OLM 5.1. Estimation of the multivariate response function

In principle, the multivariate response function provides all the information necessary for the prediction of geographic distribution when the state of all the relevant environmental variables, including the regulating ones, are known. In practice, determination of this function is difficult even in the simplest cases. We shall introduce an exceptionally complex model-based experimental study of a duckweed species (*Lemna minor*) to illustrate how the multivariate response function can be composed even if it is impossible to eliminate some density effects.

Duckweeds are relatively well studied species. Growth curves of populations of three different *Lemna* species (Figure 3.7, p. 46) were published already during the early sixties (Clatworthy and Harper 1962). Similar studies have been carried out ever since then, because these species have been widely utilized in wastewater treatments and as fodder for livestock and fish for more than 30 years.

Although duckweed populations grow exponentially under constant conditions in aquacultures with regular harvesting, it has been observed in several studies that the estimated *pgr* (called *specific growth rate* in this branch of ecology) depends on initial population density (i.e., on duckweed biomass per square meter of covered water surface), and also on harvesting frequency (see references in Lasfar et al. 2007). As population growth depends not only on environmental conditions but also increases with initial population density and harvesting frequency, which both vary from study to study, the estimated *pgr*s are different even if all other conditions are similar in the experiments. In order to filter out the density effects, r_0 was estimated by Monette et al. (2006) and Lasfar et al. (2007). As explained in the book (TBE, p. 75), r_0 is the growth rate extrapolated to zero density in continuous time models of density dependent population growth in the absence of competitor species. Linear density dependence (Eq. (6.6), p. 98) can be assumed as the plants composing a mat compete for surface area (Ch6.2, p. 99). The solution of Eq. (6.6) is

$$N_t = \frac{K\,N_0}{(K-N_0)e^{-r_0 t}+N_0} \qquad (5.1.1)$$

Although the growth rates of the experimental population depend on both their initial densities and the timing of density measurements – which means that population growth is density dependent – the growth rate can still be calculated as if the biomasses of the cultures would have grown exponentially, that is,

$$N_t = N_0 e^{rt} \qquad (5.1.2)$$

From these two equations r can be expressed as

$$r = \frac{1}{t}\ln\frac{N_t}{N_0} = \frac{1}{t}\ln\frac{K}{(K-N_0)e^{-r_0 t}+N_0} \tag{5.1.3}$$

This model was tested by Monette et al. (2006) experimentally. Their duckweed cultures were initiated at several densities and harvested after a week. Their results are summarized in Figure 5.1.1.

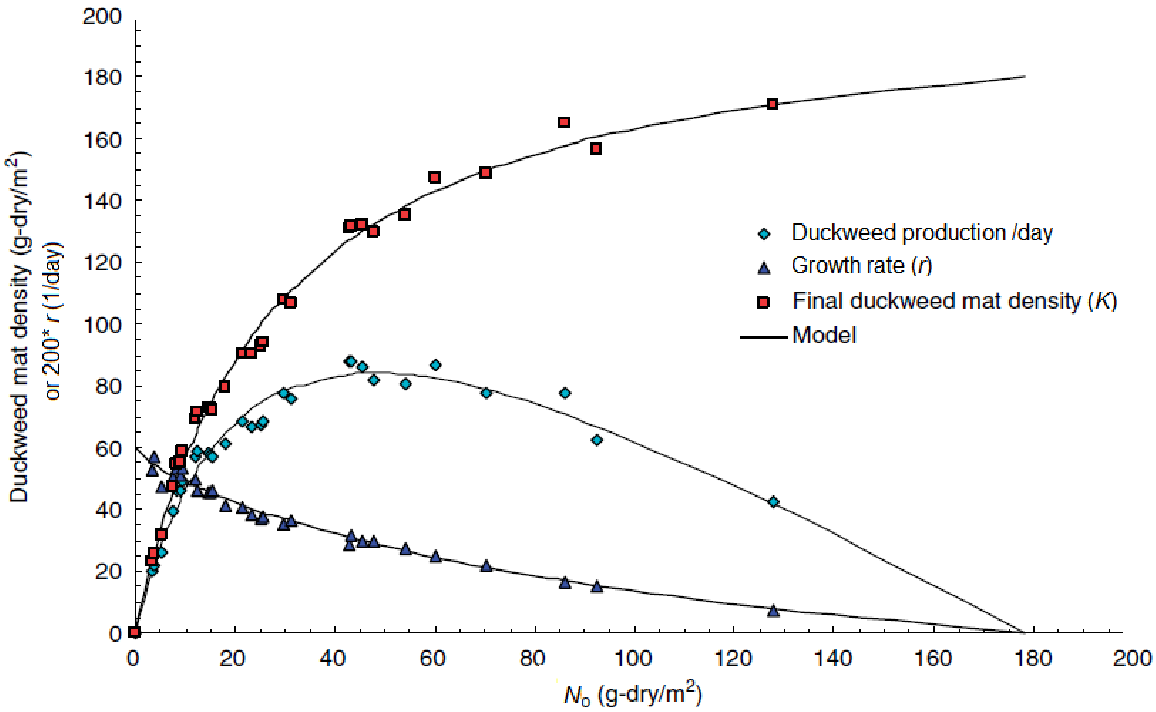

Figure 5.1.1. Predicted and observed effects of the initial duckweed mat density on population growth (after Monette et al. 2006).

Several populations were set up at different initial densities (N_0). The model of logistic growth and its estimated parameters were used for the calculation of the theoretical predictions (curves). Final duckweed density (K), population growth rate (r) and production were estimated from experiments lasting 7 days.

r_0 can be estimated from linear regression. By rearranging Eq. (5.1.3) we get

$$\frac{N_0}{N_t} = \frac{N_0}{K}(1-e^{-r_0 t}) + e^{-r_0 t}\,, \tag{5.1.4}$$

thus plotting N_0/N_t as a function of N_0 provides a straight line whose slope and intercept can be estimated, from which K and r_0 can be calculated.

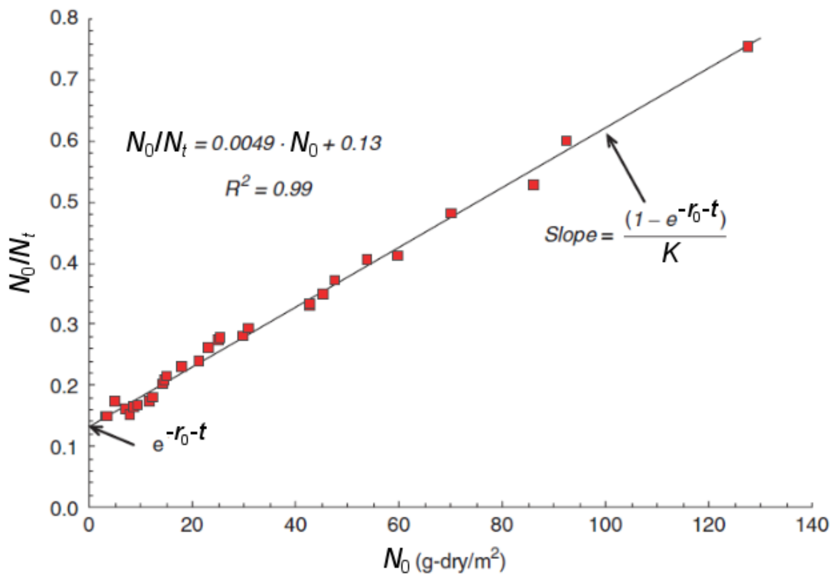

Figure 5.1.2 Estimation of r_0 and K in *Lemna minor* cultures (after Monette et al. 2006).
The populations were initiated with different *Lemna* densities and kept under nearly optimal conditions.

Having produced an estimation of *pgr* that is free from density effects, it is possible to construct $f(\boldsymbol{z}, \mathcal{M}, \mathcal{R})$, the multivariate response function. The dry weight of the duckweed mat is the variable measured, thus the populations are treated as unstructured, *i.e.*, $f(\mathcal{M}, \mathcal{R})$. The growth rate of *Lemna* populations is examined as a function of two resources ($\mathcal{R}$=R, nitrogen and phosphorus) and two modifying factors ($\mathcal{M}$: temperature and photoperiod length). As light intensity changes daily, we may consider the environments of the cultures as regularly fluctuating environments in which population growth is measured for a sufficiently long time to offset its fluctuating character (vs. stationary fluctuating environment). The univariate response functions were measured at fixed values of the rest of the t environmental variables (Figure 5.1.3.a,b, Figure 5.1.4). By assuming that the effects are independent,

$$r(R_N, R_P, T, P) = r_0(R_N, R_P, T, P) = r_{max} \cdot g(R_N) \cdot h(R_P) \cdot m(T) \cdot n(P)\,, \qquad (5.1.5)$$

where R_N and R_P are nitrogen and phosphorus concentrations, respectively; T is temperature, P is the length of the photoperiod.

The effects of the nutrients were investigated across a wide range of supply rates, so their inhibitory effects at high concentrations were considered and modelled, too.

$$r_0(R_N)|_{R_P,T,P}) = r_{0\mathrm{maxP}} \frac{R_\mathrm{P}}{(R_\mathrm{P}+K_\mathrm{P})} \frac{K_\mathrm{IP}}{(R_\mathrm{P}+K_\mathrm{IP})}\,, \qquad (5.1.6)$$

where $r_{0\mathrm{maxP}}$ is the maximal extrapolated growth rate obtained at a certain temperature, photoperiod and N-concentration; the two other factors stand for the Holling type II functional response (Ch6.4.1, p. 106) and the inhibitory effects, respectively.

Temperature response at fixed nutrient concentrations and photoperiod was modelled by a version of the Arrhenius equation

$$r_0(T)|_{\mathrm{R_N,R_P,P}} = r_{0\mathrm{maxT}}\theta_1^{[(T-\mathrm{T_{op}})/\mathrm{T_{op}}]^2}\theta_2^{(T-\mathrm{T_{op}})/\mathrm{T_{op}}}, \qquad (5.1.7)$$

where $r_{0\mathrm{maxT}}$ is the growth rate at $\mathrm{T_{op}}$ and θ_1 and θ_2 are constants. As the researchers inquired into the behaviour of *Lemna* populations in waste management systems in which operational nutrient concentrations are always above the saturation levels (Holling type II functional response), the nutrient concentrations were fixed within the optimal range, and $r_0 = r_{\mathrm{opt}}$ (Table 5.1., p. 75). The photoperiod effect was modelled in the same way. With these methods the estimates of r_{max} for Lemna minor varied between 0.41 and 0.46/day.

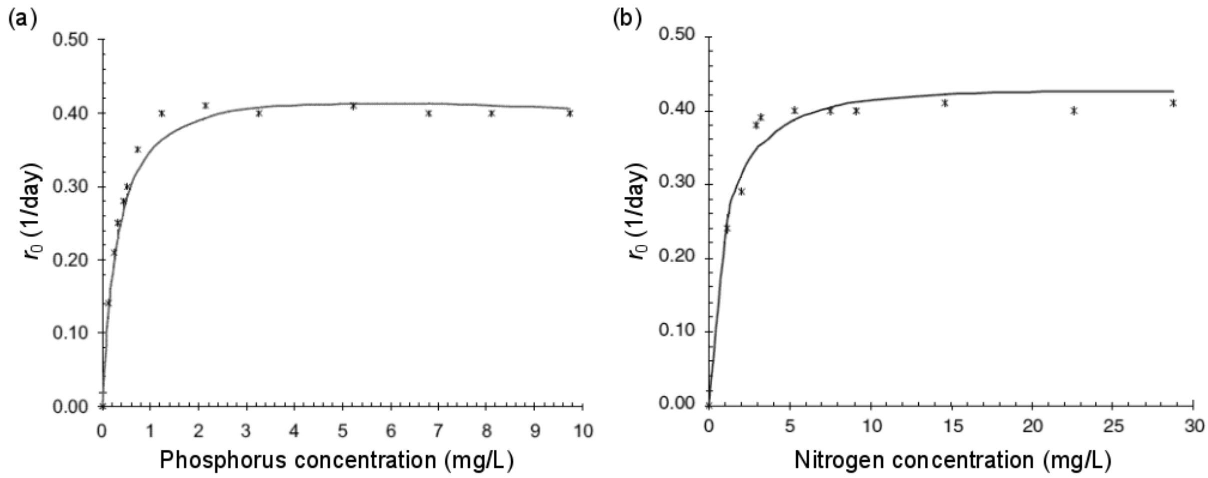

Figure 5.1.3 Numerical response functions of *Lemna minor* to nutrient concentrations in their low ranges (after Lasfar et al. 2007).

a) effect of P concentration; N concentration fixed at 92 mg/L; b) effect of N concentration; P concentration fixed at 14 mg/L. Temperature was fixed at 27 °C, the photoperiod at 14.5 hours in both series of experiments. solid line: predicted curve based on the multivariate response function. R^* is positive but very small, that explains why it is not visible on the presented scale.

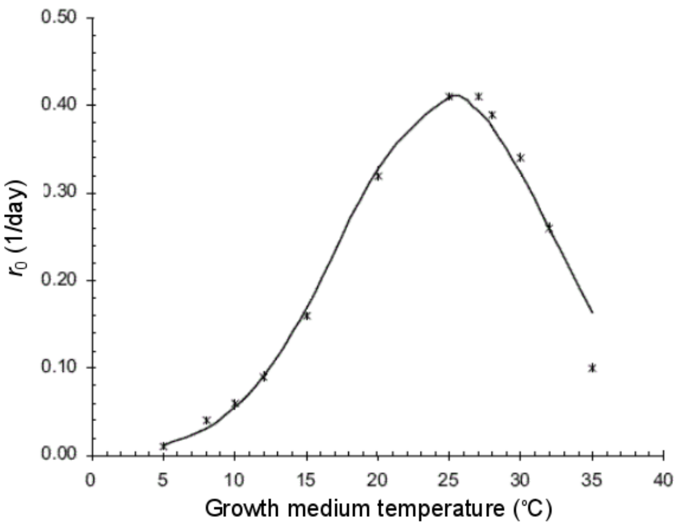

Figure 5.1.4 Temperature tolerance of Lemna minor (after Lasfar et al. 2007).

As resource (N and P) concentrations were fixed above saturation levels (90 and 15 mg/L, resp.), r_0=r_{opt}; photoperiod length was 14.5 hours. Solid line: model prediction.

Duckweeds are also investigated in their natural environments (Kufel et al. 2010, Kufel et al. 2012, Smith 2014). In the next OLM we will stress the importance of considering the level of the regulating variables and/or the presence of competitors in predicting geographic distribution. The competitors affect each other through modifying the level of their common regulating variables. Kufel et al. (2010) found that the frequently detected low biomass of *Lemna minor* in the presence of water soldier *Stratiotes aloides* is associated with low concentrations of soluble phosphorus .

References

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