Coding Optimization for an Ecological non-linear Age-structured Fish Population Model with a Shepherd Recruitment Function

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Abstract: The study of the optimally density-regulated recruitment plays a crucial role in the overall management and determining of fishing efforts of marine fish populations. This paper will develop a Matlab code can determine what an optimal recruitment density regulation strategy would be for the un-fished population and what it changes to when fishing efforts are applied. This code can determine threshold values used to avoid fisheries from collapsing. The code will be applied to the Gulf of California Pacific sardine (Sardinops caeruleus) population. An age structured design with a Shepherd density regulating stock-recruitment function is used in this study. In this work, the parameter which is varied is captured in the Shepherd recruitment function and is associated with behavioral interventions such as selecting different drift routes and clumping on resources that will increase egg-larvae survival to the recruitment stage. A detailed background study of other models is explored, then a derivation of the Shepherd recruitment model is developed from the traditional discrete model. A special MATLAB code is then developed to illustrate the pair-wise invasive plots for the model structures. The code is for theoretical analysis of fish population models.

Key-Words: Strategy dynamics, Age-structure, Convergence stable, Neighborhood invader, Evolutionary stable

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1 Introduction

Darwinian dynamics, as proposed by [1] attributes the ecological and evolutionary driving forces behind natural selection (NS) to the inherit traits in populations which can vary slightly between members of the same specie. In a restricted resource environment, where optimal practices matter, a small variation in trait resulting in a more efficient strategy leading to increased fitness (increased frequency/density) will lead to the displacement of the less effective trait holders. From [2], when consecutive strategy displacements end in a trait that can't be improved upon when practised by an equilibrium population, it is termed an evolutionary stable strategy (ESS) and represents an unbeatable set of behavioural interventions securing population persistence regarding that strategy. When strategy displacement is directional and converges to the ESS, it is also termed a convergence stable strategy [3], [4], [5], [6]. If a strategy, when practised by a rare population, can displace an equilibrium population practising a different strategy, it is referred to as a neighbourhood invader strategy (NIS) property [7], [8], [9], [10]. From [11], if a strategy is a CSS ending in an ESS and an NIS it is termed an evolutionary neighbourhood invader strategy (ESNIS) and is the optimal strategy the code will attempt to find for a population dynamics. A population whose structure allows for an ESNIS behavioural set should be able to rebound from a low-density position and persist (return to itself) even in the presence of alternative strategies. In the following discussions, strategy replacements are the displacements of a population practising one set of behaviours, with a population practising a small variation on these behaviours, but which leads to an increase in recruitment survival. The term 'a small variation in behaviour' is associated with the term 'neighbouring strategies'. The study of ESSs has a potential of future studies, especially in periodically fluctuating environments [12],[13].

From [14], [15] and [16] developing an optimization mechanism for determining an ESNIS will require a strategy adaptive dynamics (AD) framework. AD, which is used to drive the intended code, embarks on the increased fitness strategy replacement quest by measuring the density gain of introducing the current established equilibrium population to a new set of behaviours (a new strategy) and projecting the result onto a two-dimensional strategy adaptive landscape with the current strategy on the horizontal axes and the measure of density gain on the vertical axes. If the new strategy leads to an increase in the current population's density, it has positive gain over the current strategy, which will lead to the replacement of the current strategy by the new strategy and that natural selection will favour it.

Defining a suitable fitness proxy for measuring density gain of one strategy over another, the non-age-structured model will be used as a demonstration, with results extended to the age-structured model. A two equation canonical strategy dynamics set (CE) is used in the non-age structured case where the first generates the pure equilibrium density vector $\bar{X}$ of the uncontested common population X practising strategy u by recusing the population model

$$X_{n+1} = R(u, X_n)X_n \tag{1}$$

until an N periodic equilibrium is reached and $X_{n+N} = X_n$. R is the fitness function which was the Shepherd function in the model used by [17] and relates population densities. The equilibrium is defined by

$$\begin{aligned} X_{n+N} &= R^N(u, \bar{X_u})X_n \qquad (2)\\ \text{where} \quad R^N(u, \bar{X_u}) &= \prod_{k=0}^{N-1} R(u, X_{n+k}) \end{aligned}$$

and $\bar{X}(u) = \{X(i)\},\ i = n, .., n+N-1$ is the equilibrium vector of X generated at u in the absence of a new strategy. Since

$$R(u, X_n) = \frac{X_{n+1}}{X_n}, \tag{3}$$

the complicated expression for R^N can be avoided by expressing (2) instead as the density ratio combination

$$R^N(u, \bar{X_u}) = \prod_{k=0}^{N-1} \frac{X_{n+k+1}}{X_{n+k}} \tag{4}$$

The second equation in the CE set generates the gain vector $\bar{GX}$ by introducing the established population $\bar{X}(u) = \bar{X}_u$ to a new set of behaviours defined by the strategy v. This is accomplished by evaluating $R^N(v, \bar{X_u})$ which identifies with the G-function and the s-function in [18]. The gain vector is generated as

$$\begin{aligned} GX_{n+N} &= R^N(v, \bar{X_u})GX_u \qquad (5)\\ \text{where} \quad R^N(v, \bar{X_u}) &= \prod_{k=0}^{N-1} \frac{GX_{n+k+1}}{GX_{n+k}} \end{aligned}$$

Although $R^N(v, \bar{X_u})$ can serve as a fitness proxy where positive gain is defined as values above unity and negative gain as values below, its mathematical definition is complicated compromising the application of AD in pursuit of an ESNIS especially for large periods. A more suitable replacement for $R^N(v, \bar{X_u})$ with positive and negative gain rather displaying as positive and negative values is the invasion exponent I as defined in [19] which captures the gain over one period instead as

$$\begin{aligned} I(v, \bar{X_u}) &= \frac{1}{N} ln\left(R^N(v, \bar{X}(u))\right)\\ &= \frac{1}{N}\sum_{k=0}^{N-1} ln\left(\frac{GX_{n+1+k}}{GX_{n+k}}\right) \qquad (6) \end{aligned}$$

Since for the pure population at equilibrium, $I(u, \bar{X_u}) = 0$, v offers improved fitness over u if $I(v, \bar{X_u})$ is positive and vice versa. The landscape referred to earlier is the u vs $I(v, \bar{X_u})$ landscape which terminates on a hilltop if $v = w$ is an ESS with further adjustment leading to negative gain in both directions. The ESS strategy w will manifest as a peak on the landscape. In determining if w is also an NIS, equilibrium populations evolving from alternative neighbouring strategy values $u \neq w$ are introduced to the behaviour set defined by w through the fitness proxy $I(w, \bar{X_u})$. Positive gain in both directions indicates that if the strategy w was introduced by a small density population, that it will invade and displace its neighbours. Projecting $I(w, \bar{X_u})$ (vertical axes) onto the adaptive landscape for values of u (on the horizontal axes) neighbouring w, the NIS property will manifest as a valley.

The Shepherd function was chosen as the recruitment function in the age-structured model, as it contains a parameter u which can be associated with regulating the egg-larvae survival to the recruitment stage and is suited to optimization. From [20], it is defined as:

$$R(u, X(n)) = \frac{r}{1 + \left(\frac{X(n)}{K}\right)^u}$$

The r in the above represents the intrinsic growth rate, which is the maximum growth rate the population can experience when X densities are very low and are measured in recruits per unit biomass. The density regulation activates when recruitment densities exceed the environmental limitation K. The extent of the regulation is driven by the parameter u and is linked to varying endogenous processes such as changing drift routes, predating, cannibalism and competition for resources ([21], [22]), used the parameter u in the Shepherd recruitment age-structured model as a tuning parameter in fitting the model to observed data but perceived u instead as an evolving strategy in the non-age-structured case. Most ecosystem forecasts use ecosystem models instead of age-structured ones[23],[24]. Population control and density control play an important role in population modelling, although it's difficult to show [25],[26]. They calculated the ESS by instead using the 2-equation mutual invasion CE set

$$\begin{aligned} X_{n+1} &= R(u, X_n + y_n)X_n \\ &= \frac{r}{1+\left(\frac{X_n+y_n}{K}\right)^u}X_n \\ y_{n+1} &= R(v, X_n + y_n)y_n \\ &= \frac{r}{1+\left(\frac{X_n+y_n}{K}\right)^v}y_n, \end{aligned} \tag{7}$$

In the above, the population X is the equilibrium or common population with strategy u competing against a small mutational population y with strategy v in a shared environment with a density limitation where at first $y << X$. Wins and losses were recorded on pair-wise invasive plots (PIP) for consecutive matches played by the mutual invasion pairs over a wide range of u and v values. The PIP plots could determine the ESS.

The 1982 UN convention implemented control of fishing efforts. This imposed fishing controls all over the world to facilitate re-growth of the fish population [27]. The study by [28] considered probabilistic approach on fishing efforts. This model improved the understanding of fish population changes in the seas. Different studies have explored other recruitment functions based on spatial population structures [29], comparison of integrated fisheries stock assessment and integrated population models [30], inclusion of weather and climatic conditions in harvesting controls [31], and the declining of acidic conditions in seas is leading to improvement of fish population [32]. None of these studies considered a special MATLAB code to understand the Shepherd recruitment function. This work explores the use of a code that can solve models based on the Shepherd function.

2 The Age-structured Model

2.1 Population Dynamics

Borrowing from the age-structure design in [10] where density regulation is assumed present only at the recruitment level, the Shepherd function is included as the compensatory survival rate $\psi(u, X_{n-1}) = R_S(u, X_{n-1})$ of the recruitment population X_{n-1} comprising the vulnerable egg-larvae stages to the first spawning age group $x_1(n)$ one time step later as [18, 33, 20]

$$x_1(n) = s_o\psi(u, X(n-1))X(n-1) \tag{8}$$

Besides the compensatory survival rate, the recruitment population is also subjected to a non density regulated survival rate s_o in (8). The next age group,

$$x_2(n) = s_1 x_1(n-1), \tag{9}$$

is the survivors of $x_1(n-1)$ after being subjected to a non density regulated survival rate s_1. From (8), $x_1(n-1) = s_o\psi(u, X(n-2))X(n-2)$, allowing $x_2(n)$ in (9) to be written in terms of the recruitment population it generated from as

$$x_2(n) = s_1 s_o \psi(u, X(n-2))X(n-2)$$

In general, each age group in an m age group model can be expressed in terms of the recruitment population it generated from as:

$$x_i(n) = \left(\prod_{k=0}^{i-1} s_k\right)\psi(u, X(n-i))X(n-i) \qquad i = 1, .., m \tag{10}$$

where $s_k,\ k = 0, .., m-1$ are non density regulated survival rates. If further each of the $x_i(n)$ in (10) contribute constant reproduction proportions $b_i x_i(n)$, $i = 1, .., m$ towards the next recruitment tally $X(n)$,

$$\begin{aligned} X(n) &= \sum_{i=1}^{m} b_i\left(\prod_{k=0}^{i-1} s_k\right)\psi(u, X(n-i))X(n-i) \\ &= \sum_{i=1}^{m} A_i\psi(u, X_{n-i}X_{n-i} \\ &= \sum_{i=1}^{m} A_i\psi(u, X_{n-i})\frac{X_{n-i}}{X_{n-m}}X_{n-m} \\ &= R(u, X(u))X(n-m) \end{aligned} \tag{11}$$

or rather

$$X_{n+m} = R(u, X_u)X(n) \tag{12}$$

where, for $i = 1, .., m$, $A_i = b_i\left(\prod_{k=0}^{i-1} s_k\right)$ are the population parameters, $X_u = \{X_{n-i},\ i = 1, .., m\}$ is the recruitment vector over m generations (and not over one period) and $R(u, X_u) = \frac{X(n+m)}{X_n}$ is the recruitment fitness function representing the progress in recruitment densities over m generations (and not stock densities over one time interval as in the non age-structured case (2)). $\bar{X_u}$ is generated by recursing (12) until an equilibrium is reached with period N (note that $X_u \subseteq \bar{X_u}$). From (4) and (6), a simple expression for I in evaluating the gain of strategy v over u can be defined by generating the gain population vector $\bar{GX}(v, \bar{X_u})$ through recursions of

$$\begin{aligned} GX_n &= \sum_{i=1}^{m} A_i\psi(v, X_{n-i})GX_{n-i} \\ &= R(v, X_u)GX_{n-m} \end{aligned} \tag{13}$$

over N time intervals using the entries of $\bar{X_u}$. $R^N(v, \bar{X_u})$ is then defined as

$$R^N(v, \bar{X_u}) = \prod_{k=0}^{N-1}\frac{GX_{n+m+k}}{GX_{n+k}}$$

and the invasion exponent measuring the net gain over one period as

$$I(v, \bar{X}_u) = \frac{1}{N} \sum_{k=0}^{N-1} ln \left(\frac{GX_{n+m+k}}{GX_{n+k}} \right) \tag{14}$$

The (Matlab) code addressing the model parameters required for the recursion model (11) is shown in Fig.3 (see Appendix B). The code starts with $u = 10$ and simulates NS by embarking on a systematic search for the hilltop on the landscape defined by (14). $M = 60000$ recursions will ensure an equilibrium state of which the last $N = 8!$ captures the most popular periods but is large enough to include chaotic and quasi-periodic tendencies. A maximum of $T = 200$ strategy adaptations may avoid a runaway search for the CSS. From the chosen initial strategy $u = 10$, adaptations $u = u + f$ are made in increments of the evolution step size f where at first $f = 1$ until the CSS is over stepped after which f is reduced to $\frac{f}{10}$ and adaptations are made in the opposite direction. After every over step, f is further reduced, and the direction changed, which simulates NS converging on an evolutionary attracting strategy. During numerical calculations, values are less than $thresh = 0.0001$ are taken as zero. The remainder of the coefficients are model specific and will be defined in section 3 for a hypothetical model corresponding to $m = 3$ and a real world model corresponding to $m = 6$.

2.2 Strategy Adaptive Dynamics

Tapping from literature in evolutionary ecology such as [3], [4], [5], the ESNIS sought after is an unbeatable set of behavioural interventions securing population persistence in the presence of small mutational changes in these behaviours and has three properties; it's population must be unbeatable when at an equilibrium/common density (ESS), invasive at low densities (NIS) and, most importantly, must be evolutionary possible through directional adaptations (CSS). In this section the direction of adaptations in u will be determined for a CSS ending in an ESS optimization. From [18], the mutational strategies straddling $u, v = u \pm h$, with gain step size $|h| << 1$ are on the CSS convergence path if one of them can invade the common population $\bar{X}(u)$. The common strategy is adapted to $u = u + f$ in the direction of the invader, a process that is repeated until u reaches the ESS w after which neither of the two $v = w \pm h$ are able to invade $\bar{X}_w$, defining a hilltop. If $v = u + h$ is an invader, equation (14) will be positive

$$I(v, \bar{X}_u) > 0, \bar{X}_u = \bar{X}(u) \tag{15}$$

A first order Taylor expansion of $I(v, \bar{X}_u) = I(u + h, \bar{X})$ leads to

$$\begin{aligned} I(u+h, \bar{X}_u) &= I(u, \bar{X}_u) + \left(\frac{\partial I}{\partial v} \right)_{v=u} h + O(h^2) \\ &\approx \left(\frac{\partial I}{\partial v} \right)_{v=u} h \end{aligned} \tag{16}$$

since $I(u, \bar{X}_u) = 0$, and the truncation error $O(h^2)$ is taken as negligible on account of $|h| << 1$. From [4] and [34], the fitness gradient $\frac{\partial I}{\partial v}_{v=u}$ indicates the direction of improved strategies in accordance with Fisher's fundamental theorem of NS where

$$\begin{aligned} u_{n+1} &= u_n + \alpha \left(\frac{\partial I}{\partial v} \right)_{v=u} \\ &= u(n) + f \end{aligned} \tag{17}$$

Here $f = \alpha \left(\frac{\partial I}{\partial v} \right)_{v=u}$ is the strategy evolution step size. The speed term α in f varies according to population size, structure and genetic possibilities [4]. From (17), when $\left(\frac{\partial I}{\partial v} \right)_{v=u} > 0$, NS will favor strategy adaptations to the right of u and vice versa. Adaptations to u in the code is in terms of the evolutionary step size f (initiated at $f = 1$) added to u in accordance to the sign of the fitness gradient. The CSS code in Fig.5 (see Appendix B) approximates the fitness gradient for a given u with equilibrium population $\bar{X}_u(u)$ by repeating the calculations leading to (16) for $v = u - h$ which results in a second equation which, when subtracted from (16), results in the central difference equation expression

$$\left(\frac{\partial I}{\partial v} \right)_{v=u} \approx \frac{I(u+h, \bar{X}_u) - I(u-h, \bar{X}_u)}{2h} \tag{18}$$

With reference to Fig.4 (see Appendix B), for every pure population $\bar{X}_u$, two gain populations $G\bar{X}R(u + h, \bar{X}_u)$ and $G\bar{X}L(u - h, \bar{X}_u)$ with $h = 0.001$ must be generated by recusing (11) over M time intervals, firstly for the pure population and then the gain populations as they require the entries of the already generated $\bar{X}_u$. Each of the three populations will require m initial conditions in in the range $\left[_{0,K}\right]$ and will require the assembly of m previous generations with amplitudes defined by $A_{_i}$, $i = 1, .., m$. Once a strategy $u = w$ is calculated for which $\left(\frac{\partial I}{\partial v} \right)_{v=u=w} \approx thresh$, u is termed an evolutionary singular strategy (ess) (see [18]) and, as it also represents a hilltop on the (u, I) adaptive landscape, it is a local ESS. The hilltop status is determined by calculating the second derivative using the numerical approximation

$$\partial_{vv}|_{v=u=w} \approx \frac{D_I}{h^2} \tag{19}$$

$$D_I = I(u+h,\bar{X}_u) - 2I(u,\bar{X}_u) + I(u-h,\bar{X}_u)$$

which must be negative [4]. The evaluation of the fitness gradient is captured in Fig.5 (see Appendix B)where

$$\begin{aligned} I(u+h,\bar{X}_u) &= IXR \\ I(u-h,\bar{X}_u) &= IXL \\ I(u,\bar{X}_u) &= IX \end{aligned}$$

Each adaptation to u is a distance f from u in the direction determined by the sign ss of (18). If ss is positive, f is positive and vice versa. If ss at time step n is oppositely signed from ss at step $n-1$, the hilltop was stepped over and it is time to reduce the step size to $f = \frac{f}{10}$ and apply adaptations in the opposite direction until the hilltop is stepped over again, requiring a further reduction $f = \frac{f}{10}$ which will define the CSS convergence path [8, 14, 17]. If this converging process exceeds T adaptations without (18) reaching $thresh$ and (19) testing negative, the hilltop does not exist for the chosen model parameters and the process is terminated with the $break$ command. This part of the code is shown in Fig.6 (see Appendix B) with Matlab instruction $\sim=$ for $\neq$. The code must terminate if a hilltop $u = w$ is reached, representing optimal behaviour from the common population's point of view in regulating recruitment densities favoured by NS. The question now is if w also represents an optimal strategy from a rare invader's point of view, the outcome w of the CSS ending in an ESS code is tested against the NIS property.

It will be assumed that the CSS $u = w$ belongs to the rare population x generated at w and the investigation conducted is to determine under which circumstances x will be able to invade any equilibrium population $\bar{Y}_u$ if the commonly used (equilibrium) u is near the rarely used w. If w is a NIS, the gain invasion exponent (14) will show positive growth

$$I(w,\bar{Y}_u) > 0 \qquad (20)$$

for a variety of nearby $\bar{Y}(u) = \bar{Y}_u$ populations. It will be assumed that one such choice in a local neighbourhood of w is $u = w+h$ and that the equilibrium $\bar{Y}_u$ is only slightly different to the equilibrium $\bar{X}(w) = \bar{X}_w$ as u and w are near neighbours on the strategy evolution axes. The Taylor expansion of $\bar{Y}_u$ will result in

$$\bar{Y}(w+h) = \bar{Y}(w) + \left(\frac{\partial \bar{Y}}{\partial u}\right)_{u=w} h + O(h^2) \qquad (21)$$

Omitting $O(h^2)$ terms in (21) and realizing that $\bar{Y}_w = \bar{X}_w$, the expansion of the Invasion exponent (20) simplifies to

$$\begin{aligned} I(w,\bar{Y}_{w+h}) &\approx I(w,\bar{Y}_w + \left(\frac{\partial \bar{Y}}{\partial u}\right) h) \\ &\approx I(w,\bar{X}_w) + \left(\frac{\partial I}{\partial \bar{Y}}\right)\left(\frac{\partial \bar{Y}}{\partial u}\right) h \\ &= \left(\frac{\partial I}{\partial \bar{Y}}\right)\left(\frac{\partial \bar{Y}}{\partial u}\right) h \qquad (22) \\ &= \left(\frac{dI}{du}\right)_{\substack{u=w \\ \bar{Y}=\bar{X}}} h, \qquad (23) \end{aligned}$$

$$\left[\left(\frac{\partial I}{\partial \bar{Y}}\right) = \left(\frac{\partial I}{\partial \bar{Y}}\right)_{\bar{Y}=\bar{X}}, \left(\frac{\partial \bar{Y}}{\partial u}\right) = \left(\frac{\partial \bar{Y}}{\partial u}\right)_{u=w}\right]$$

If w is an NIS, equation (23) must be positive for all u in a local neighbourhood of w which is possible if both $\frac{dI}{du}$ and h are either positive or negative and increasingly so as h becomes larger with $I(w,\bar{Y}_u) = 0$ at $u = w$. This defines $I(w,\bar{Y}_w)$ as a minimum on the I vs u adaptive landscape. In formulating a code friendly expression for $\frac{dI}{du}$, $\bar{Y}_u$ in (22) is evaluated at $u = w-h$ resulting in the expression

$$I(w,\bar{Y}_{w-h}) \approx -\left(\frac{dI}{du}\right)_{\substack{u=w \\ \bar{Y}=\bar{X}}} h \qquad (24)$$

which enables the calculation of $\frac{dI}{du}$ by subtracting (24) from (23) as the nested central difference equation

$$\frac{dI}{du} = \frac{I(w,\bar{Y}_{w+h}) - I(w,\bar{Y}_{w-h})}{2h} \qquad (25)$$

with the second derivative defined as,

$$I_{YY}|_{\substack{u=w \\ \bar{Y}=\bar{X}}} \approx \frac{D_I}{h^2} > 0 \qquad (26)$$

$$D_I = I(w,\bar{Y}_{w+h}) - 2I(w,\bar{Y}_w) + I(w,\bar{Y}_{w-h})$$

The code determines w's NIS status by calculating (25) and (26) using the pure populations $\bar{Y}_{w-h} = \bar{YL}$ and $\bar{Y}_{w+h} = \bar{YR}$ and their respective gain populations $G\bar{Y}L$ and $G\bar{Y}R$ as shown in Fig.7 and Fig.8 (see Appendix B).

3 Model Structure and Plots

The code was executed for the following two models: Hypothetical model: An $m = 3$ population with

$$\begin{aligned} \bar{s} &= [0.25\ ,\ 0.6\ ,\ 0.7] \\ \bar{b} &= [1.5\ ,\ 2\ ,\ 4] \\ K &= 1 \text{ and } in = 0.8 \end{aligned}$$

Real world model: An $m = 6$ Pacific sardine population off the Gulf of Mexico with parameters estimated from Nevárez-Martínez *et al* (1999) as

$$\begin{aligned} \bar{s} &= [0.25\ ,\ A\ ,\ A\ ,\ A\ ,\ A\ ,\ A] \\ \bar{b} &= [2.3\ ,\ 2.3\ ,\ 2.3\ ,\ 2.3\ ,\ 2.3\ ,\ 2.3] \\ K &= 1 \text{ and } in = 0.1 \end{aligned}$$

$$where\ A = e^{-0.77-F} \tag{27}$$

The F is the fishing mortality factor where $F = 0$ represents the un-fished population.

As in the non age-structured case in [17], the optimum strategy w was calculated for a range of $1 < r < 2$ values resulting in Figure 1 (See Appendix A) for the hypothetical model which serves as demonstration for the concepts introduced in this paper and the effect the choice of r has on model dynamics. These plots show the adaptive landscape in the first column with the ESS and NIS properties manifesting as maxima and minima where they exist. The equilibrium population output $\bar{X_w}$ is in the second column and the PIP plot in the third column.

1. Adaptive landscape plots: The Invasion exponents of the gain populations $I(v, \bar{X_w}) = IX$, were plotted over the range $v = w - 0.5 : 0.01 : w + 0.5$. The NIS property was either confirmed or ruled out by plotting the invasion exponents of the gain populations $I(w, \bar{Y_u}) = IY$ over the grid $u = w - 0.5 : 0.01 : w + 0.5$. The two plots share the same axes with the net gain IX and IY on the vertical axes and the strategy u or v on the horizontal axes.
2. Population plot: The equilibrium recruitment population densities $\bar{X_w}$ spanning the last 30 time units of the M recursions are plotted against discrete time n.
3. PIP plot: These plots are similar to the PIP's discussed in Diecmann and Ferriere (2004) and Geritz *et al.* (1998) and serve as a graphic platform for analysing the local ESS, CSS and NIS properties of w as well as other interesting occurrences. The mutual invasion CE model, adapted to the age-structured case was run over a grid with the vertical axes representing rare populations practising strategies $v = w - 0.5 : 0.01 : w + 0.5$ and the horizontal axes representing equilibrium/common strategies $u = w - 0.5 : 0.01 : w + 0.5$. The initial values of the rare population Y_n practising v were entered as 0.01 and those of the common population X_n practising u was entered as 0.8. The competition ran over 50 000 time units for each pair with the average y_{av} and X_{av} populations calculated from the output over the last 1000 time units. When a population's average was less than 0.01, it was regarded as displaced (extinct).

3.1 The PIP Plots

Borrowing from Geritz *et al.* (1998), the interpretation of the colour codes in the PIP plots in the third columns of Figure 1 are listed in Appendix A. The various degrees of cooperation between populations ranging from full to none are determined by the mutual invasion model outcomes X_{av} and y_{av}.

1. Circle ○: Full cooperation at $50 : 50$ was observed when $u = v$ (competing against itself) or when strategies were perfectly symmetrical about w. NS favours both parties when rare, leading to a possible dimorphic partnership with an equilibrium showing equal occupation status. These pairs satisfy $\|X_{av} - y_{av}\| < 0.01$ and are situated along the minor diagonal (bottom left to top right) as well as the major diagonal (top left to bottom right).
2. Grey along the major diagonal: Almost full cooperation at $65 : 35$ was observed when both parties were almost symmetrical about w but one party was slightly closer to w leading to NS favouring both when rare but the closer party had the advantaged with approximately a 65% occupation status. This outcome remains unchanged whether the closer party is initiated as rare or common. Two cases were observed:
    - Case 1: The dark grey regions along the major diagonal, the commonly used strategy u is marginally closer to w with outcome $X_{av} > y_{av}$.
    - Case 2: The light grey regions along the major diagonal are regions where the rare strategy v is closer to w and $y_{av} > X_{av}$.
3. Grey along the minor diagonal: There was low cooperation at $95 : 5$ when both parties are near neighbours (almost identical) but the rare party v is slightly closer to w. This outcome was detected in two cases:
    - Case 3: When strategies u and v were approximately 0.01 units apart, NS could not distinguish between them and the status quo remained, with the rare population occupying approximately 5% of the environment. These pairs, corresponding with $X_{av} >> y_{av}$, are indicated in dark grey along the minor diagonal.
    - Case 4: When the strategy difference between u and v was more significant at approximately 0.1 units, NS detected the rare strategy as an improvement, which lead to the rare population becoming common while the common population became rare. These pairs, corresponding with $y_{av} >>$

X_{av}, are indicated in light grey along the minor diagonal.

4. Black and white: There was no cooperation at $100:0$ when NS strongly favours only one strategy to the point of a 100% occupation status, displacing the other party. Two cases arose:
    - Case 5: The black regions are combinations where the common strategists u displace the rare strategists v with no cooperation. These strategies are at least 0.15 units apart with the common strategists closer to w. Fitting a vertical line through a chosen u on the horizontal axes starting and ending in a black region will straddle regions of cooperation (white, gray, and dark gray). The u value for which the vertical interruption is minimal defines an optimum and is by definition a local ESS as this u value will displace all rare strategists in its neighbourhood.
    - Case 6: The white regions are combinations where the common u strategists are displaced by the rare v strategists with no cooperation. These strategies are at least 0.2 units apart with the rare strategists closer to w. Fitting horizontal lines through v values starting and ending in a white region also straddle regions of cooperation, as the distances between strategies are not distinct enough for NS to have a clear preference. The horizontal line with the least amount of interruption is by definition a NIS as this v strategy can displace all common strategists in its neighbourhood to a larger extent.
5. Identifying the CSS: w must be an ESS, NIS and CSS to be a likely outcome of evolution. From the above discussion, the ESS and NIS status of w can be determined on the PIP plots by drawing horizontal and vertical lines through (w, w) but the manifestation of the CSS condition on the PIP plot must still be demonstrated. For w to be a CSS, the strategy path leading to w must be defined by small strategy adaptation where a rare population $v = u_{i+1}$ closer to w must be detectable to NS to the extent of no cooperation with the common strategist $u = u_i$ which describes strategy pairs in the white regions bordering the minor diagonal. After displacing the common strategists, the new population must first reach an equilibrium (the black edge of the minor diagonal) before a next rare invasive strategy $v = u_{i+2}$ even closer to w is introduced. Connecting coordinates $(u = u_i, v = u_{i+1})$ in a white region to the equilibrium are $(u = u_{i+1}, v = u_{i+1})$ in the black region to the next invasion are $(u = u_{i+1}, v = u_{i+2})$ in the white region, animates a stair climbing process along the minor diagonal towards w. In each of these near neighbour cases along the minor diagonal (including the light and dark grey regions described by cases 3 and 4), if v is entered as common and u as rare, the closer v strategists displace the rare strategists (black region), proving that evolution won't change direction but will keep climbing the staircase towards w. This one-way stairway defines the CSS path and ensures that Darwinian dynamics returns strategies back to the ESS should there be slight perturbation in the strategy or rather the behaviour it represents.

3.2 Model Discussion

In the hypothetical case it was observed in the outcome of the ESNIS search that the closer r is to its bottom boundary $r = 1$, the higher the value of w is and the higher the period is of the population output. This can be ascribed to a low intrinsic growth rate, which will necessitate abrupt behavioural interventions to promote population stability. The closer r is to the upper limit $r = 2$ however, less drastic interventions are required for population densities to return to normal. Specifically pertaining to Figure.1 (See Appendix A),

Row i) $r = 1.36$ and $w = 17.33$: All three properties are observed. The population output has a period 4.
Row ii) $r = 1.47$ and two w outputs, one at $w = 12$ (when the code was initiated at $u = 10$) and the other at $w = 11.04$ (when the code was initiated at $u = 10.5$): The optimal strategy $w = 12$ is an ESS as the vertical line passing through $u = 12$ defines a minimum cooperation situation compared to its immediate neighbours. It is however, not a CSS as, from the PIP plot, there is no stairway leading towards it. In [8] this configuration was referred to as a 'Garden-of-Eden' in 1989 and an unlikely outcome to NS. When the strategy search was instead initiated at $u = 10.5$,the code terminated in $w = 11.04$ but, as the stairway only exists to the left of this ESS,it is not a CSS. Neither of these two ESS's have the NIS property, which is confirmed by the adaptive landscape plots for both outcomes. The population output when $w = 11.04$ has a period 4.
Row iii) $r = 1.65$ and $w = 8.05$: All three properties are observed. The population output has period 2.

The sardine population was run with a constant $r = 1.65$ for different fishing mortality rates to determine when the population can no longer support an ESNIS. Specifically pertaining to Figure 2 (See Appendix A),
Row i) With no fishing, the population shows a period

two abundance with an ESNIS strategy of $w = 7.794$. Row ii) When a fishing mortality of $F = 0.22$ is applied, the population could maintain a period two ESNIS of $w = 9.462$ which shows that a change in behaviour was required to accommodate lower age specific survival rates. The peaks and troughs are more exaggerated when compared to the unfished population.

Row iii) Moving fishing mortality up to $F = 0.42$ lead to a quasi periodic outcome with population abundance estimated at every 4 to 5 years. The population is no longer capable of an ESNIS but only an ESS with $w = 13.758$ (See Figure 2 (See Appendix A). This population is more likely to run the risk of collapse if this rate of fishing continues, as its dynamics no longer allow for behavioural intervention that can rebound densities to maintain the population.

4 Conclusion and Future Research

The code developed in this paper simulated the behavioural changes population dynamics allow when circumstances change. It is therefore suitable to an extent for the investigation of fishing mortality rates provided model parameters can be estimated to match observed abundance rates. The code and paper is intended for experimentation for persons new to the field of ecological optimization. Future research will include more real-world data analyses and observed changes in strategy over time. The paper made derivation of the Shepherd recruitment function from the traditional discrete model and showed a detailed analysis of the function and a unique MATLAB code that is included in the appendices (See Appendix B). The paper shares the code, in other studies no code has been included. The method can be used as an alternative method to solve models similar to the Shepherd recruitment function. Also, developments from the code can easily be made to include other factors, such as stochastic effects and other environmental factors.

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Appendix A

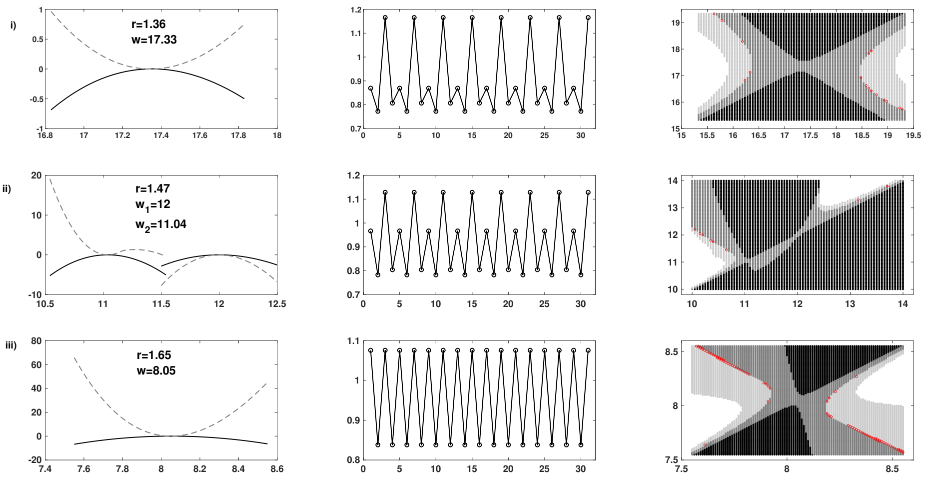


Fig. 1: For $m =$ 3: i) For $r = 1.36, w = 17.33$ is an ESS. ii) For $r = 1.47$, $w = 12$ is a ‘Garden of Eden’ ESS but $w = 11.04$ is a CSS and ESS. iii) For $r = 1.65, w = 8.05$ is a ESNIS

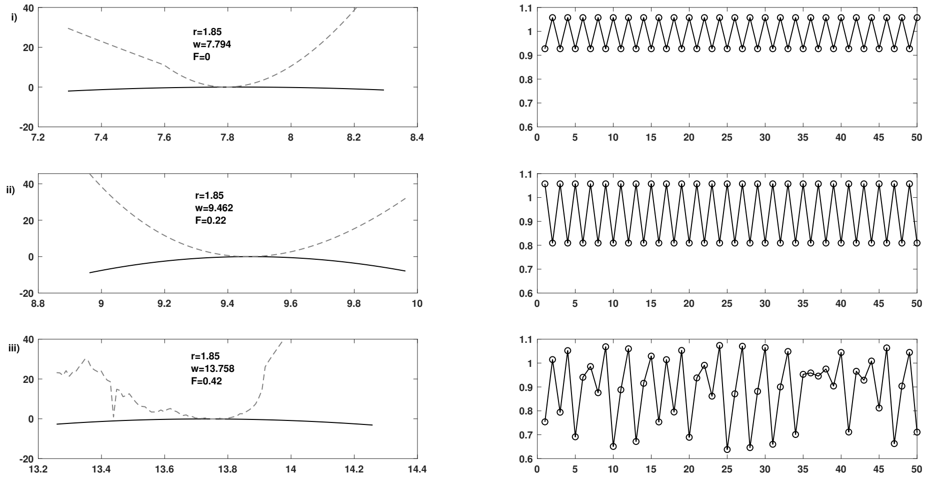
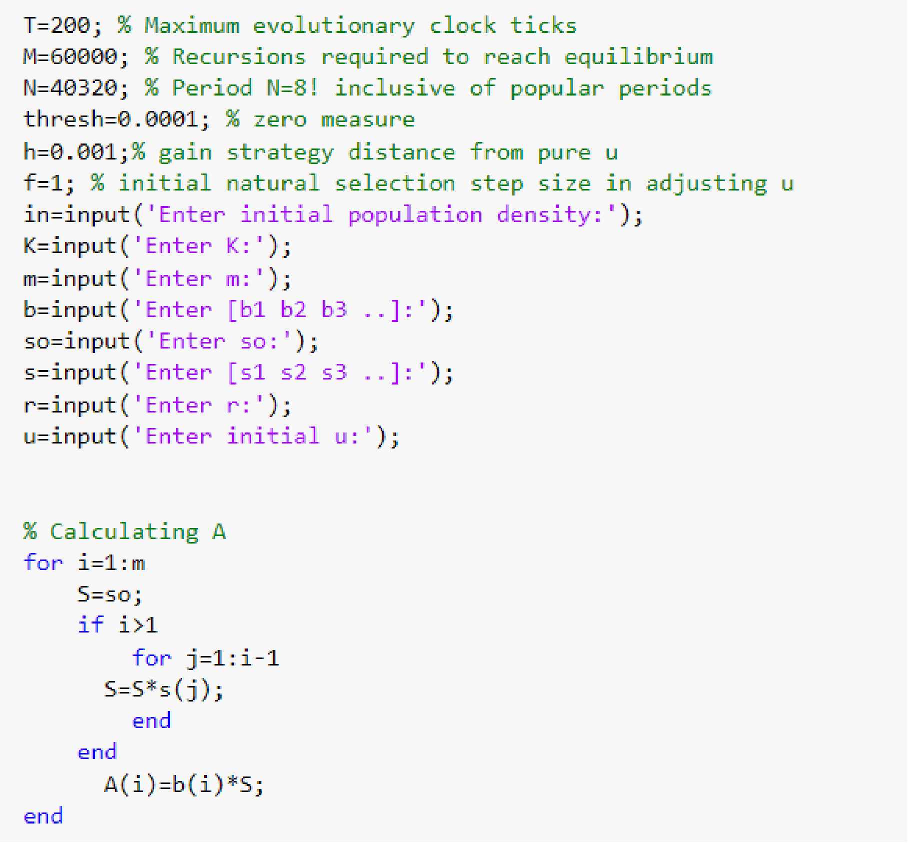


Fig. 2: For $m =$ 6 and $r = 1.65$: i) For $F = 0, w = 7.794$ is an ESNIS. ii) For $F = 0.22, w = 9.462$ is an ESNIS. iii) $F = 0.42, w = 13.758$ is an ESS and CSS

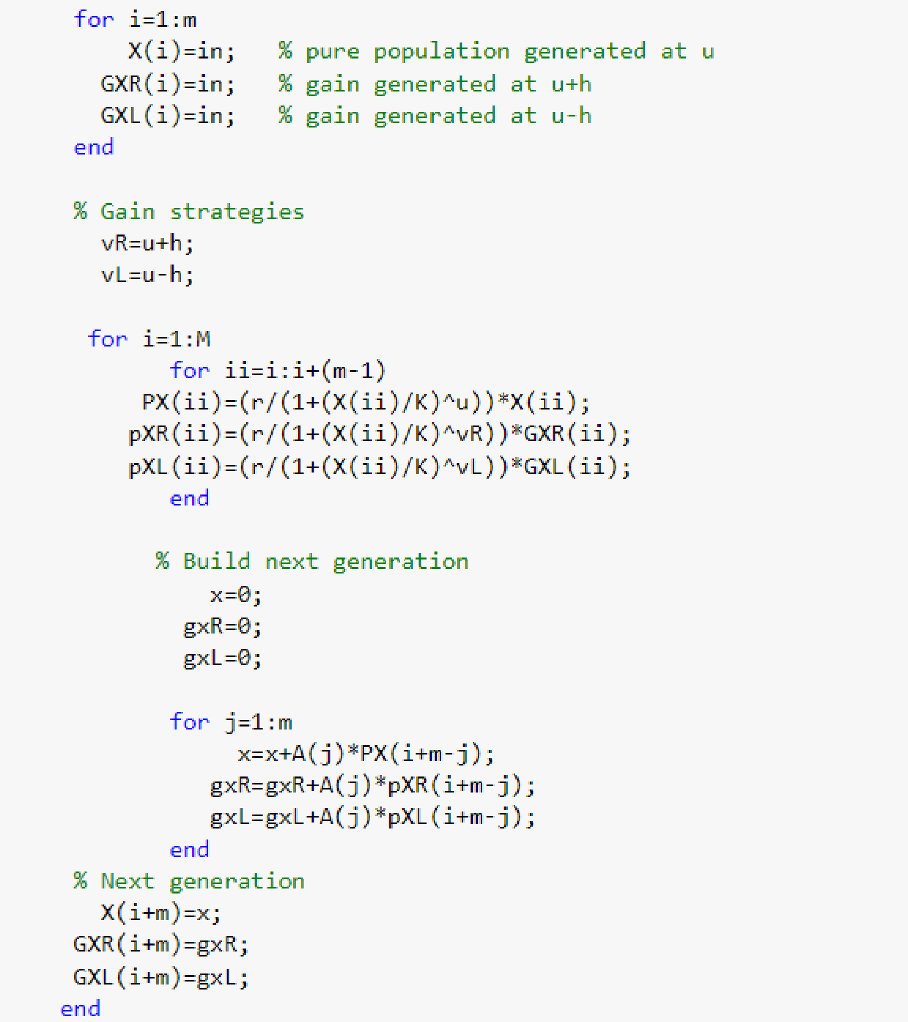
Appendix B

In this appendix, all codes used in the text of this paper are shown.



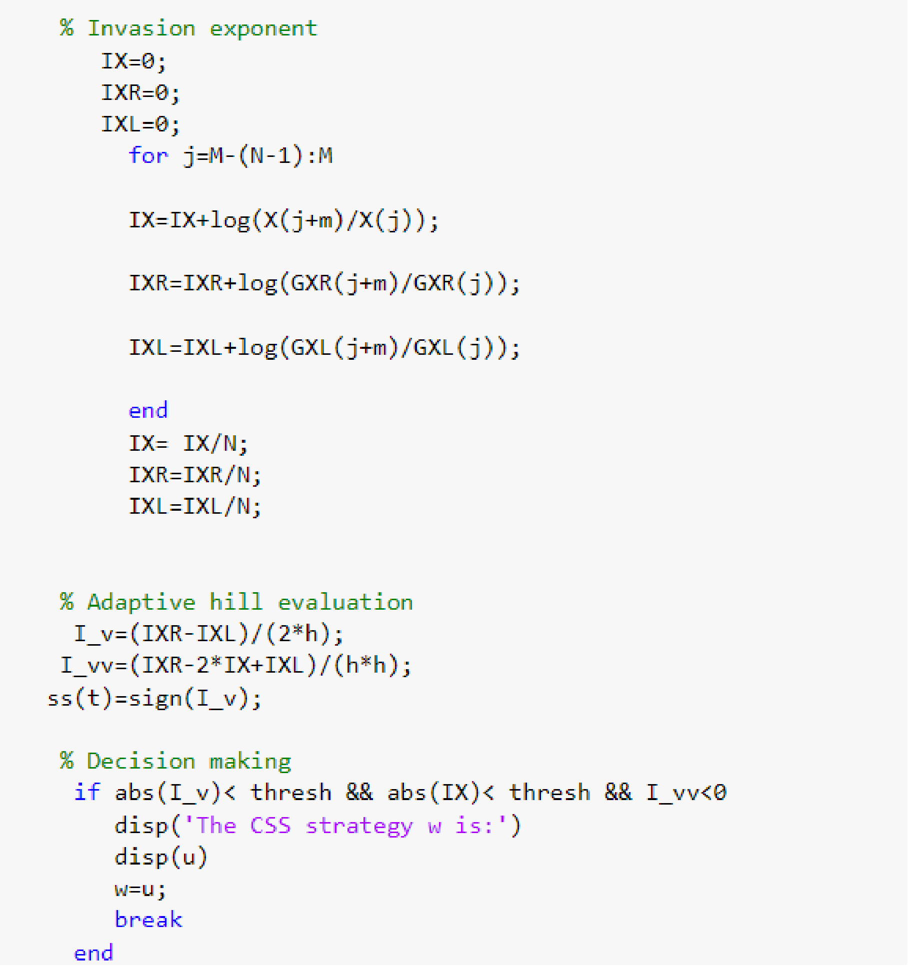
```
T=200; % Maximum evolutionary clock ticks
M=60000; % Recursions required to reach equilibrium
N=40320; % Period N=8! inclusive of popular periods
thresh=0.0001; % zero measure
h=0.001;% gain strategy distance from pure u
f=1; % initial natural selection step size in adjusting u
in=input('Enter initial population density:');
K=input('Enter K:');
m=input('Enter m:');
b=input('Enter [b1 b2 b3 ..]:');
so=input('Enter so:');
s=input('Enter [s1 s2 s3 ..]:');
r=input('Enter r:');
u=input('Enter initial u:');


% Calculating A
for i=1:m
    S=so;
    if i>1
        for j=1:i-1
      S=S*s(j);
        end
    end
      A(i)=b(i)*S;
end
```

Fig. 3: Matlab code addressing model parameter entries and A_i calculations



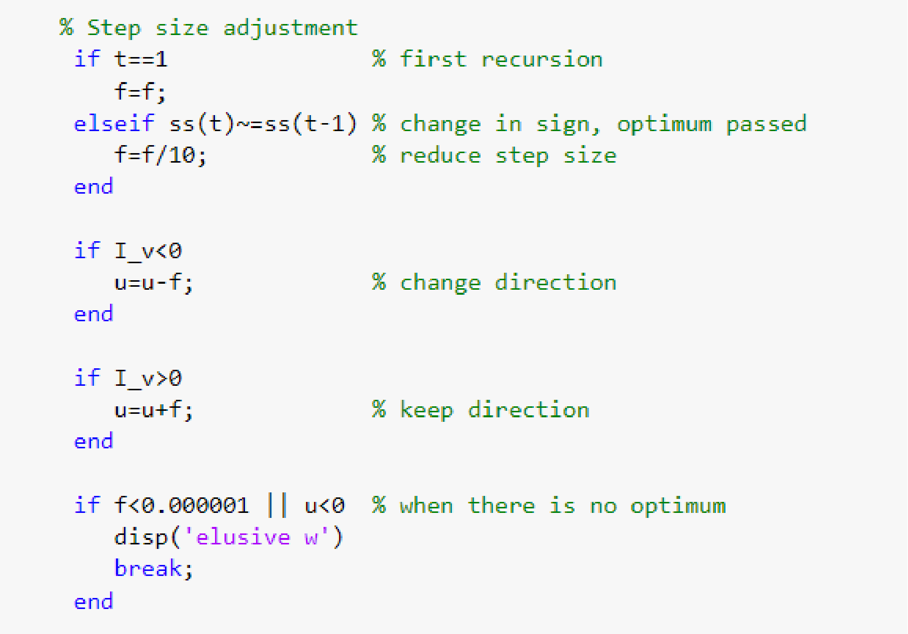
```
 for i=1:m
     X(i)=in;   % pure population generated at u
   GXR(i)=in;   % gain generated at u+h
   GXL(i)=in;   % gain generated at u-h
 end

 % Gain strategies
   vR=u+h;
   vL=u-h;

  for i=1:M
        for ii=i:i+(m-1)
      PX(ii)=(r/(1+(X(ii)/K)^u))*X(ii);
     pXR(ii)=(r/(1+(X(ii)/K)^vR))*GXR(ii);
     pXL(ii)=(r/(1+(X(ii)/K)^vL))*GXL(ii);
        end

       % Build next generation
           x=0;
         gxR=0;
         gxL=0;

        for j=1:m
             x=x+A(j)*PX(i+m-j);
           gxR=gxR+A(j)*pXR(i+m-j);
           gxL=gxL+A(j)*pXL(i+m-j);
        end
 % Next generation
   X(i+m)=x;
 GXR(i+m)=gxR;
 GXL(i+m)=gxL;
end
```

Fig. 4: Matlab code addressing the calculation of the next generation recruitment population as well as the gain populations.



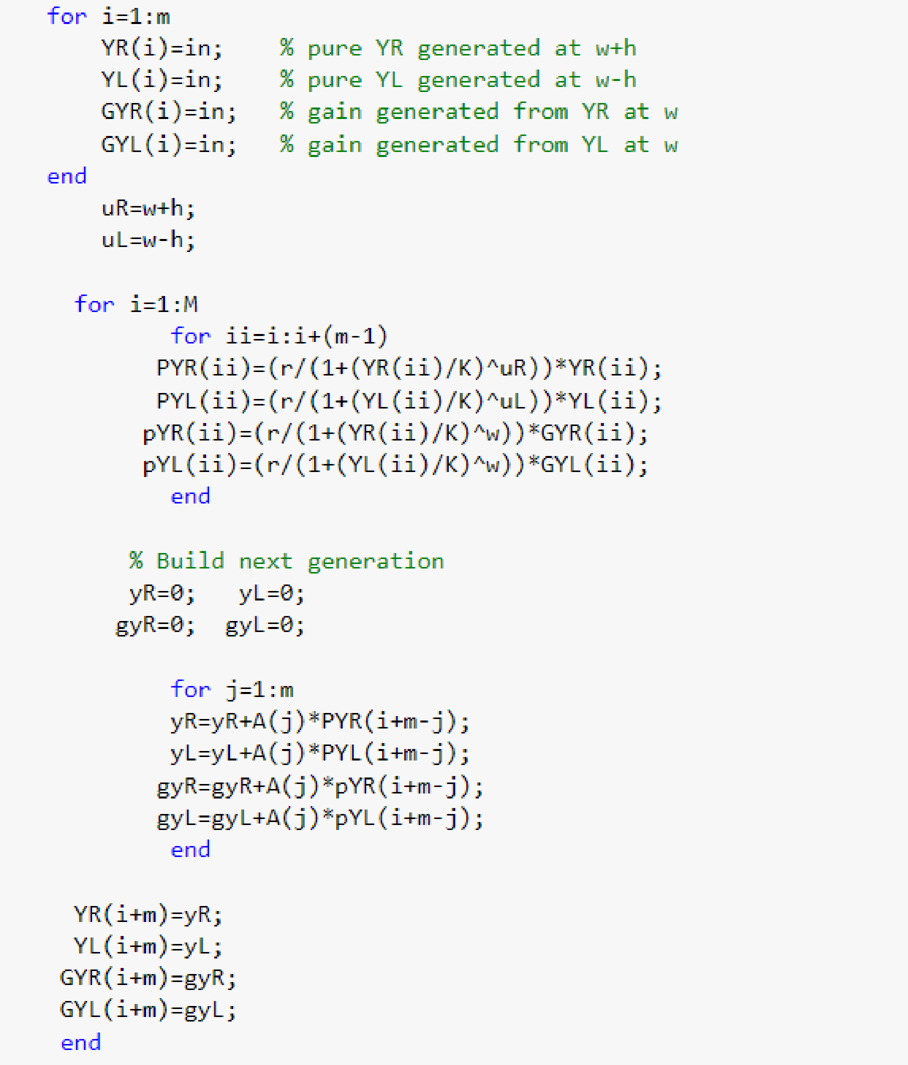
```
 % Invasion exponent
    IX=0;
    IXR=0;
    IXL=0;
      for j=M-(N-1):M

      IX=IX+log(X(j+m)/X(j));

      IXR=IXR+log(GXR(j+m)/GXR(j));

      IXL=IXL+log(GXL(j+m)/GXL(j));

      end
      IX= IX/N;
      IXR=IXR/N;
      IXL=IXL/N;


 % Adaptive hill evaluation
  I_v=(IXR-IXL)/(2*h);
 I_vv=(IXR-2*IX+IXL)/(h*h);
ss(t)=sign(I_v);

 % Decision making
  if abs(I_v)< thresh && abs(IX)< thresh && I_vv<0
     disp('The CSS strategy w is:')
     disp(u)
     w=u;
     break
  end
```

Fig. 5: Matlab code for calculating the gain of v over u.



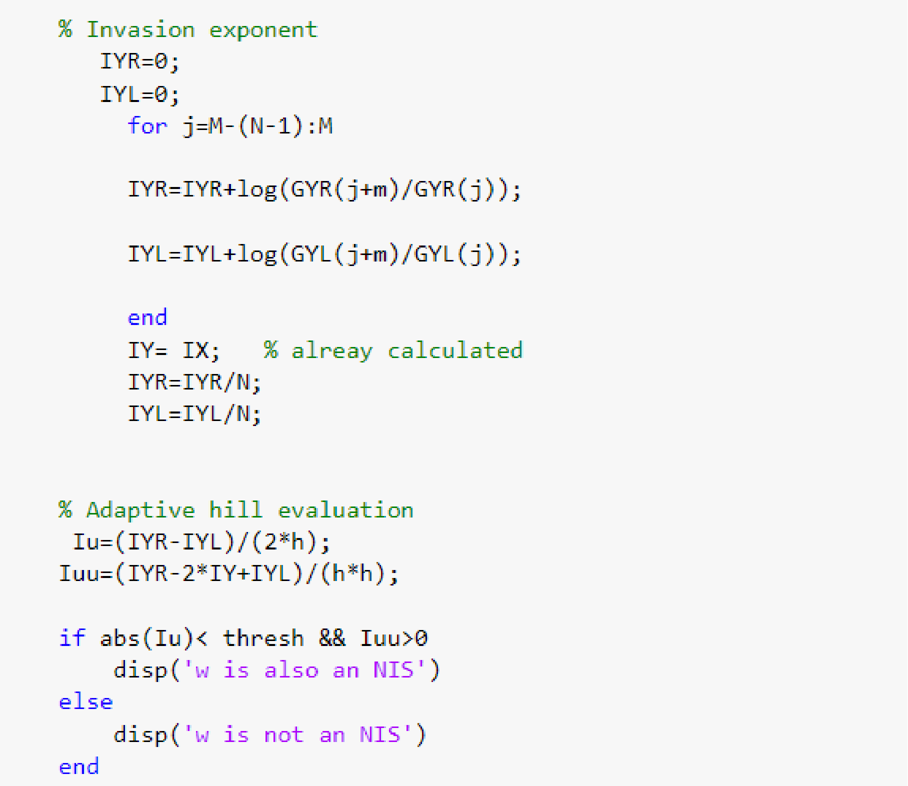
```
 % Step size adjustment
  if t==1                 % first recursion
     f=f;
  elseif ss(t)~=ss(t-1) % change in sign, optimum passed
     f=f/10;              % reduce step size
  end

  if I_v<0
     u=u-f;               % change direction
  end

  if I_v>0
     u=u+f;               % keep direction
  end

  if f<0.000001 || u<0  % when there is no optimum
     disp('elusive w')
     break;
  end
```

Fig. 6: Matlab code for determining evolution step size f and direction of improved fitness



```
for i=1:m
    YR(i)=in;    % pure YR generated at w+h
    YL(i)=in;    % pure YL generated at w-h
    GYR(i)=in;   % gain generated from YR at w
    GYL(i)=in;   % gain generated from YL at w
end
    uR=w+h;
    uL=w-h;

  for i=1:M
         for ii=i:i+(m-1)
        PYR(ii)=(r/(1+(YR(ii)/K)^uR))*YR(ii);
        PYL(ii)=(r/(1+(YL(ii)/K)^uL))*YL(ii);
       pYR(ii)=(r/(1+(YR(ii)/K)^w))*GYR(ii);
       pYL(ii)=(r/(1+(YL(ii)/K)^w))*GYL(ii);
         end

      % Build next generation
      yR=0;   yL=0;
     gyR=0;  gyL=0;

         for j=1:m
         yR=yR+A(j)*PYR(i+m-j);
         yL=yL+A(j)*PYL(i+m-j);
        gyR=gyR+A(j)*pYR(i+m-j);
        gyL=gyL+A(j)*pYL(i+m-j);
         end

  YR(i+m)=yR;
  YL(i+m)=yL;
 GYR(i+m)=gyR;
 GYL(i+m)=gyL;
 end
```

Fig. 7: Matlab code for generating the gain populations either side of the CSS population $\bar{X}_w$



```
% Invasion exponent
   IYR=0;
   IYL=0;
     for j=M-(N-1):M

     IYR=IYR+log(GYR(j+m)/GYR(j));

     IYL=IYL+log(GYL(j+m)/GYL(j));

     end
     IY= IX;   % alreay calculated
     IYR=IYR/N;
     IYL=IYL/N;


% Adaptive hill evaluation
 Iu=(IYR-IYL)/(2*h);
Iuu=(IYR-2*IY+IYL)/(h*h);

if abs(Iu)< thresh && Iuu>0
    disp('w is also an NIS')
else
    disp('w is not an NIS')
end
```

Fig. 8: Matlab code for determining if the CSS, w, is also a NIS

Contribution of Individual Authors to the Creation of a Scientific Article (Ghostwriting Policy)

The authors equally contributed in the present research, at all stages from the formulation of the problem to the final findings and solution.

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Conflict of Interest

The authors have no conflicts of interest to declare that are relevant to the content of this article.

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