_{k=1}^{m-a} D_k \frac{3}{1 - p_k^3} (p_k)^{3-i} y(n + i)
\]

7) In general, for a period \( T \) with \( A_1 \) the first non zero term:

\[ A_1 x(n - m + 1) = \sum_{k=1}^{m-a} D_k \frac{T}{1 - p_k^T} \sum_{i=1}^{T} (p_k)^{T-i} y(n + i)
\]

If \( A_k \) is the first non zero term of \( \tilde{A} \), the summation in equation (6) will initiate at \( k = a \) and there will be \( m - a \) roots which will change the summation upper limit of equation (15) to \( m - a \). The general formula expressing the recruitment densities in terms of stock densities with a finite period \( T \) and first non zero model parameter \( A_a \) is given by

\[ A_a x(n - m + 1) = \sum_{k=1}^{m-a} D_k \frac{T}{1 - p_k^T} \sum_{i=1}^{T} (p_k)^{T-i} y(n + m - 1 + i)
\]

(20)

8) The formula that extracts \( \psi(n) \) from \( x(n) = \psi(n)y(n) \) in (20) is then

\[ \psi(n) = \frac{1}{A_a y(n)} \sum_{k=1}^{m-a} D_k \frac{T}{1 - p_k^T} \sum_{i=1}^{T} (p_k)^{T-i} y(n + m - 1 + i)
\]

(21)

The ROC is the region bounded by the largest causal pole and the smallest anti-causal pole. Formula (21) requires stock data in the present and future which can be changed to present vs past by replacing \( n \) in \( y(n + m - 1 + i) \) with its periodic equivalent \( n - hT \) where \( h = 1, 2, \ldots \). Formula (21) holds for all finite \( T \) and \( m \). In quasi-periodic cases where \( T \) is sufficiently large but can be defined as finite within a boundary of tolerance, if all poles lie within the unit circle as \( |p_k|^T \approx 0 \) for all \( k \). In pure causal events, large \( T \) values will reduce (21) to the quasi-causal approximation

\[ \psi(n) \approx \frac{1}{A_a y(n)} \sum_{k=1}^{m-c} D_k \frac{T}{1 - p_k^T} \sum_{i=1}^{T} (p_k)^{T-i} y(n + m - 1 + i)
\]

(22)
IV. RESULTS AND DISCUSSION

Returning to the Simulink model I, this section will demonstrate how (21) is used to extract $\psi(n)$ from the output $y(n)$ of subsystem B and population parameters $\bar{A}$. After the extraction, the true form of $\psi(n)$ from subsystem A will be compared to that of the extraction model (21) for comparison. The extraction equation will be applied to another two hypothetical models, model II with $T = 4$ and $m = 6$ and model III with $T =$ quasi-causal and $m = 6$. For model I,

| Model number | $I$ |
|--------------|-----|
| age groups   | $m = 2$ |
| age group parameters $\bar{A}$ | $[0.4 \ 0.56]$ |
| $T$ = stock output $\bar{y}$ | $[0.7520 \ 1.1229 \ 0.8903]$ |

The single pole calculated from $0.4z + 0.56$ is $p = -1.4$ with anti causal ROC $|z| < 1.4$. No partial fractions are required in this case with $D_1 = 1$ which reduces formula (21) to

$$
\psi(n) = \frac{p^2y(n+2) + py(n+3) + y(n+4)}{A_y(n)(1 - p^2)} (23)
$$

The application of Simulink requires a present versus past relationship (cause and effect) which motivates shifting $y(n+2)$, $y(n+3)$, $y(n+4)$ to their respective periodic equivalents $y(n-1)$, $y(n)$ and $y(n-2)$,

$$
\psi(n) = \frac{p^2y(n-1) + py(n) + y(n-2)}{A_y(n)(1 - p^2)} (24)
$$

The extraction process is captured in the Simulink diagram Fig.4 with output:

$$
\bar{\psi} = [1.6118 \ 0.4710 \ 1.2798]
$$

which corresponds with the true values generated from subsystem A for the Shepherd $\psi$ function and model parameters $K = 1$, $r = 1.75$ and $w = 8.618$. A comparison of the true and extracted density regulation is shown in Fig.5.

For the second model,

| Model number | $II$ |
|--------------|-----|
| age groups   | $m = 6$ |
| age group parameters $\bar{A}$ | $[0.2 \ 0.5 \ 0.2 \ 0.1 \ 0.01 \ 0.001]$ |
| $T$ = stock output $\bar{y}$ | $[1.0885 \ 1.0506 \ 0.8757 \ 0.9188]$ |

The five poles from

$$
0.2z^5 + 0.5z^4 + 0.2z^3 + 0.1z^2 + 0.01z + 0.001
$$

as well as the associated partial fraction coefficients are

- $p_1 = -2.1366 \quad D_1 = 0.0547$
- $p_2 = -0.1301 + 0.4088i \quad D_2 = 2.0662 + 2.9998i$
- $p_3 = -0.1301 - 0.4088i \quad D_3 = 2.0662 - 2.9998i$
- $p_4 = -0.0516 + 0.1003i \quad D_4 = -2.0935 - 14.1426i$
- $p_5 = -0.0516 - 0.1003i \quad D_5 = -2.0935 + 14.1426i$

with ROC $0.4289 < |z| < 2.1366$. The output of the extraction formula is:

$$
\bar{\psi} = [0.6475 \ 0.7696 \ 1.4011 \ 1.2522]
$$

which is consistent with choosing the parameters in the Shepherd function as $r = 1.9$, $K = 1$ and $w = 7.78$. The true and extracted regulation is compared in Fig.6.

In the third model,

| Model number | $III$ |
|--------------|-----|
| age groups   | $m = 6$ |
| age group parameters $\bar{A}$ | $[0 \ 0.3 \ 0.25 \ 0.3 \ 0.2]$ |

quasi-periodic stock output see Fig.7.

The stock output is almost periodic output with period $T = 210$ if the tolerance is set to $|y(n+T) - y(n)| < 0.001$ and $T = 9$ if it is relaxed to $|y(n+T) - y(n)| < 0.01$. The first non zero entry is $A_9 = 0.3$ with poles calculated from $0.3z^3 + 0.25z^2 + 0.3z + 0.2$ all located inside the unit circle with

- $p_1 = -0.7240 \quad D_1 = 0.7322$
- $p_2 = -0.0547 + 0.958i \quad D_2 = -0.3661 - 0.2558i$
- $p_3 = -0.0547 - 0.958i \quad D_3 = -0.3661 + 0.2558i$

and causal ROC $|z| > 0.9596$. For $T = 210$, the quasi-causal formula (22) is used and for $T = 9$, the original formula (21) is used. The extracted density regulations for these two cases are shown in Fig.8. They approximately correspond to the density regulation generated by subsystem A when choosing $r = 1.9$, $w = 4.812$ and $K = 1$ which is also shown in Fig.8. On a practical side, the relaxed $T = 9$ version requires less data for a similar extraction result.

V. CONCLUSION

In a cruise control model, the functionality of the actuator is determined by separating its contribution from the data output stored in the electronic control unit (ECU) and then comparing it to expected values through a diagnostic comparison [2]. This is what the extraction formula does for the ecological model, it separates the density component from the data stored in the periodic output which can then be used to mathematically identify the SR or it can be compared to previous values from which changes in population behavior can be determined. Schoombie and Getz (1998) linked the parameter $w$ in the non age-structured Shepherd model to the intensity of the behavioral interventions of a fish population in keeping stock (not recruitment) densities within the boundaries of $K$. They determined through a series of competitions (game theory) between an equilibrium population and a low density mutation practicing a slightly different version of $w$ that an ESS $w$ exists representing an invasion immune set of exclusive behavioral interventions in keeping densities within the boundaries of $K$. Future research will investigate the potential of using the extraction formula in determining where on the
strategy evolution landscape a population is with regards to its ESS. The extraction formula requires a model with a periodic equilibrium, constant survival and reproduction rates and the SR at the recruitment level of the age-structured model which puts it into the category of a novel application, yet, it opens the door to alternative modeling procedures and the freedom to experiment with manipulation tools such as the Z-transform from different fields.

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Fig. 6: $\psi(n)$ comparison for model $II$ with $m = 6$, $\bar{A} = [0.2 0.5 0.2 0.1 0.01 0.001]$ and true $\psi(n)$ calculated from $r = 1.9$, $w = 7.78$, $K = 1$ and $T = 4$.

Fig. 7: Quasi-periodic output $\bar{y}$ for model $III$ with $m = 6$ and $\bar{A} = [0 0 0.3 0.25 0.3 0.2]$.

Fig. 8: $\psi(n)$ comparison for model $III$ with $m = 6$, $\bar{A} = [0 0 0.3 0.25 0.3 0.2]$ with true $\psi(n)$ calculated from $w = 4.812$, $K = 1$ and $r = 1.9$. The quasi-causal extraction formula was used for $T = 201$ and the original formula for $T=9$.

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