

Effects of Immigration on the Dynamics of Simple Population Models

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Many simple population models exhibit the period doubling route to chaos as a single parameter, commonly the growth rate, is increased. Here we examine the effect of an immigration process on such models and explain why in the case of one-dimensional ("single-humped") maps, immigration often tends to suppress chaos and stabilise equilibrium behaviour or cyclical oscillations of long period. The conditions for which an increase of immigration "simplifies" population dynamics are examined. © 1999 Academic Press

1. INTRODUCTION

Consider a single population whose growth is controlled by simple deterministic birth and death processes. We are interested in exploring what might result if there were a constant (typically small) influx of individuals into the population via an immigration process. Under what conditions would this influx stabilise or destabilise the population's equilibrium? Or, if the population cycles in time, possibly even displaying erratic chaotic behaviour, does this immigration serve to simplify (e.g., by restoring equilibrium) or complexify the dynamics? Recently there has been considerable interest in these elementary, but nevertheless important questions, which form the basis for understanding the role of immigration and its influence on population dynamics (Holt 1983, McCallum 1992, Stone 1993, Ruxton 1994, Sole and Bascompte 1994, Doebeli 1995, Rohani and Miramontes 1995, Sinha and Parthasarathy 1996, Ruxton and Rohani 1998).

Holt (1983) was one of the first to recognise that an influx of immigrants from surrounding peripheral island

populations could stabilise a chaotic mainland population. Independently, McCallum (1992) arrived at similar conclusions motivated by an interest in the highly variable population dynamics of the crown of thorns starfish *Acanthaster planci* and its associated larval recruitment patterns. These findings were analysed in Stone (1993), where the actual mechanism by which immigration suppressed chaos and stabilised simpler dynamical responses was elaborated. It was found that immigration has the potential to modify the well-known period-doubling route to chaos and to induce unusual period-doubling reversals. Rohani and Miromantes (1995) followed these ideas, focusing their study on host-parasitoid systems where the phenomenon of period-doubling reversals also appeared upon allowance of immigration. The common thread in all the above analyses lay in the observation that immigration is often, although not always, capable of buffering an oscillatory population and conferring it with a stable equilibrium. This general conclusion, however, has not been without controversy. Doebeli (1995), for example, in attempting to synthesize general relationships between immigration and stability, argued that many of the results of these earlier studies "should be viewed with caution." In this paper we attempt to develop these issues further.

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2. STABILIZATION PROPERTIES OF IMMIGRATION

Consider the general discrete-time single population model:

$$x_{n+1} = F_c(x_n) = f(x_n) + c. \quad (1)$$

In this equation, x_n represents the population abundance at a certain time, x_{n+1} represents that abundance one time step later, and c is a non-negative constant representing immigration into the population. The function f is usually nonlinear and takes density-dependent growth into account via birth–death processes. The equilibrium or fixed point(s) x_c^* may be found by solving the equation $x_c^* = F_c(x_c^*)$. The mathematical stability of an equilibrium point x_c^* can be deduced by linearising (1) about equilibrium by setting $x_n = x_c^* + \delta$ and applying a Taylor expansion. Close to equilibrium, terms of δ^2 and higher are negligible and the linearized equation reads

$$\delta_{n+1} = F'_c(x_c^*) \delta_n, \quad (2)$$

where $F'_c(x_c^*)$ is the derivative of F_c evaluated at x_c^* . One sees immediately that the equilibrium point is locally stable if

$$|F'_c(x_c^*)| < 1, \quad (3)$$

and the system will then eventually return to the equilibrium point after a small perturbation. Under this condition, the higher the value of $|F'_c(x_c^*)|$, the weaker the stability of the equilibrium point, and the longer it will take to recover from a perturbation from equilibrium (Stone *et al.* 1996). More specifically, setting $a = F'_c(x_c^*)$ we see that the return to equilibrium is geometric with

$$\delta_n = a^n \delta_0. \quad (4)$$

Thus, $|F'_c(x_c^*)|$ can be regarded as a measure of the stability of x_c^* ; high stability corresponds to low absolute values of the derivative at equilibrium. On the other hand, if x_c^* is not stable, then $|F'_c(x_c^*)|$ is a measure of the speed at which a system initially close to an equilibrium will be repelled from that equilibrium.

When $F'_c(x_c^*) = 0$ the equilibrium is defined as *super-stable* since perturbations decay to equilibrium in a manner that depends on higher order terms, rather than the linearisation (2). For example, if $F''_c(x_c^*) \neq 0$,

$$\delta_n \sim K^{2n} \delta_0^{2n}, \quad (5)$$

where K is a constant. The speed of return to equilibrium is now considerably faster than geometric, thus justifying the terminology “superstable”.

The effects of immigration on the stability of the equilibrium point can be easily deduced when F_c is single-humped and $F'_c(x_c^*) < 0$. (Here, by “single-humped,” we mean a typically smooth and non-negative function with exactly one critical point, a maximum, and at most one point of inflection to the right of the maximum.) A graphical analysis of Eq. (1) under these conditions reveals that an increase in the immigration parameter c must increase x_c^* . Thus, if $F''_c(x_c^*) < 0$, and since $F'_c(x_c^*) < 0$, a small additional increase in immigration will increase $|F'_c(x_c^*)|$ and hence destabilize the equilibrium point. Similarly if $F''_c(x_c^*) > 0$, an increase in immigration will stabilize the equilibrium point.

To summarise the statements above (cf. Doebeli 1995):

(S1) The equilibrium point x_c^* is stable if $|F'_c(x_c^*)| < 1$. The stability of the equilibrium x_c^* depends on the value of the derivative at equilibrium. The smaller the value of $|F'_c(x_c^*)|$, the “stronger” the stability and the faster the return time to equilibrium after a small perturbation. The (local) stability of x_c^* is strengthened by a small increase in immigration if $|F''_c(x_c^*)| > 0$, while it is weakened if $|F''_c(x_c^*)| < 0$.

It is important to note that the simple local stability conditions for the equilibrium point given in (S1) convey little indication on the effect of immigration on the existence or stability of periodic orbits or chaos, as will be discussed further below.

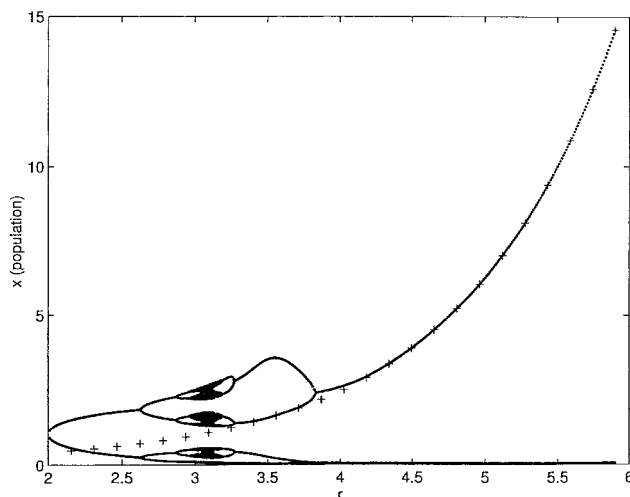


FIG. 1. Bifurcation diagram of the Ricker map, Eq. (6), with immigration parameter $c = 0.055$. The points marked “+” are calculated from the approximation (10) derived in the text.

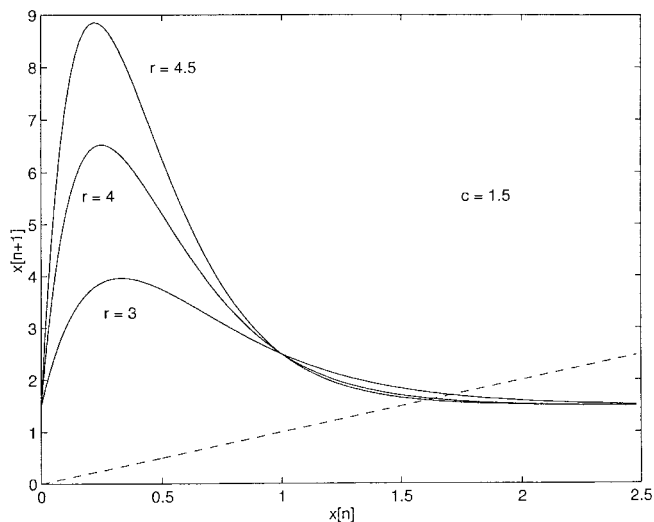


FIG. 2. Return map $F_c(x)$ when $c = 1.5$ (Eq. 6).

Examine now the well-known Ricker map with a parameter c representing immigration into the population:

$$x_{n+1} = F_c(x_n) = x_n \exp[r(1-x)] + c. \quad (6)$$

When $c = 0$ (i.e., no immigration), the classical period-doubling route to chaos may be observed as the growth rate r is increased (May 1976). One of the major aims of Stone (1993) was to show that adding even a small amount of immigration (i.e., taking c slightly greater than zero) causes the period-doubling route to chaos to eventually reverse itself. Increasing the parameter r first produces a series of period-doubling bifurcations, but as

r gets larger still, then a sequence of period-halving bifurcations follow (see Fig. 1); these period-halving bifurcations do not occur when $c = 0$. As discussed there, the reversal of the period-doubling route to chaos is common to a broad class of single-humped functions $F_c(x)$, and is not a particular property of the Ricker map.

In order to understand why immigration inhibits chaos at larger growth rates and tends to “stabilise” the Ricker map, we first consider an exaggerated case where immigration constitutes a sizeable fraction, say in the range of 15–40%, of the maximum possible population (which may be calculated as $F_c(1/r)$). Figure 2, for example, plots $F_c(x)$ versus x for such a case with $c = 1.5$, for several values of r . One sees how the immigration term in this map creates a “floor” below which the population can never fall (McCallum 1992, Stone 1993, Ruxton and Rohani 1998). The equilibrium may be determined graphically, and lies exactly at the intersection point of the graph F_c and the 45-degree line ($x_{n+1} = x_n$). The derivative $F'_c(x_c^*)$ is therefore the slope of the graph F_c at this intersection point, and for the cases examined in Fig. 2, one sees visually that $F'_c(x_c^*) \approx 0$. This can be attributed to the long, almost horizontal plateau in the tail of the Ricker map for large values of x . Sufficient immigration c serves to vertically translate this horizontal plateau, so that it intersects the 45° line, thereby producing an equilibrium x_c^* for which $F'_c(x_c^*) \approx 0$. Equilibria created by this mechanism can be highly stable and approach superstability.

These last points are illustrated in Fig. 3a, where the iterates of the Ricker map are plotted when $r = 1.99$ for different immigration levels c . (Note that the Ricker map bifurcates from an equilibrium to a 2-cycle at $r = 2$, so

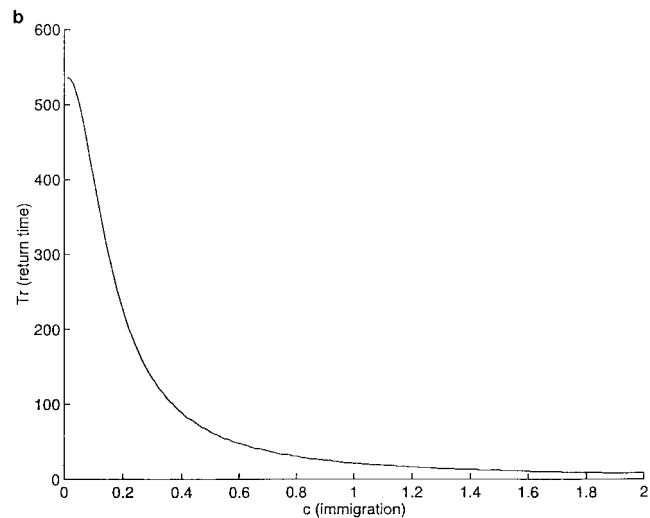
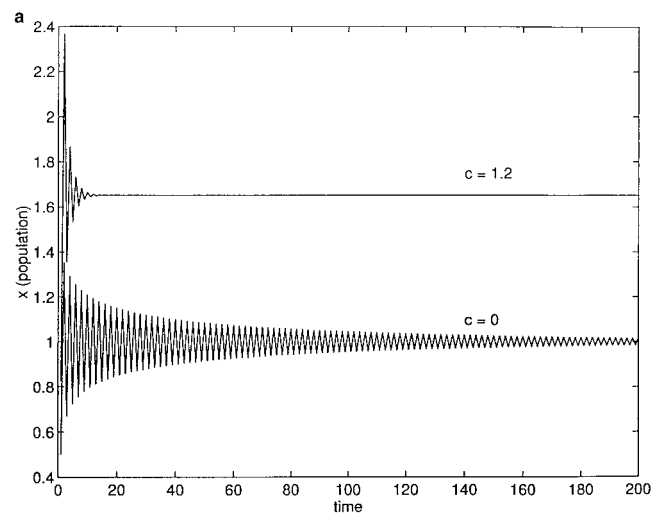


FIG. 3. Ricker map (6) when $r = 1.99$. (a) Time series evolution of the map after an initial perturbation demonstrating return time, T_r , to equilibrium. (b) Plot of the return time, T_r , as a function of the immigration parameter c .

that the equilibrium at $r = 1.99$ has only weak stability (since $|F'_c|$ is close to unity.) Both time-series in Fig. 3a begin from an initial condition $x_0 = 0.5x_c^*$, i.e., at 50% of the model population's equilibrium value, and decay back to the equilibrium at different speeds. Now define the return time T_r as the number of iterations required for the model beginning with the initial condition $x_0 = 0.5x_c^*$ to decay back to within 0.1% of its equilibrium (Stone *et al.* 1996). In this example, the population without immigration ($c = 0$) requires some 540 iterations before settling to within 0.1% of its equilibrium level, and thus has a return time $T_r = 540$. But the population in which immigration is large $c = 1.5$ has the astonishingly short return time of $T_r = 9$. This rapid

return rate is due to the near superstability conferred upon the population's equilibrium by the large immigration influx. More generally, we have plotted the return time T_r as a function of immigration c (Fig. 3b). The graph shows that immigration has the potential to dramatically reduce the return time T_r .

The high stability imparted to the population dynamics by immigration does not only occur for the relatively large levels of immigration just investigated. Consider an immigration influx that is roughly of the order 1–5% of the maximum population. In this example we choose $c = 0.055$, confirming with the bifurcation diagram in Fig. 1. Note from Fig. 1 that at large values of r there is a persistent two-cycle in the regime

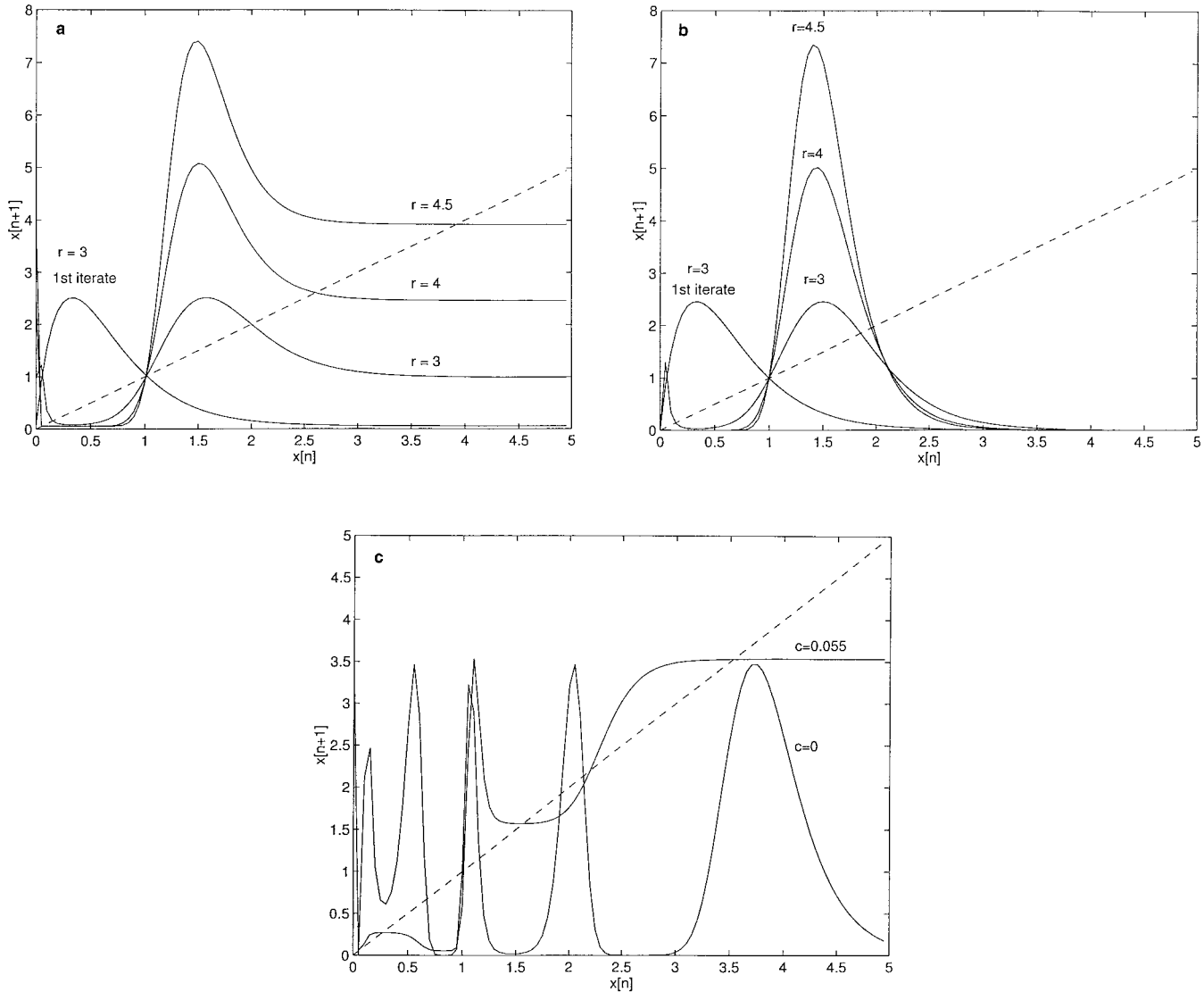


FIG. 4. (a) the first and second iterate (i.e., $(F_c(x))$ and $(F_c^2(x))$) of the Ricker map when $c = 0.055$ for different values of r . (b) Same as (a) except with $c = 0$. (c) The fourth iterate $F_c^{(4)}$ when $r = 3.5$ with $c = 0$ and $c = 0.055$.

where we would normally have expected chaotic dynamics had there been no immigration ($c=0$). Iteration of the map on this two-cycle yields the sequence

$$p \rightarrow q \rightarrow p \rightarrow q \rightarrow p \rightarrow \dots \quad (7)$$

where the steady states p and q must satisfy

$$q = F_c(p) \quad \text{and} \quad p = F_c(q). \quad (8)$$

Alternatively, we may write the points p and q as fixed points of the second iterate of the map F_c , i.e.,

$$q = F_c^2(q) \quad \text{and} \quad p = F_c^2(p), \quad (9)$$

where $F_c^2(x) = F_c(F_c(x))$.

We have graphed $F_c^2(x)$ in Fig. 4a for three values of r when $c = 0.055$; it should be compared with Fig. 4b for the case in which $c = 0$. One sees that the small level of immigration has a major impact on the map $F_c^2(x)$ and its fixed points. In particular, for the examples in Fig. 4a, when $r > 3$, the slope of $F_c^2(x)$ at the fixed points, $F_c^2(x)$, is approximately zero. These maps thus enjoy a highly stable (almost superstable) 2-cycle.

The fixed points p and q of $F_c^2(x)$, as seen in Fig. 4a, may be approximated as follows. Since the parameters of the Ricker map (6) chosen satisfy $r \gg 1 \gg c > 0$ (so that $ce^r \gg 1$), then for $x \gg 1$, $F_c(x) \approx c$ while $F_c(c) \gg 1$. Iteration of the map thus approximates the sequence (7) where $p \approx c$ and $q \approx F_c(c)$. This explains the existence of the two fixed points seen in Fig. 4a for the map $F_c^2(x)$ when $r > 3$, and moreover allows their numerical values to be calculated to a good approximation.

Consider the bifurcation diagram in Fig. 1 once again. According to the approximations above, the larger fixed point q of the 2-cycle should be well approximated by

$$q = F_c(c) = ce^{r(1-c)} + c. \quad (10)$$

The predicted values of q are plotted in Fig. 1 as a function of r and are in excellent agreement with the numerically obtained values.

The stability of the 2-cycle at the points $p \approx c$ and $q \approx F_c(c)$ may also be estimated. First note that because $q = F_c(c) \gg 1$, $F_c(q)$ lies well into the horizontal plateau of the map F_c , so that $F_c'(q) \approx 0$. But the stability of the points p and q depend on the derivative:

$$F_c^2'(p) = F_c^2'(q) = F_c'(p)F_c'(q) \approx 0. \quad (11)$$

In other words, the 2-cycle also inherits very strong stability properties. The development of the strong 2-cycle when growth rates (r) are high seems to be a feature of many simple “single hump” population models.

An indication of the effect of immigration on higher order iterates of the map F_c may be gained from an examination of Fig. 4c. Here we examine the fourth iterate of F (i.e., F^4) for $r = 3.5$ for the case when there is no immigration ($c = 0$) as well as the case where immigration conforms with that in Fig. 1 ($c = 0.055$). All 4-cycles are located at the intersection of the graph F^4 and the 45° line. It is hard to miss the striking horizontal “plateau” induced by immigration in the map F^4 which cuts the 45° line, thereby creating an extremely stable 4-cycle.

3. DOES IMMIGRATION SIMPLIFY DYNAMICS?

As observed in Fig. 1, the Ricker map, when subject to immigration, initially follows the period-doubling route to chaos as the growth rate r is increased. A series of period-halving bifurcations ensue when r increases beyond some threshold value. Depending on the level of immigration, the period-halving bifurcations can begin before the onset of chaos (Stone 1993). Thus by suppressing or controlling the map’s chaotic dynamics immigration can in this sense destroy the so-called quantitative universality described in Feigenbaum (1978). It is interesting to reread Feigenbaum’s (1978) original paper, where he begins with a description of a biological population model that takes the form of a one-dimensional map $f(p)$, qualitatively similar to the Ricker map, with a long concave “tail” so that F “goes to zero for large p ” (see his Fig. 1). Thus even the map in Fig. 1 of Feigenbaum would fail to follow the “universal” period-doubling route to chaos in the presence of small levels of immigration. On the other hand, as is well known and will be discussed below, adding an immigration term to the familiar single-humped logistic map $F_c(x) = rx(1-x) + c$ will never yield period-halving bifurcations. We are thus led to ask the question: under what conditions does the addition of immigration lead to “simplified” dynamics via period-halving bifurcations? Similarly, under what conditions does immigration generate a more complex sequence of period-doubling bifurcations?

To our knowledge Doebeli (1995) is the only one who has examined this question and attempted to provide criteria as to whether or not immigration stabilised the dynamics of a model population. According to Doebeli in his Introduction, "...stabilization is understood, not in the mathematical, but the intuitive sense; as a process leading to more regular and simple dynamics." We note, however, that the usual notions of stability are not equivalent to the notion of dynamical simplicity. (For example, a stable two-cycle can be more stable in terms of return time from a perturbation than a "simpler" stable equilibrium point.) Nevertheless, Doebeli argued that it is possible to equate the local stability of the equilibrium with the simplicity of the system. More specifically, he claimed that the response of the system to immigration depends on the rate of change of $|F'_c|$ at the equilibrium point. Based on this idea, Doebeli provided a recipe for deducing whether or not immigration will lead to simpler dynamics. He argued that this can be easily determined by examining (1) (under the general assumption that $F'(x_c^*) < 0$) when there is *no* immigration ($c = 0$); where, in his terminology, the equilibrium point is denoted by x^* :

(S2) "...the effect of immigration depends on whether the modulus $|F'_c(x)|$ is increasing or decreasing at x^* ..." and hence if $F''_c(x^*) > 0$, immigration "... will have a simplifying effect on dynamics. It will have a contrary effect if $F''_c(x^*)$ is negative."

In other words, Doebeli suggested that one need only evaluate the local stability specifically when there is no immigration ($c = 0$) to qualitatively determine how a system, no matter what immigration levels it experiences, will be affected by changes in immigration.

We see two major problems with criterion (S2). First, as we have already touched on, it equates simplicity with local stability of the equilibrium. Although the effect of additional immigration on the stability of the equilibrium point is correctly described by (S1), there is no general connection between the stability of the equilibrium point and the simplicity of the system's dynamics, as Doebeli's arguments leading to statement (S2) would imply. Second, it (wrongly) suggests that the local stability behaviour of the equilibrium evaluated when $c = 0$ has some global validity in characterizing the model's stability when $c > 0$. The following examples make these difficulties more transparent.

Examine first the logistic map with constant immigration

$$x_{t+1} = F_c(x_t) = Rx_t(1 - x_t) + c, \quad (12)$$

where both R and c are assumed to be non-negative. Note that this map is, up to a linear change of coordinates, identical to the logistic map without immigration

$$x_{t+1} = f(x_t) = rx_t(1 - x_t), \quad (13)$$

the two maps being connected via the relation $(r - 1)^2 = (R - 1)^2 + 4Rc$. It is useful to analyze the simpler map f as a means of understanding the dynamics of F_c . When $r > 2$, $f'(x) = r - 2rx^* = 2 - r < 0$ and is a decreasing function of r . Hence $F'_c(x^*)$ is a decreasing function of c . According to Doebeli's argument and criterion (S2), since $f''(x^*) = F''_c(x^*) = -2r < 0$, the dynamics of both of these system should become more complicated as either r or c increases. However, this is not necessarily the case. As is well known, when r is greater than a critical point r_* ($r_* \approx 3.57$) the system is generally chaotic, but "windows of stability" exist within the region $r_* \leq r \leq 4$, where there are stable periodic orbits (May, 1976). By increasing either r or c , it is therefore possible to move systems from a chaotic state with no stable periodic orbits to a state which possesses a stable periodic cycle. At such a transition, an increase in r or c makes the dynamics of such a system simpler and its stability stronger. In other words, even though $F''_c(x^*) < 0$ and $|F'_c(x_c^*)|$ is an increasing function of immigration, additional immigration can still lead to simpler dynamics, contrary to statement (S2). Therefore the stability of x^* reflects neither the global stability characteristics nor the dynamical simplicity of the system.

Maynard Smith and Slatkin's (1973) population model provides another interesting case study:

$$x_{t+1} = F_c(x_t) = \frac{\lambda x_t}{1 + (ax_t)^b} + c. \quad (14)$$

McCallum (1992) already showed that the effects of immigration on this system are quite complicated, and while adding a small amount of immigration may stabilise a chaotic system, adding a small amount of additional immigration can then destabilise the system once again. Figure 5 shows a bifurcation diagram for this system with $\lambda = 2.2$, $a = 0.5$, and $b = 5.088$ and where the immigration parameter c is varied in the interval $[0, 0.5]$. The dynamics without immigration are complex and aperiodic. The non-trivial unstable equilibrium point is located at $x^* \approx 2.073$, and the values of the first and second derivatives at equilibrium are $F'_0(x^*) \approx -1.775$ and $F''_0(x^*) \approx -0.720$. According to Doebeli's criterion (S2), immigration should make the dynamics more complex since $F''_0(x^*)$ is negative and hence $|F'_c|$ at equilibrium

will be larger with a small amount of immigration than it is with none at all. In fact, $|F'_c(x_c^*)| > |F'_c(x^*)|$ for all c in the interval $[0, 0.5]$, so for any amount of immigration c in this interval, the local stability of the equilibrium point is less with immigration than without. Therefore, Doebeli's criterion would imply that the dynamics of the system with immigration (for $0 < c \leq 0.5$) should be more complex than without immigration. However, as can be seen from Fig. 5, as the immigration parameter c is increased from 0 to 0.5, the system undergoes a sequence of period-halving bifurcations. That is, contrary to the predictions of Doebeli's criteria, immigration causes the system to become simpler.

The question then of when a change in a parameter "simplifies" or "stabilises" a system seems to be a non-trivial mathematical problem. While the concavity of the function at the equilibrium point does give some hint of whether immigration will induce period-doubling or period-halving bifurcations (Stone 1993), the sign of $F''_c(x^*)$ cannot by itself predict what the effect of immigration will be.

As another example, consider again the system (14), now with the parameters $a = 0.6$, $b = 10$, $\lambda = 1.2$ and with the immigration parameter c varying from 0 to 1 (see Fig. 6). With no immigration, the system has a stable equilibrium x^* and in this case, $|F'_c(x^*)|$ is a clear indicator of the stability of the system. In addition $F''_c(x^*) < 0$, which indicates that a small amount of immigration can weaken the stability of the system and perhaps make the dynamics more complex. And as can be seen, increasing immigration at first induces a

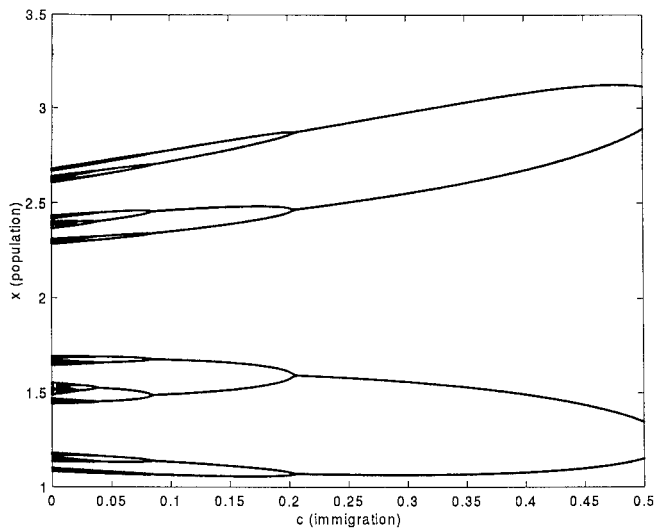


FIG. 5. Bifurcation diagram for Eq. (14) with $\lambda = 2.2$, $a = 0.5$, $b = 5.088$, and the immigration parameter c varying between 0 and 0.5.

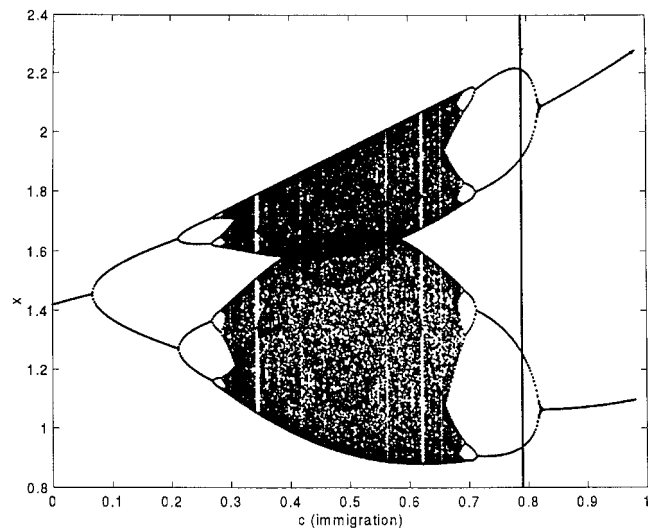


FIG. 6. Bifurcation diagram for Eq. (14) with $\lambda = 1.2$, $a = 0.6$, $b = 10$, and the immigration parameter c varying between 0 and 1.

sequence of period-doubling bifurcations. However, higher amounts of immigration induce a period-halving cascade, which finally results for very large amounts of immigration, in once again a stable equilibrium (not shown). The relative change of $|F'_c(x^*)|$ is not here a good indicator of the dividing line between the regimes where the dynamics become more complex (period-doubling) or more simple (period-halving); $|F'_c(x^*)|$ continues to increase with additional immigration even at the beginning of the period-halving cascade, where the dynamics are clearly simplifying (contrary to the predictions of S2). It is only at about $c = 0.79$ (indicated by the vertical line in Fig. 6), where the system has an attracting orbit of period 4, that $|F'_c(x_c^*)|$ begins to decrease.

4. DISCUSSION

We do not know of simple but general criteria that completely characterise the effect of immigration on population dynamics; it is not clear that such criteria even exist. There are, however, in the context of the population model (1), some observations that can be made, under the assumption that $F_c(x)$ is a single-humped non-negative function. First, a large enough quantity of immigration into the system (i.e., a sufficiently large value of c) will always simplify the system. This is because the fixed point will then be located in the (almost) flat plateau region in the tail of F_c (Stone 1993) and therefore be stable since $|F'_c(x_c^*)| \approx 0 < 1$. More formally, since $f = F_0$ (see Eq. (1)) is non-negative and decreasing for

x greater than the local maximum, $\lim_{x \rightarrow \infty} f'(x) = 0$. Hence, in particular, there must exist a number $M > 0$ such that if $x > M$ then $|f'(x)| < 1$. If $c > M$, then $x_c^* \geq c > M$, since f is nonnegative. Thus, $|F_c'(x_c^*)| = f'(x_c^*) < 1$, whence x_c^* is a stable equilibrium. Therefore, immigration at a level greater than M will always induce a stable fixed point.

Second, in wide classes of models, where with no immigration an increase in some parameter causes period-doubling bifurcations leading to chaos, even a small amount of immigration into the population is often enough to eventually reverse this process and, for sufficiently large values of the parameter, cause period-halving bifurcations. Interestingly, this same type of phenomema occurs in many other settings (Wilder *et al.* 1994, Astrom *et al.* 1996, McCann and Hastings 1997). We have noted it, for example, in a continuous SEIR epidemic model. McCann and Hastings (1997) observed similar behaviour in a foodweb model when the introduction of omnivory created a population floor bounding population minima away from zero, in a manner rather like the immigration effect discussed here. Last, we note that until now most theoretical studies dealing with the effects of immigration on population models have focused on equilibrium analyses of the map F_c . We have demonstrated here that the higher iterates of the map, i.e., F_c^n display dramatic sensitivity to very small levels of immigration.

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