

OLM 6.2 Potential large-scale consequences of a temperature-dependent Allee-effect

Strong Allee-effect renders extinction one of the stable states of a system (Figure 6.3, p.98). This implies that colonization can be successful only if the invader population size (of individuals or propagules) exceeds the Allee threshold, i.e., population size at the unstable equilibrium (extinction threshold, Ch6.1.2, p.98). If this occurs rarely, then even non-isolated habitats providing environmental conditions within the range of the species' ecological tolerance will remain unoccupied for long periods of time. Moreover, the dependence of growth rate on population density changes with external conditions like temperature, which may affect both the position of the unstable fixed point and the dispersal rate through multiple mechanisms in case of ectotherm organisms. This OLM presents some examples.

Andrew Kramer and his colleagues (2008) looked for an explanation to the phenomenon that the relatively large (>2 mm) copepod *Hesperodiatomus shoshone* is missing from the alpine lakes of Sierra Nevada in which its fish predator, the trout, had gone extinct decades earlier, and in which *Daphnia melanica*, a species usually co-occurring with *H. shoshone*, has already re-established its populations. *H. shoshone* populations, like other species of the zooplankton, maintain egg banks buried in the sediment of the lakes, which makes them capable of fast recovery after the fish population was wiped out. Of the 44 lakes studied by Knapp and Sarnelle (2008), which had been stocked with fish earlier but were actually fishless, they could establish the earlier presence of the species from the sediment in 41. *D. melanica* populations were re-established in 82% of these lakes, whereas *H. shoshone* re-appeared only in 54% (Figure 6.2.1).

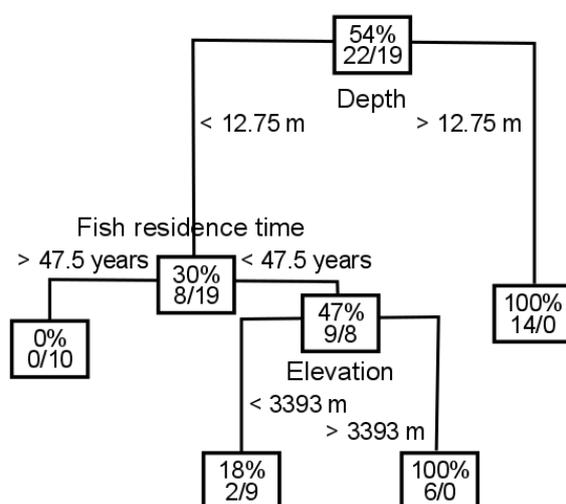


Figure 6.2.1 The probability of *H. shoshone* recovery as a function of lake depth, elevation and the duration of fish residence (after Knapp and Sarnelle 2008).

The percentages at the nodes are the proportions of lakes in which the *H. shoshone* population recovered, the numbers are those of lakes with and without recovery. The lengths of the branches of the tree are proportional to the variance explained by the actual factor. Egg bank size increases with lake depth and decreases with fish residence time.

The researchers suspected that the relevant mechanism behind this pattern might be an Allee effect due to difficulties in mate finding (mating limitation; Table 6.1, p.104), based on the reasonable assumption that in the shallow lakes which have been occupied for long times by fish the egg bank was depleted. Moreover, the dispersal abilities of *H. shoshone* are limited and unlike the parthenogenetic *D. mellanica* *H. shoshone* is obligately sexual. Since its habitat is rather large compared to its mobility, it is possible that the encounter rate of potential mates is low at low population densities.

How are encounter rates and critical densities related? Let us discuss this following Gerritsen (1980). At low population densities only a proportion p_m of females encounter males and reproduce. Accordingly, the lifetime reproductive success of an average female (Eq.(8.17), p.155) can be partitioned into two components: the reproductive success of females finding mates and that of one's which fail finding mates:

$$R_0 = (1 - p_m)0 + p_m \sum_i l_i m_i \quad (6.2.1)$$

where $\sum_i l_i m_i$ is the lifetime reproductive success of mate-finding females.

Here we focus only on the mechanisms operating at low population density and disregard negative feedback at higher densities. As a first approximation we may assume random walk, i.e., that the individuals move independently of one another. Under this assumption the number of encounters per unit time will be Poisson distributed and the probability that a female individual meets at least one male during time t is

$$p_m = 1 - e^{-Zt} \quad (6.2.2)$$

where Z is the encounter rate, i.e., the expected number of encounters per unit time. With R_0 specified, the critical frequency of encounters (Z^*) above which the population is capable of growth can be calculated (TBox 8.2, p.155). For $R_0 = 1$ (i.e., at zero growth) the previous two equations combine to

$$1 - e^{-Z^*t} = \frac{1}{\sum_i l_i m_i} \quad (6.2.3)$$

from which

$$Z^* = -\frac{1}{t} \ln \left(\frac{\sum_i l_i m_i - 1}{\sum_i l_i m_i} \right) \quad (6.2.4)$$

For the population to increase the encounter rate should exceed Z^* .

In the random encounter model for computing the encounter rate (Gerritsen and Strickler 1977), i.e., for random walk and encounters, the encounter rate is a function of population density (N), encounter radius (d) and speed of movement (v):

$$Z = -\frac{4\pi}{3}d^2Nv \quad (6.2.5)$$

With half of the population assumed to be males, N is actually half of the observed population size. Substituting the expression thus obtained into Eq.(6.2.4) and rearranging yields N^* , the critical density under which the population shrinks and goes extinct:

$$N^* = -\frac{3}{4\pi t d^2 v} \ln\left(\frac{\sum_i l_i m_i - 1}{\sum_i l_i m_i}\right) \quad (6.2.6)$$

The critical density due to constrained encounter probability can be derived from more complicated models as well; for example, by considering movement patterns (Kiørboe 2008).

We see that all the terms of the expression depend on temperature – especially in ectotherm organisms –, and the dependence may not be unidirectional. The probability of encounters increases between faster moving individuals (v), and in warmer water the molecules move faster, too, which may decrease the encounter radius (d) if mate perception is chemically mediated. However, the other fitness components may also be temperature dependent in various ways. All this means that the net effect of changes in temperature can be expected to be species and habitat dependent.

Estimating the critical density from Eq. (6.2.6) is a difficult task in itself, because it requires data on the lifetime reproductive success of females, as well as on the speed of individual movement and encounter radius under different conditions. Kramer et al. (2008) have estimated the critical density of *H. shoshone* to fall within the 0.5-5 copepods/m³ range. To verify the hypothesis that it is the critical density that stands in the way of species recovery in the alpine lakes they have set up a series of experiments consisting of three elements. They have selected six lakes from which all copepods were extinguished by introduced fish in the past for good so that no copepods reappeared later. They put a small mesh cage into each lake, containing a density of 3000 copepods/ m³ each. These isolated populations increased at a pace similar to natural populations, proving that the lakes were still suitable habitats for the species. They also conducted whole-lake copepod reintroductions in each of the six lakes, releasing different numbers of individuals at the centres of the lakes and checking the populations for growth through a 3-year period. They found that it was only in the lake with the highest *H. shoshone* propagule density (3.9 individuals/m³) that the population started exponential growth and the proportion of fertilized females in this lake was most similar to that found in inhabited natural lakes.

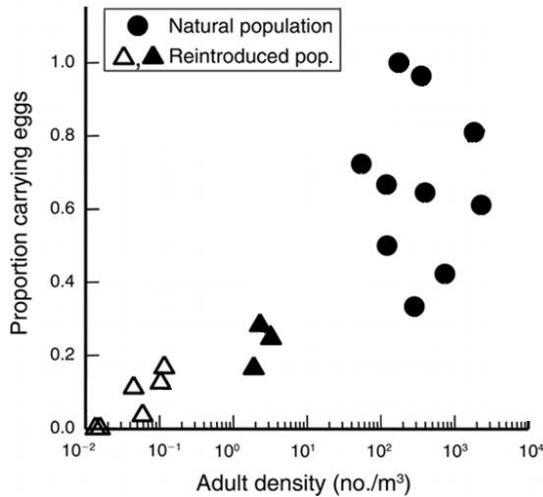


Figure 6.2.2 Evidence for the difficulty of finding mates (after Kramer et al. 2008).

Results of the whole-lake reintroduction experiments with the copepod *H. shoshone* from the period 2003-2005 (triangles). Reintroduction was successful only in Square lake (filled triangles). Each point represents data from one year in one lake. The relatively high scatter of the data from natural populations (circles) may be the result of censuses taken in different seasons.

The third element of the study was a mesocosm experiment with another common copepod species (*Skistodiaptomus pallidus*) demonstrating that growth rate of the populations increased with increasing initial population density in the low-density range.

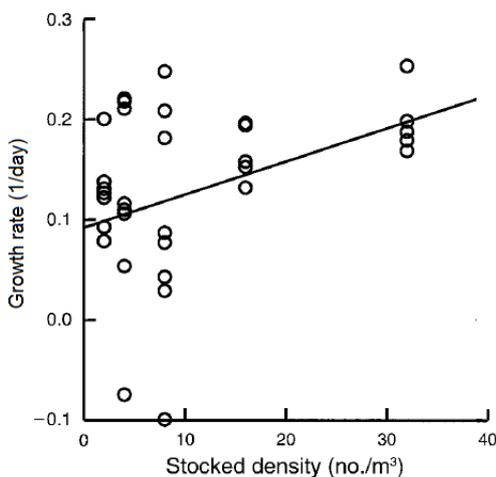


Figure 6.2.3 The relation between pgr and initial population density in the mesocosm experiment with *Skistodiaptomus pallidus* (Kramer et al. 2008).

The higher variance of lower-density populations can be caused by demographic stochasticity.

These three experiments support the hypothesis that the lack of obligate sexual zooplankton species from some highly isolated habitats can be explained with the Allee effect. A more recent model-based study (Wittmann et al. 2011) has revealed that a strong, temperature dependent Allee effect (i.e., an unstable equilibrium at a positive density of resting eggs) is inevitable in cyclically parthenogenetic zooplankton species as well. The reason for this is that for the production of resting eggs which ensure population survival in adverse environmental conditions it is necessary that males, which are produced parthenogenetically at a temperature dependent rate (the sex of a parthenogenetic individual is dependent on the environmental conditions in these species), find females of the appropriate

developmental stage. These conditions have to be included in the classical life cycle graphs and the corresponding life cycle models.

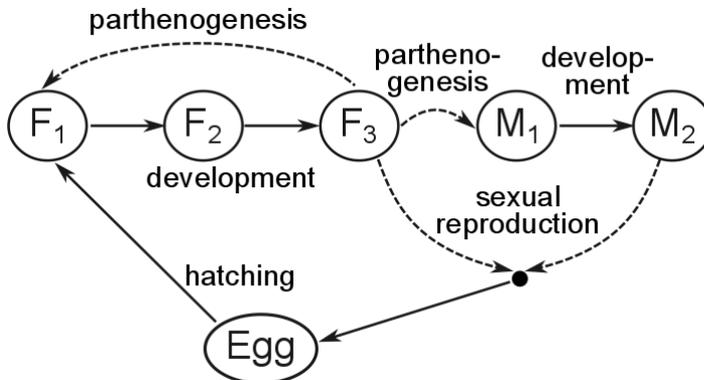


Figure 6.2.4 Modified life-cycle graph of *Bythotrephes longimanus* (after Wittmann et al. 2011).

Life-history stages: F: female, M: male, Egg: resting egg. A hierarchical stage-structure model was built in which the within-season transition rates were represented by differential equations whereas between year-changes of resting egg densities were modelled by a discrete-time equation.

A detailed, mechanistic model was developed for the study of the invasion dynamics of the spiny water flea, *Bythotrephes longimanus*, a freshwater cladoceran, a generalist predator with a strongly temperature dependent life-cycle (Figure 6.2.4). The model was parameterized with data from laboratory experiments as well as from a long-term survey of a natural population (Wittmann et al. 2011). *B. longimanus* started its carrier in North-America at the beginning of eighties when it was accidentally introduced into Lake Ontario, supposedly from the Lake Ladoga system. Analytical and simulation studies both support that a temperature-dependent Allee threshold (Figure 6.2.5) is an essential feature of this type of life-cycle.

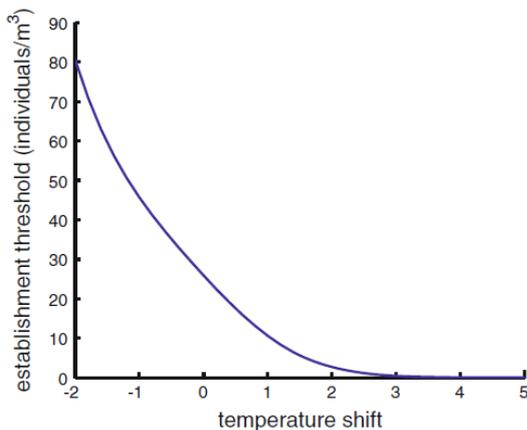


Figure 6.2.5. Temperature dependence of the critical density of spiny water flea, *Bythotrephes longimanus* (Wittmann et al. 2011).

Simulation results parameterized from field data. The daily average temperature value measured in the reference population has been shifted (increased or decreased) by the value on the abscissa.

Such results are not restricted to temperature-sensitive zooplankon species, but temperature-dependent strong Allee effects (critical densities) can be expected in other ectotherm species as well. Wheeler et al. (2012) built a similarly semi-discrete model with temperature dependent vital rates for the alpine butterfly *Parnassius smintheus* and found a temperature-dependent Allee threshold too. The Allee threshold for gypsy moth presented on Figure 6.11 (TBE, p. 105) is probably also due to restricted encounter rates at low densities (Figure 6.2.6) and is suspected to be temperature-dependent.

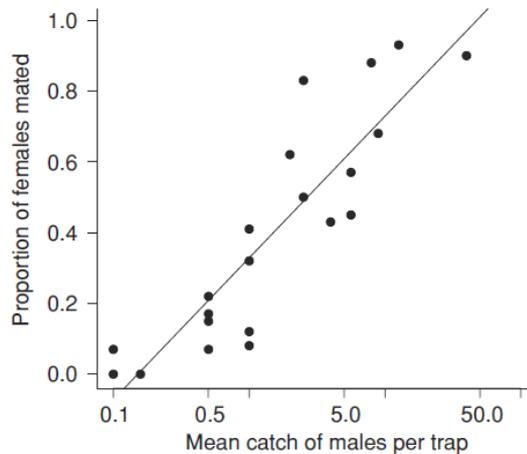


Figure 6.2.6 The effect of population size on the proportion of fertilized females of *Lymantria dyspar*.

The density of males (horizontal axis) was measured using pheromone traps. In order to determine the fertilization probability of females, lab-hatched virgin females were tethered on trees for 24 hours, and checked for conception via dissection (data from Tcheslavskaja et al. 2002, Gascoigne et al. 2009).

Even though the models and the mechanisms studied here are case specific, we may not only draw conclusions regarding the expected highly temperature sensitive Allee thresholds in ectotherm organisms, but also take the more general message home that in order to understand large-scale distribution patterns the thorough knowledge and the appropriate modelling of individual life cycles are indispensable.

References

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