

Chapter 1

Environmental Microcatastrophes

This opening chapter presents an approach which is often used to investigate the behavior of complex systems when the number of equations that allow for interactions of their many parameters is too large and the direct methods are impracticable. A good way to illustrate the approach is to apply it to a forest ecosystem in terms of its resistance against pest insects and environmental microcatastrophes associated with insect outbreaks. They are called “microcatastrophes” as it is a single ecosystem that runs a risk of destruction.

Population outbreaks, in which populations suddenly increase many times, have occurred in nature long before the appearance of man, for instance, the well-known disasters such as plagues of mice, lemmings or locusts. Man interferes with the natural dynamics of animal populations, being able to both provoke and stop outbreaks. In some cases man-induced outbreaks can result from introducing a new species to a country that naturally lacks conditions to control its numbers (say, natural enemies). This was the case of rabbit brought to Australia by European settlers, or Colorado beetle, a potato pest, accidentally brought to Europe and Asia. On the other hand, there exist chemical and biological methods of mitigating risks from insects and other pests.

Forest pests offer a classical model of natural population outbreaks, such as, for instance, outbreaks of black fir beetle (*Monohamus urussovi* Fish.) that inhabits the Sayan Mountains in Siberia. At the beginning of its outbreak, the population of insects in a forest is very small but then it grows suddenly, increases tenfold for a few years, and sweeps over the forest to destroy a great part of trees; eventually, the outbreak fades and the population returns to its previous moderate numbers.

We study the important problems of population dynamics, such as stabilization of populations, cyclic processes in population density, and population outbreaks, using a very simple model. Although simple, it can describe and predict outbreaks of insect populations just by means of straightforward plotting without any resort to calculations.

Phase portraits

Prediction of the population density in a coming year from its density in a current year is a key point in studies of population dynamics. If the number of insects of some species living in some area is K in a current year and M in the following year, the ratio M/K measures the growth (if $M/K > 1$) or decline (if $M/K < 1$) of the population. The ratio M/K is called the reproduction rate of the species in a given habitat. The population number is proportional to the surface area and M/K is constant throughout the habitat if individuals are evenly distributed and the environment is more or less uniform. In such cases population dynamics can be studied in selected sample areas of, say, one square mile. In fact, M/K may differ through different parts of the forest and, what is most important, through different years. The current number of insects obviously influences reproduction as it controls the availability of food and habitat resources. For example, a too large population (overpopulation) slows down its reproduction because less progeny can survive in the conditions of severe competition.

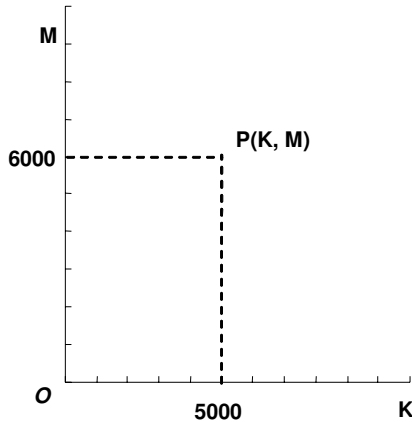


Fig. 1. A single standard observation on the phase plane (K, M) , where K is the number of insects in a year, M is the number of insects a year after.

Thus there is no simple rule to predict the population density in some year from its density in the previous year. The problem can be solved using the method of phase portraits. Phase portraits are plotted in the Cartesian coordinates as points in the phase plane with the coordinates made by pairs of numbers (K, M) which are called standard observations and obtained by counting insects of a given species living within a given area in a current year (K) and insects in the same area in the following year (M). The K and M axes are assumed to have the same scale (Fig. 1), for example, 1000 individuals. A standard observation is represented in Fig. 1 by the point P with the coordinates (K, M) , with $K = 5000$ and $M = 6000$, or 5000 individuals in a current year and 6000 insects a year later.

The totality of standard observations for several years (in the same or different areas) plotted in the phase plane makes up a “cloud” of points (Fig. 2), which is called the *phase portrait* of the respective population.

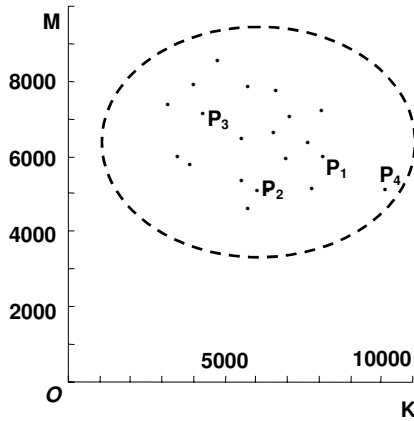


Fig. 2. Phase portrait of a population comprising standard observations for several pairs of successive years.

Each point in the cloud represents two counts (K and M) of population density in two successive years (Fig. 2). For instance, the point P_1 corresponds to 8000 insects counted in 1995 (K axis) and 6000 insects in 1996 (M axis) and P_2 shows the population change from 6000 insects in 1996 to 5000 in 1997; P_3 and P_4 are for 4000 insects in 2000 and 7000 in 2001 and 10000 insects in 2002 and 5000 in 2003, respectively, etc.

Even though different points of the cloud can correspond to the same area (and different years), in the general case they are related to different areas and image the results of numerous long-term observations each taken at two successive years. A question arises whether the data obtained this way represent any dependence between the population numbers K in the current year and its numbers M in the next year on the same plot. Generally, there is no such dependence as any K can have more than one M in the cloud because besides the initial number of insects their reproduction depends on the environment, weather, or living quality of the selected habitats.

However, in many important cases environment factors are less essential than the initial population density K , and the cloud of Fig. 2 then becomes elongate (Fig. 3a). The cloud stretching and narrowing (provided that observations are complete) mean that the population in

the following year ranges within a narrow interval (M_1 , M_2) for any specific K .

A cloud which is narrow enough can be approximated by a curve (Fig. 3b). This is an approximate phase portrait giving a tentative idea of

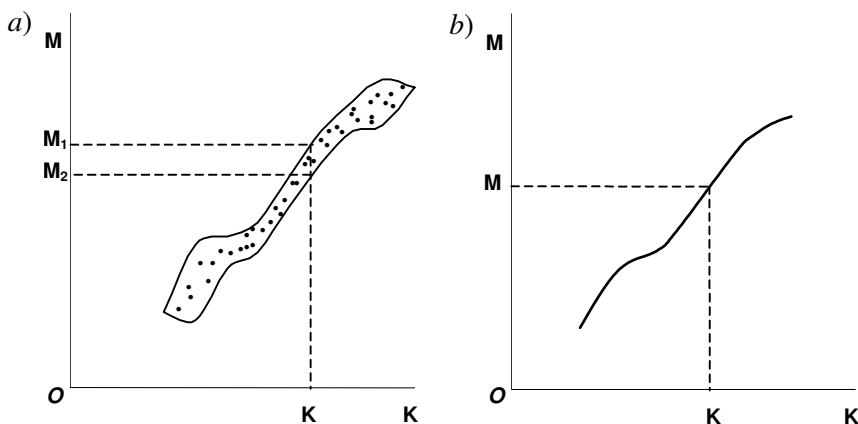


Fig. 3. Narrow phase portrait of a population (a), and its approximation by a curve (b).

reproduction without allowance for environment and climate controls. Thus any K corresponds to a single M (Fig. 3b) and their relationship is a function where K is the argument and M is the function.

In simple cases, functions are defined by equations such that a function is easily obtained from its argument ($M = K^2$, $M = (K+1)^3$, or $M = \log K^2$, etc.). These equations are usually mathematically proved or obtained from physical theories for simple natural phenomena. Yet, the processes challenged in environment science (or in other sciences such as biology, economics or sociology) are often too confusing to be described by mathematical equations but can be approximated by empirical relationships [Kolmogoroff, 1937, etc.] like the curve in Fig. 3b.

Substituting a curve (Fig. 3b) for a narrow cloud (Fig. 3a) is a very common procedure applied to any empirical function (obtained from experiment). The cloud of standard observations can be in fact much narrower than that shown in Fig. 3a, and the approximation 3b is in this case more exact. We assume this approximation to be valid in population

dynamics problems, as well as other problems of environment, sociology, and economics discussed below. Of course, this assumption requires a support from experience, and it does agree with practice quite often.

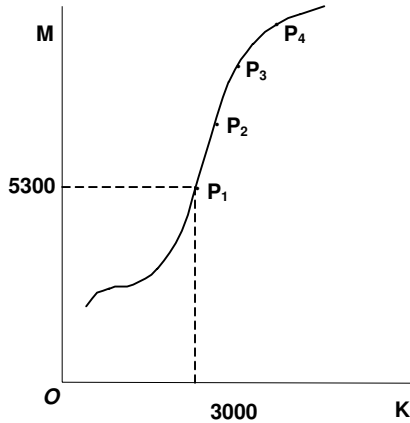


Fig. 4. Standard observations P_1, P_2, \dots , plotted to make an empirical reproduction curve considered as the phase portrait of a population.

The phase portraits of processes (e.g., see the series of points P_1, P_2, \dots , etc. in Fig. 4, standard observations over many years making up an empirical reproduction curve) are plotted assuming that the processes can be described by clouds almost coinciding with a curve. Thus the phase portraits considered below are actually the phase curves, or the plots of some functions.

The most general trends are evident already from the very shape of phase curves (Fig. 5). For instance, curve 1 everywhere rises (greater M correspond to greater K) and is an increasing function $M(K)$, whereas curve 2 everywhere falls (greater K corresponds to smaller M) being a decreasing function. The function of curve 3 first decreases and then increases having reached its minimum. Similarly, it is easy to plot a function with a maximum.

Curve 1 is convex. This means that any chord connecting two points cuts off an arc above the chord. A convex curve looks like an upside-down cup. Curve 3 is concave, i.e., its any chord truncates it to make an

arc below. A concave curve looks like a right-up cup. Curve 2 is first concave and then convex, and its concave and convex segments are separated by a point of inflection.

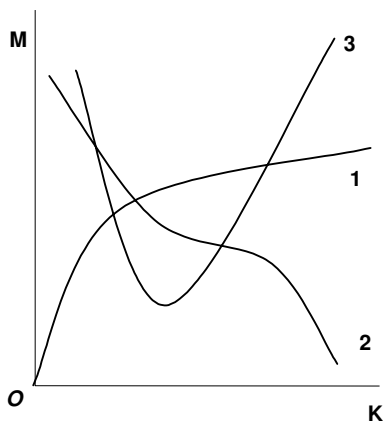


Fig. 5. Most general types of reproduction curves: increasing curve (1), decreasing curve (2), concave curve with minimum point (3).

Reflection from bisector

Phase portraits obtained from long-term observations can be used to predict changes many years in advance. This is best achieved by a straightforward geometric device applicable to many problems other than population dynamics.

Many populations have their phase portraits in the form of a convex curve that begins from the origin of coordinates O and crosses the bisector of the quadrantal angle at a single point (point 1 in Fig. 6).

Consider this common case in more detail. The origin of coordinates O represents the simplest and a quite natural standard observation when there are no insects at all in a current year ($K = 0$) and, naturally, no insects in the following year ($M = 0$). Of course, repeated observations drive to the same result, as predicted by the phase portrait: zero population in any current year and zero population in the following year.

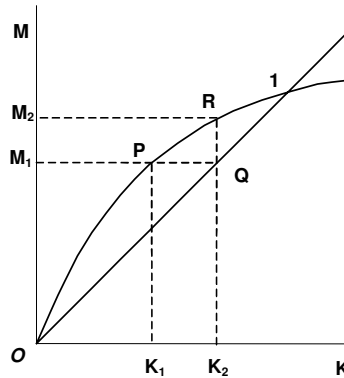


Fig. 6. Method of reflection from bisector applied to a convex reproduction curve.

This means that the population is extinct. A point on the phase curve where the population is constant ($M = K$) is its equilibrium point and the corresponding state of the population is its equilibrium state. Therefore, the bisector which is the totality of all points $M = K$ is of special importance to our further studies. The plot in Fig. 6 has a single equilibrium point besides O where the phase curve crosses the bisector (point 1). Let it have the coordinates K_s, M_s where “ s ” stands for “stable (equilibrium)”; then, $M_s = K_s$, i.e., the number of individuals (K_s) in a current year is exactly the same as in the following year (M_s), etc. Such exact equality is of course rare in practice but K can approach K_s . We show later what comes from that, and now consider the population a year after the first year of observation. It can be predicted from M_1 corresponding to K_1 (K_1 is taken positive but less than K_s . See the phase curve of Fig. 6). The same population another year later is predicted by repeated use of the same phase curve: It is the M -coordinate M_2 of the point R with K_2 equal to M_1 , as M_1 is then the initial population, and M_2 is the population a year after it was M_1 . To simplify the transition from P to R , see that both OK_2 and OM_1 are the sides of a square with the vertex Q on the bisector (as $OK_2 = OM_1$ and the bisector is the locus of points equidistant from both axes). Thus, the point Q can be easily found by drawing a horizontal line through P to cross the bisector. The point R has the same K_2 as in Q , and R is thus obtained by drawing a vertical line through Q to cross the bisector.

Therefore, the population M_2 a year after it was M_1 can be inferred geometrically: to pass from the point P of the phase curve to the point R , simply draw a horizontal line through P to cross the bisector in the point Q and then a vertical line through Q to cross the phase curve in R .

Then only M_1 and M_2 are to be used, without plotting K_1 , K_2 and the segments K_1P and K_2Q (Fig. 6). To predict the population M_2 , it is enough to plot the rectangle M_1QRM_2 knowing M_1 . The segments PQ and QR are at equal angles to the bisector (45°), like the light reflected by a mirror. That is why the device is called reflection from bisector.

Simple population processes

We begin with simplest processes described by increasing functions. Fig. 7 images a common and very important case of $M(K)$ relationship represented by a convex phase curve starting from the origin point O and crossing the bisector at a single point (point 1). The coordinate origin ($K = M = 0$) is an equilibrium point, but not an interesting one since the population does not exist there at all. The point acquires special importance when P approaches O and the population is extinct but it is evidently not the case for the considered type of the curve since population density at the interval above the bisector R is always to the right of P , and $K_2 > K_1$ (Fig. 6). Moreover, due to the convexity of the curve its chord OP goes down when P moves to the right (see Fig. 7) and, therefore, the slope of OP relative to the K -axis also decreases (the slope is measured by the ratio of the ordinate (M -coordinate) of P to its abscissa (K -coordinate) and equals the tangent of the angle of OP to the K -axis). Thus, the ratio M/K diminishes when K grows. The ratio, which is the reproduction rate of a population, measures how many times the next generation is larger (if $M/K > 1$) or smaller (if $M/K < 1$) than the previous one. On the contrary, the reproduction rate grows when K diminishes, and reaches the highest value at $K = 0$ associated with biologically vanishing population density. Mathematically, the highest value is achieved through passage to the limit: as K tends to zero, the slope ratio of the chord OP , equal to M/K , tends to some limit called the derivative of the function $M(K)$ at $K = 0$ and denoted as $M'(0)$. In terms of geometry the limit is the slope of the tangent to the curve at the point O .

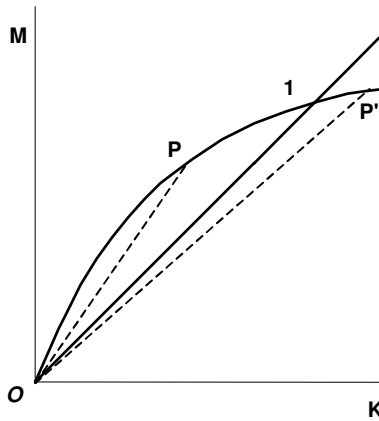


Fig. 7. $M(K)$ function represented by a convex phase curve which includes the origin point O and crosses the bisector at a single point (point 1).

The biological meaning of the result is that the reproduction rate of a population decreases after it has occupied the best habitats for feeding and laying eggs. Slower reproduction can also result from other factors such as contamination of environment with the population's life wastes, or infectious diseases. The competition for habitats might serve to avoid the negative effects. The ratio M/K is above unity till point 1 (at $K < K_s$, where K_s is the K -coordinate of 1) (Fig. 7) which means that $M > K$ and the population grows year by year. However, at $K > K_s$ the slope of OP becomes below unity, i.e., $M < K$ and the population reduces, which can be interpreted as the overpopulation effect [Baltensweiler, 1964; 1970; Baltensweiler et al., 1977].

Equilibrium states corresponding to the points $M(K) = K$ are of special interest. Once fallen at this point, the population obviously stays there forever. Of course, the result has only theoretical significance, since any casual disturbance can push the system out of the equilibrium state. That is why we concern mainly the states of stable equilibrium which a population tends always to return to after minor deviations. In our case the convex phase curve can cross the bisector at only one point. Let it be point 1, its K -coordinate be K_s , and its M -coordinate be $M_s = K_s$.

We show below that point 1 is a point of stable equilibrium of a population.

Let the point $P_0 (K_0, M_0)$ in Fig. 8 mark the state of a population having its initial density K_0 (K -coordinate of P_0) and the density M_0 in the next year (M -coordinate of P_0). The projections on the axes are omitted to make the picture better readable.

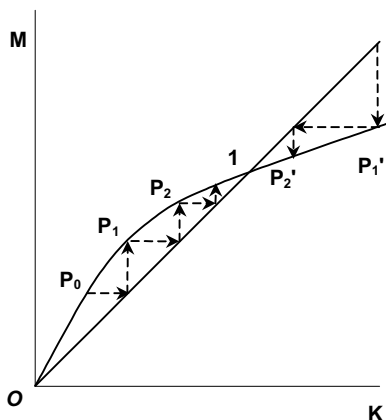


Fig. 8. Population dynamics for a convex phase curve.

At $K_0 < K_s$ (P_0 is on the left of 1), the reflection from the bisector moves P_0 into P_1 imaging the population state in the next year with the population density equal to the K -coordinate K_1 of the point P_1 (Fig. 8). Repeating this procedure gives P_2 with the K -coordinate K_2 equal to the population density in the following year after P_1 , etc. The points P_0, P_1, P_2, \dots arbitrarily approach point 1, so any population that initially was on the left of 1 evolves to approach the point of stable equilibrium (point 1) arbitrarily close (Fig. 8). On the other hand, if the initial state P_0' was on the right of 1, it grades into P_1', P_2', P_3', \dots , approaching 1 from the right. The effect of some casual factors can move the point P off or make it leap over state 1, but the population tends to recover its stable state from either direction. This is the phenomenon called a state of stable equilibrium of a population: whichever be its initial distance from the point of stable equilibrium, the population eventually stabilizes near it

(at the type of the curve $M(K)$ we discuss). Therefore, the population density is always near K_s unless some extraordinary disturbance occurs.

In another case, as simple as the previous one, of a concave $M(K)$ crossing the bisector at a single point (point 1, Fig. 9), any population state P_0 between 0 and 1 successively grades into the states P_1, P_2, \dots , approaching 0, and the population vanishes. If the initial state of the population P_0' is to the right of 1, its following states P_1', P_2', \dots , correspond to the tendency of an unlimited growth. This situation is obviously impossible in nature, and the curve of Fig. 9 thus does not provide a realistic image of the reproduction dynamics at high K ; it can no longer be concave (see below).

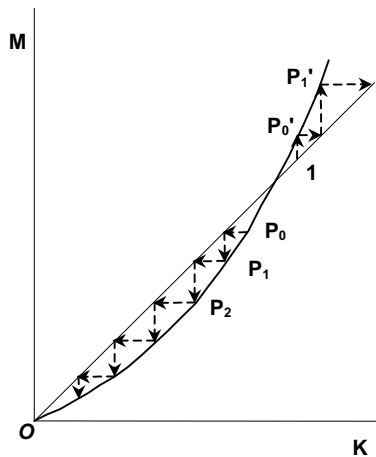


Fig. 9. Population dynamics for a concave phase curve.

Point 1 is again an equilibrium point, but in this case it is a point of unstable equilibrium when any minor deviation drives the population either to extinction (deviation to the left of the equilibrium) or to unlimited growth (deviation to the right of the equilibrium). This state obviously cannot persist and thus eludes any observation in nature. These points are important rather because they are the “divides” between different domains of population dynamics [*Isaev and Khlebopros, 1973; Nature, Our Soviet correspondent, 1973*].

The curve of Fig. 8 and, hence, populations of stable density, are commonly found in nature at invariable conditions. The curve of Fig. 9 is, on the contrary, unrealistic in general, and only its concave part is essential showing the decay of a population towards the left end.

More complex population processes

So far we have focused upon increasing functions $M(K)$ and thus could predict only the dynamics associated with population growth or decline till its equilibrium state (including zero point corresponding to extinction). Yet, some species demonstrate a different type of population dynamics, likewise existing in nature, and their phase functions are not always increasing. The assumption that a population decreases at high K means overpopulation and can be checked in the field.

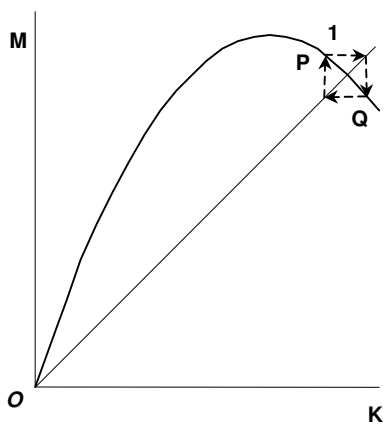


Fig. 10. Idealized closed cycle for a convex phase curve.

Figure 10 shows the curve $M(K)$ with an interval of rapid decrease after equilibrium point 1. A population that happens to be in the state P (or Q) (the vertices of the square halved up by the bisector), is in the state Q (or P) the following year and so on, and its density oscillates periodically.

This “exact” cycle is of course impossible in reality, because the initial state is never exactly P or Q . A natural process of this kind can be interpreted as cyclic only to some approximation. These nearly cyclic processes actually get disturbed with time. Figure 11 images the density dynamics of a population pushed off its cyclicity and evolving in a spiral way. The K -coordinate of K can vary in a rather broad range about the equilibrium (K -coordinate of 1). These processes are called quasi-chaotic, and this equilibrium point is called unstable since the population density can significantly deviate from the equilibrium infinitely many times.

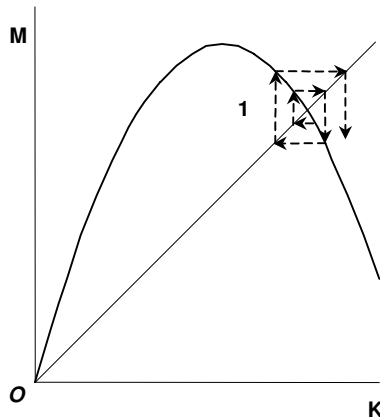


Fig. 11. Quasi-chaotic population dynamics for a convex phase curve.

Many natural processes behave so that their phase curves cross the bisector at three points 1, 2, 3 (excluding the origin O), which is the case of special importance. In this case population density has three equilibrium points, except zero where it becomes extinct. Figure 12 shows the most common case of an increasing phase function $M(K)$.

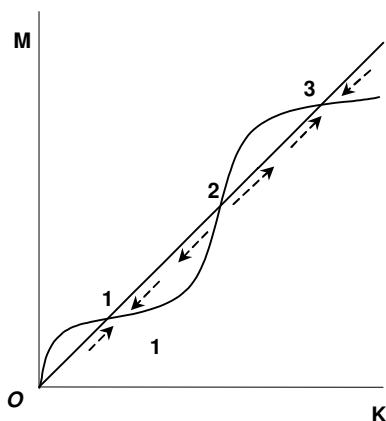


Fig. 12. Phase curve that crosses the bisector at three points of stable (points 1 and 3) and unstable (point 2) equilibrium.

We turn to the biological meaning of the curve of Fig. 12 after having formally applied reflection from bisector.

The initial states between points 0 and 1 move to the right approaching point 1, and the initial states between points 1 and 2 move to the left, likewise approaching point 1. Therefore, point 1 is again the point of stable equilibrium, with the only difference that a too strong deviation towards population growth makes the population move to the right rather than turn back to point 1, since the states between 2 and 3, that likewise are above the bisector, move rightward like the points between 0 and 1. So, point 2 marks unstable equilibrium as in the case of Fig. 9. Point 3, on the contrary, corresponds to stable equilibrium, like point 1, and is associated with a higher population density relative to point 1. Remember that stability of a population is meant as “local”, and the system never recovers after too large deviations from the equilibrium.

We can easily apply the same constructions as in Figures 8 and 9 to the more complex curve of Fig. 12 at intervals 0-1, 1-2, 2-3, and the interval to the right of 3.

The interval 0-1 is favorable for a species survival as any population within it grows till point 1 of stable equilibrium where it stays (slightly oscillating around it due to casual effects). Interval 1-2 is unfavorable and is associated with population density decrease till stable point 1.

Interval 2-3 is again favorable and brings the population to stable equilibrium 3. If the curve does not cross the bisector at other points after 3, all states to the right of 3 approach it while the population decreases. Further intersections, if any, are alternately the points of stable and unstable equilibria. As far as we know, natural insect populations never show more than three equilibria (except zero).

A question naturally arises: which biological conditions control the specific shape of the phase curve of a population? These conditions are known, for example, for the forest pest of black fir beetle. The curves of the type of Fig. 8 describe its populations in young forests in plainland or in forests at the steppe border in highlands. Black fir beetle attacks weak and ill trees in those forests by getting into their inner bark where it lays eggs. The pest does not attack strong trees which protect themselves by coating the eggs with gum. Equilibrium point 1 in Fig. 8 corresponds to the pest population of stable density that live in a forest with a constant percentage of weak trees to provide food and breeding place.

The conditions of higher mountains, where climate is colder and wetter, are more favorable, and the initial population density K is associated with a larger density M in the following year, so that the phase curve of Fig. 8 rises up to take the shape of Fig. 12. Interval 2-3 corresponds to another feeding pattern specific to the case when the population density is so high that pests have to attack sound trees for the shortage of weak ones, and sound trees can no longer resist. Unlike the case of infinitely enduring ecological equilibrium between the forest and the pests in plainland and low highlands, the new feeding pattern threatens the very existence of the forest. Yet, insects can use interval 2-3 only after their density reaches point 2. Normally this never happens and the population stays in some vicinity of stable equilibrium 1 since it cannot grow within 1-2. Abnormal conditions arise when a highly dense population comes from outside, which is quite possible for flying insects. Then the density of pests grows at the account of the invaders rather than the natives who are unable to overcome the unfavorable interval between 1 and 2. As soon as the population exceeds point 2, interval 2-3 “sets into work” and the population density rises up to new stable equilibrium 3 to produce an outbreak. Population density at state 3 may be ten times that

at normal state 1 in black fir beetle and dozens thousand times in other insects, which makes interval 2-3 too long to show in a picture.

The conditions are especially favorable in mountain top regions (in low highlands), where a mature forest has a different phase curve than in Fig. 12, namely it rises relative to the latter (Fig. 13). Biologically the upward shift means that the same population density K in a mature forest produces a higher density M the following year than in the worse conditions of Fig. 12. The risen phase curve crosses the bisector again at a single point (point 3) while points 1 and 2 disappear.

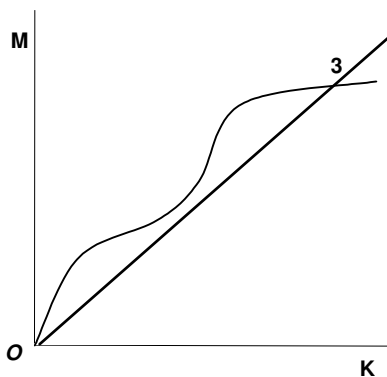


Fig. 13. Phase curve associated with the conditions most favorable for pests or with a weakened forest.

A pest population with this phase curve reproduces till point 3 and an outbreak becomes inevitable. Once the population becomes dense enough, insects attack mature forest and that feeding pattern persists until the whole forest dies out. Driven by the food lack, the dense population migrates downhill and triggers the formerly inactive interval 2-3 of the curve of Fig. 12. Then the pests develop an outbreak which propagates downhill like a wave destroying the forest. Finally the outbreak reaches its lower part corresponding to the phase curve in Fig. 8. The population cannot reach a too large density there since it can only diminish within the region to the right of 1; the excess insects die out and the outbreak stops [Isaev *et al.*, 1984].

Pests usually spare young trees, and the forest thus can recover after outbreaks, starting with the age relevant for the insects. Then the tops and slopes of mountains become again covered with mature forest, roughly uniform in age, where another outbreak can occur in a while. The periodic outbreaks devastate forests in the same way as forest fires, with the only difference that forests can recover after outbreaks of pests and fires can often be fatal. In such cases, the mountains get covered with grass, or with a forest of a different type. That is why overmature forest with trees of different ages is never found in upper mountains where air or satellite images most often show young forests.

Interference of man can deform the phase curve, most often to the worse. In nature the curve of Fig. 13 rises under conditions that are especially favorable for insects when they can feed on strong trees. Yet, the same thing happens in a forest weakened by felling, or by industrial air pollution. This is the way man can provoke insect outbreaks.

On the other hand, man can mitigate the risk of outbreaks, or stop them, by means of chemical or biological extermination of pests; then the phase curve goes down, as in Fig. 14, and returns to the form of that in Fig. 8.

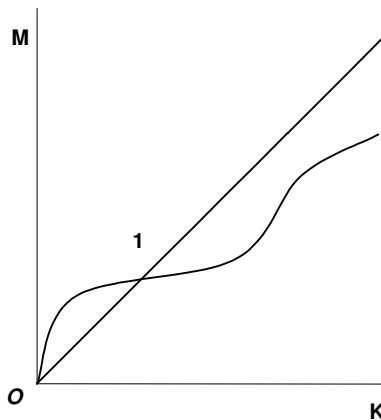


Fig. 14. Phase curve associated with manmade extermination of pests.

Up to this point, we have dealt with population outbreaks of pests and their interaction with the host forest, but the model has more general

implications. A few examples below show outbreaks relevant to people and their activity.

Locust outbreaks are the most familiar. In terms of taxonomy, the locust is a species allied to grasshopper living in arid steppes, particularly in the steppes of Eastern Asia. In normal conditions they are not social insects, and live like ordinary grasshoppers. However, if their density becomes excessive for any reason (not quite understood as yet), they grow wings, normally reduced, and acquire the ability to fly. Then, gathering in immense swarms, they become what is called locusts, and fly to other countries, devastating vegetation, and migrate on and on as far as they eat up all food, exactly as the forest pests do.

Another example is the vanished forests of Ancient Greece. Throughout historic time, this mountainous country has been woodless, with bare rocky ranges. However, the mountains were covered with forest in prehistoric times, as is remembered in the Greek oral tradition and confirmed by paleogeographic data. The scarce population of that time could hardly disforest the land. There is a hypothesis that the deforestation may have been caused by domestic goats which ran wild and went through an outbreak. The goats ate up the young tree suckers, the forest never recovered, and rains washed the soil away from the slopes. Thus, the familiar classical Greek landscape results from a man-induced environmental disaster. The same impact, for instance, related to exhaustive pasturing, can provoke desertification. Perhaps, Sahara might have appeared in this way.

We can also cite an example of rabbits that were brought by immigrants to Australia where they could not find enough natural enemies since the population of local predatory marsupials had been thinned out at that time. Consequently, the uncontrolled rabbit population grew in an outbreak that endangered the entire agricultural production of Australia. Eventually people had to build fences throughout the continent to keep the rabbits away.

The species of *homo sapiens* may have likewise undergone an outbreak when people learned to hunt mammoths and thus passed to a new feeding pattern. When mammoths became extinct, the human population may have considerably decreased. Another outbreak of human reproduction apparently occurred in the twentieth century.

A case of erroneous ecological measures

The reproduction of salmon provided an instructive example of misprediction and related erroneous measures. Adult salmon inhabit open sea but come to spawn to the rivers of the Russian Far East and America. Each seven-year-old fish returns to its birthplace where many fish gather for spawning. The Russian zone of catch was established as a 12 miles wide border where only Russian fishermen were allowed, but Japanese fishermen fished extensively along the border margins. To stop that practice, ichthyologists suggested the government to extend the boundary up to 24 miles, assuming that this would automatically increase the yield. However, the catch actually decreased and increased only later, after several seven-year cycles. To explain what actually happened, we interpret the reasoning of the ichthyologists (who used a different approach) in terms of our model (Fig. 15), where population numbers K and M correspond to two successive septennials and thus are spaced at seven years. (The model is the same whether we count fries or fish returning to spawn).

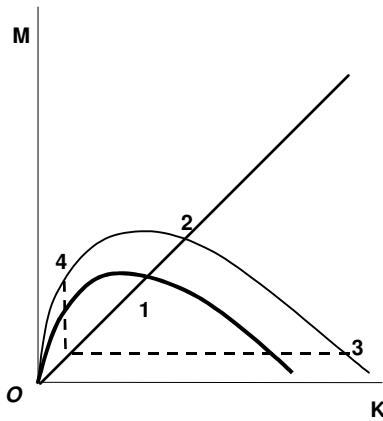


Fig. 15. Phase portraits of the salmon population before (heavy line) and after (thin line above) the broadening of the forbidden catch zone.

Salmon is a species which decreases its numbers abruptly at overpopulation, i.e., its phase curve bends sharply downward. The phase

curve shown by heavy line in Fig. 15 corresponds to the catch before the broadening of the forbidden zone and the curve shown by thin line to that after the change. In the former case the population was at the state of stable equilibrium 1; in the latter case it was presumed to pass to a new equilibrium state 2, with a greater population.

In fact, the catch fell strongly only for the fish coming to spawn because the change of the forbidden zone did not apply to the catch in open sea or in rivers. As a result, much more individuals could successfully reach the spawning place. Describing the new situation in terms of phase portraits requires primarily the knowledge of what would be the initial population at the point where we start with the new phase curve. We may assume that the fish density in the spawning places would be excessive, leading to reverse dependence between the progeny and the numbers of spawning fish. Therefore, fish, in fact, hindered one another in spawning so much that the damage could not be kept up by the greater numbers of spawning individuals.

The first reproduction cycle after broadening the forbidden zone is represented by point 3 of the new phase curve, where K is much greater than the former stable number of fish coming to spawn (the K -coordinate of point 1). However, after seven years we obtain a number M smaller than the previous stable value. One might predict that after several further septennial cycles (first such cycle corresponds to point 4 of the new phase curve), the population should stabilize at point 2, and thus become greater than at the former point 1. That is what really occurred.

Classification of outbreaks

Typical phase portraits allow classification of all possible kinds of outbreaks understood as any sudden change in population density. We limit ourselves to the cases when the curve $M(K)$, starting at the origin of coordinates, crosses the bisector at three other points: point 1 corresponds to the lowest nonzero population density, point 2 to an intermediate population density, and point 3 to the highest population density. Each of the three can be, in principle, stable or unstable, but only certain combinations of stability types are possible. Our assumption

agrees with the fact that no more than three equilibrium states are observed in nature, at least in insects.

Intermediate equilibrium point 2, even if it is stable against small deviations, rarely holds on for a long time, and thus this type of population is rare for long-living species. Indeed, suppose that such a point is stable, as shown in Fig. 16.

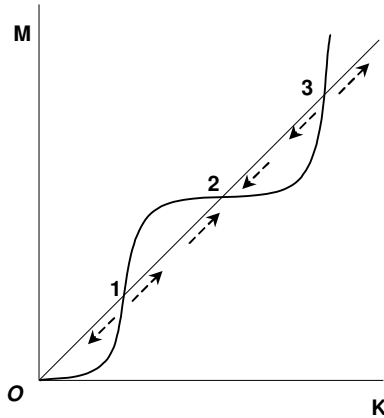


Fig. 16. Phase curve that crosses the bisector at three points: lowest nonzero population density (point 1), intermediate population density (point 2), highest population density (point 3).

The zero point is also necessarily stable in this case (Fig. 16). Of course, a population that fits this phase curve arrives at point 2 and can never pass the unfavorable zone 1–2 downwards. However, some events can upset the normal behavior of the population and suddenly increase or decrease its density, as in the case of flying insects brought to some locality, to move the population to the right of point 3 into the interval which was out of reach before. In the same way, some disaster can push the population of Fig. 16 to interval 0–1, make it move to the point O and eventually become extinct. Therefore, species with the dynamics corresponding to Fig. 16 are relatively rare, and can be neglected in rough classifications like the one we suggest. (Compare this case with the behavior corresponding to the phase curve of Fig. 8 when a

population never fails to return to stable equilibrium 1, even after great deviations.)

The population of species close to extinction usually decreases too much in density, as is probably the case of whales because of abusive hunting and increasing pollution of the oceanic water. There are, however, species able to prevent population thinning by means of the so-called Allee effect. They form geographically dispersed groups with a relatively dense population in each, which keeps them within interval 1-2 of the phase curve, i.e., above critical point 1. The Allee effect is worth mentioning as it extends Lorenz's general law which implies that the instinct of intraspecific aggression forces species to settle uniformly over their habitats. Note that the curve of Fig. 16 must bend downwards to the right of point 3 because of the limited resources and the related constraints on population growth.

No fourth equilibrium point having been so far found in insects [Isaev and Khlebopros, 1977; Berryman *et al.*, 1987; Bazikin *et al.*, 1997; Isaev *et al.*, 1984; 2001], we may restrict ourselves to the cases of unstable point 2. Then there are several alternatives^a.

Points 1 and 3 correspond to stable equilibrium [May, 1971; 1973; Isaev and Khlebopros, 1973; *Nature*, *Our Soviet correspondent*, 1973] (Fig. 17):

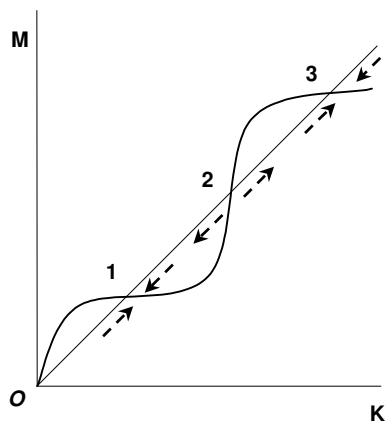


Fig. 17. Case of stable points 1 and 3.

^a They can be investigated using reflection from bisector in the same way as above.

Point 1 is stable, and point 3 is unstable (corresponding to unstable equilibrium) (Fig. 18). Note that explanation to Fig. 11 shows why point 3 is unstable.

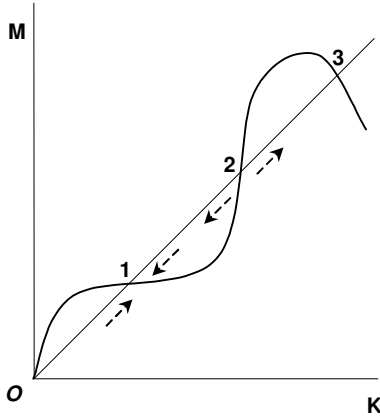


Fig. 18. Case of stable point 1 and unstable point 3.

Point 1 is unstable and point 3 is stable (Fig. 19):

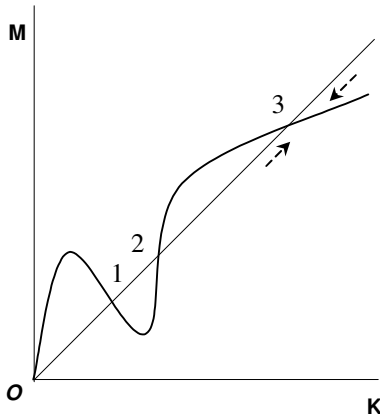


Fig. 19. Case of unstable point 1 and stable point 3.

Points 1 and 3 are both unstable (Fig. 20):

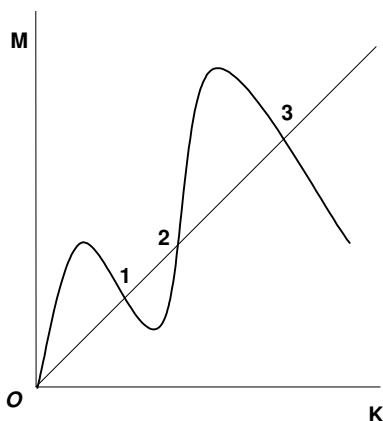


Fig. 20. Case of unstable points 1 and 3.

Figures 18, 19 and 20 image the cases when a population moving from unstable points 1 or 3 can leap over point 2. They are the cases of high-amplitude oscillations which may trigger outbreaks. First explanation of these effects was suggested in *Isaev and Khlebopros* [1977] and more details can be found in *Isaev et al.* [1984; 2001], and *Bazykin et al.* [1997].

Note that some species have adapted in a way that their population outbreaks spare their host ecosystem. For example, some pests of conifers in the Swiss Alps eat only the lower half of needles and ignore the cruder upper half [*Schwerdtfeger*, 1952; 1956]. Thus, trees can survive and grow new needles. Several species of this kind have been found in Russia as well and must exist elsewhere in forest lands. This feeding pattern is good for both the forest and the pest as the parasite is interested in preserving its food resource. In further chapters we discuss other examples of recoverable and unrecoverable resources in relation to the economic activity of man.

Classification of population processes

The straightforward approach we described is not immediately applicable to population processes in general which are as a rule far more complicated. Namely, generations not always take turns at regular intervals, yearly as in insects, or every seven years as in salmon, or any. Moreover, generations can overlap and coexist. The approach works only provided that the following conditions are satisfied:

1. All individuals of the species reproduce simultaneously at regular time intervals.
2. Every former generation dies out after its reproduction phase (which is shorter than the interphase) and before the following reproduction phase of the following generation.

Under these conditions, all possible population processes fit a comprehensive classification. This classification was suggested for the first time in *Isaev and Khlebopros* [1984] and developed in *Isaev et al.* [2001].

There are six possible patterns of population behavior for the cases when the phase curve crosses the bisector at three points (except zero where the population does not exist).

- (1) A single stable equilibrium point of the population, as in Fig. 8.
- (2) A single unstable equilibrium point, as in Fig. 10 (or Fig. 11), with quasi-random oscillations around it.
- (3) Two stable equilibrium points and one unstable equilibrium point, a “point of escape”, as in Fig. 12 (or Fig. 17).
- (4) One stable equilibrium point, one unstable equilibrium point with quasi-random oscillations, and one unstable escape point, as in Fig. 18, the population at the first unstable point being smaller than at the second one.
- (5) One stable equilibrium point, one unstable equilibrium point with quasi-random oscillations, and one unstable escape point, as in Fig. 19, the population of the first unstable point being greater than at the second one.

(6) Two unstable equilibrium points with quasi-random oscillations and one escape point, as in Fig. 20.

The phase curves with two equilibrium points are obviously unrealistic: once got to the right of the unstable point, the population would grow infinitely. The same holds true for any even number of equilibrium points. On the other hand, any odd number of equilibrium points would be theoretically possible, though the known populations have no more than three such points. Thus, our classification appears to be exhaustive for the intended biological applications.

Note that outbreaks of forest insects acquire specific features in the time of climate change like one we might now witness. Sudden warming or cooling make forests vulnerable to pest attacks, especially the forests at habitat borders, e.g. at the forest-steppe interface. On the one hand, it is because trees become exposed to conditions they were not selected for, and their pest resistance weakens. On the other hand, climate change can be bearable for adult trees but fatal for young growth, which can hinder forest recovery. As a result, the outbreaks that would have at most destroyed a part of the forest in the former climatic conditions completely replace it by a steppe ecosystem in a new climate. Climate events can even trigger pest outbreaks in territories where they were unknown for thousands of years. The climate-dependent behavior of outbreaks is explainable in terms of cumulative catastrophes often invoked in describing natural hazards.

Thus we investigated the interaction of pest insects with a forest, their habitat, and the related microcatastrophes of sudden population outbreaks which can either change drastically the state of the forest or reduce its area, or even cause different degrees of deforestation. Although apparently confusing, the behavior of the 'pests-forest' system turns out to follow quite simple laws and the outbreaks of pests develop according to a limited number of scenarios.

We arrived at this result using the method of phase portraits, a phenomenological modeling approach based on empirical input data. Phase portraits are either one-dimensional or two-dimensional images, corresponding to the number of investigated parameters of a system. In

the one-dimensional case, they are plotted in the phase planes (x_n, x_{n+1}) . Phase portraits in the plane (x_n, x_{n+1}) — applied in this chapter and in some other chapters below — show discrete changes in some system parameter measured at two successive moments of time. The phase plane (x, \dot{x}) used in some of the successive chapters displays processes that change continuously, and these portraits (or phase curves) describe the rate of changes. Two-dimensional phase portraits represent the dynamics of two parameters of a system shown along the two respective coordinate axes. In the case of insects, a two-dimensional system can include, for example, the dynamics of pests and of their natural enemies [Volterra, 1931; Kolmogoroff, 1937].

Phase portraits can be narrow or broad. In narrow phase portraits (very narrow ones can be approximated by a curve), the recorded change in system parameters is defined uniquely by their previous value (for insects it means that a change in the density of a population is defined only by its original numbers). Systems described by narrow phase portraits move along their phase curves and stop at equilibrium points: virtually forever at points of stable equilibrium and for a while at points of unstable equilibrium; the time a system can stay at an equilibrium point corresponds to the time scale of its evolution. The effect of other factors, often quite numerous, is allowed by phase portrait broadening. In the case of insects, a broad phase portrait can image the density of a population controlled by several regulating mechanisms rather than its original numbers: numbers of predators, food supply, etc. Then, a system moves within the limits of its broad phase portrait but remains anchored on the equilibrium points (see Chapter 4), which are the characteristic points of the phase portrait and invariably define the few possible scenarios of the system dynamics. This key feature of phase portraits is applied in this and in the following chapters to predict the dynamics of different natural and cultural systems.

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