

A Consideration of the Choice of Minimum K_{pred} Values for iMARNET

Aditee Mitra & Kevin Flynn; CSAR, Swansea; May 2013

Traditional M-M (Holling II) approaches define kinetics according to a given G_{max} (maximum grazing rate) and K_{pred} (half saturation constant), perhaps with inclusion of a threshold value, or as a sigmoidal function (Holling III).

The base equation for Holling II is thus $G = G_{max} \cdot \frac{[prey]}{[prey] + K_{pred}}$

In reality K_{pred} is an emergent property of predator and prey size (actually of their “reactive distance”, here considered as equal to a function of their combined radii). Further, while the Holling II approach (and also parts of the Holling III curve, depending on its formulation) describe values of grazing rate (G , $gC L^{-1}$) as function of prey concentration and which subsequently increase with decreasing prey concentration (approaching infinity with Holling II); in reality that cannot be possible. The control of G at high rates is limited by a combination of satiation feedbacks and handling rate. The former is a function of the processing of the ingested material from all sources; the latter will be affected by differences in prey types, and as a function of the structural features of prey and predator.

It is patently apparent from all the above that a single K_{pred} value for functions describing grazing upon prey of different size is inappropriate. It was for this reason, and as an aid to describing changes in prey selectivity (related to the presence of alternative prey, or to prey of different nutritional quality) that the approach of Mitra & Flynn (Mitra A, Flynn KJ, 2006 Accounting for variation in prey selectivity by zooplankton. *Ecological Modelling* 199; 82-92) was developed. While noting that Mitra & Flynn (2006) is no more computationally expensive than traditional approaches to implement, it is recognised that the Holling II approach has been widely used and will likely continue to be so for some time. Here we consider the implications of encounter rate theory to the estimation of K_{pred} .

Full details and equations will be presented in the paper being developed from this work; here, recognising the urgency for iMARNET, we present just the results to inform discussion and decision making.

In brief, the following have been computed using the approach in Mitra & Flynn (2006) coupled with equations linking ESD (equivalent spherical diameter) to C, ESD to swimming speed, and encounter rates between prey and predator calculated with reference to their respective ESDs and swimming speeds, and to turbulence. This assumes ballistic rather than diffusive (Levy flight) movements; ballistic rates of encounter will give the maximum possible values. In reality, other factors (notably satiation –induced decrease in motility) will also decrease the encounter rate. In situations where prey are limiting, it may be assumed that ballistic paths are appropriate; thus the formulation describes correctly the experimentally computed bacteria ingestion by HNF and mixotrophs reported by Zubkov and colleagues for the AMT data series (e.g., Hartman et al, 2012).

Using encounter rates we derive the value of prey concentration that enables half G_{\max} ; this is referred to as $K_{0.5}$, to differentiate it from K_{pred} . As per the details in Mitra & Flynn (2006), $K_{0.5}$ equates (approximately) to $2 \times K_{\text{pred}}$. This $K_{0.5}$ is computed with various caveats (see above as well as below). For the purpose at hand, the plots shown assume (i) no turbulence (increasing turbulence will effectively decrease the minimum K_{pred} though the effect is not great for organism sizes of $<100\mu\text{m}$ ESD), and (ii) assumes that both prey and predator are swimming (it should be noted that diatoms are less C-dense as prey items, which coupled with the absence of swimming can effectively raise the $K_{0.5}$ values significantly).

$K_{0.5}$ values are displayed in terms of C and N units for easy reference to C or N-based model platforms, assuming Redfield C:N for prey and predator ($80 \text{ mgC/m}^3 \quad 1 \mu\text{mol N/L}$). Examples are given for predator of fixed ESD (from an HNF through to a copepod), against a range of prey ESD options, and a range of maximum grazing (ingestion) rates. The grazing rates are as a specific rate (e.g., $\text{gC prey g}^{-1}\text{C predator day}^{-1}$); the value of G_{\max} , coupled with that of GGE, defines the predator growth rate maximum.

The upper plot for each predator shows a full range of prey options (bacteria through to the size of the predator). The lower plot considers prey ESD up to between 50% of the predator ESD, and $K_{0.5}$ values capped at the equivalent of $1\mu\text{mol N/L}$; the scale of G_{\max} has been altered to enhance plot interrogation.

In crude terms, assuming $\text{GGE}=50\%$, the growth rate attainable at the prey concentration indicated by the $K_{0.5}$ value is ca. 25% of the value of G_{\max} ; for example, $G_{\max}=3\text{d}^{-1}$ will at $\text{prey}=K_{0.5}$ enable a predator growth rate of ca. a doubling per day. The prey concentration indicated by $K_{0.5}$ would

at $G_{\max}=1d^{-1}$ and $GGE=50\%$ support the growth rate potential (ca. $0.25 d^{-1}$) of a “typical” copepod, or an oligotrophic μZ .

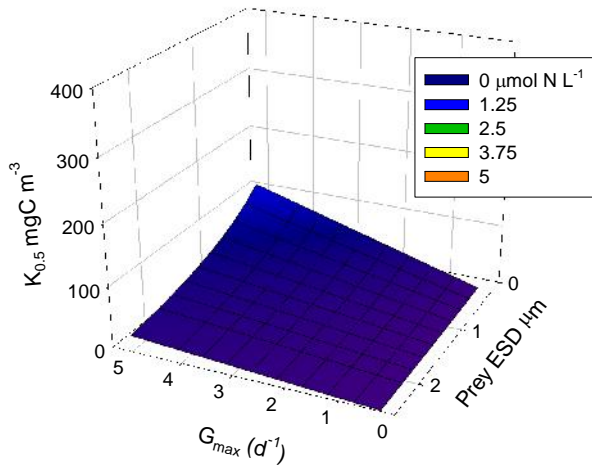
Some general comments:

- K_{pred} ($K_{0.5}$) are emergent properties of G_{\max} , predator and prey ESD and motility/turbulence - driven encounter rates. Using K_{pred} as an input driver in models must be undertaken with great caution to ensure that the value does not describe impossible grazing kinetics. Ideally the description should not be used at all, but should be replaced by a term using Holling I type descriptions for the initial phase of the interaction (see Mitra & Flynn 2006).
- In traditional grazing functions K_{pred} is often the same for all prey types. This is manifestly inappropriate, as differences in ESD have profound effects on predation rates.
- Linking predator activity to temperature will inevitably affect potential G_{\max} and thus also raise K_{pred} . In simple terms, doubling G_{\max} will double K_{pred} . Any model describing zooplankton with inclusion of a temperature term must link that value of Q_{10} also to K_{pred} . This will affect ecology with climate change, with organism types changing directly and indirectly. **However**, it would be very much preferable not to use this approach at all, but to substitute one similar to Mitra & Flynn (2006) referenced to ESD-C and motility-C relationships coupled to encounter rate calculations. The only substantive additional data input required to drive what are a series of simple equations, are ESDs for each PFT.

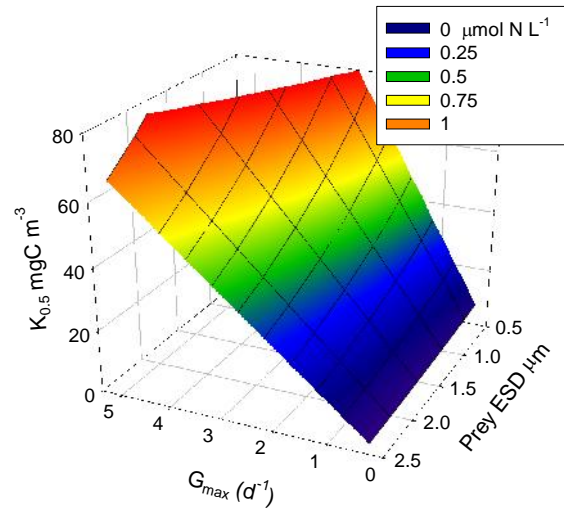
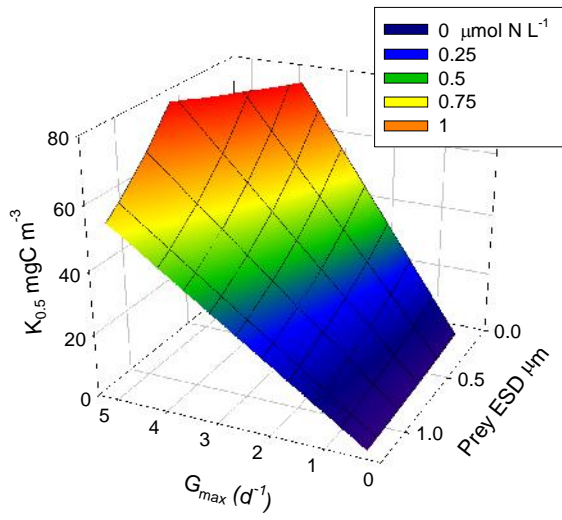
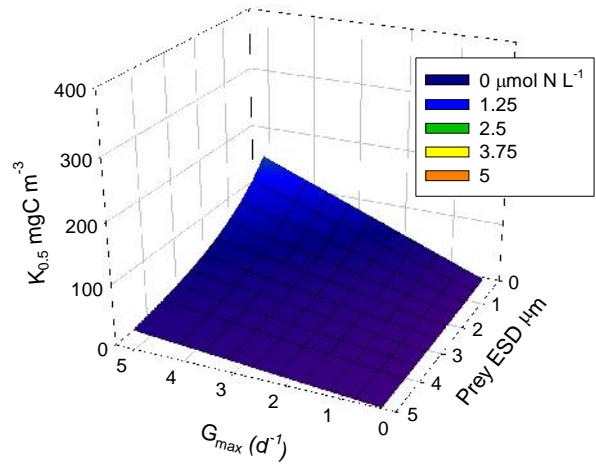
References:

- Hartmann, M., Grob, C., Tarran, G.A., Martin, A.P., Burkill, P.H., Scanlan, D.J., Zubkov, M.V., 2012. Mixotrophic basis of Atlantic oligotrophic ecosystems. *Proc. Nat. Acad. Sci.* 109:5756-5760.
- Mitra, A., Flynn, K.J., 2006. Accounting for variation in prey selectivity by zooplankton. *Ecol. Model.* 199:82-92.

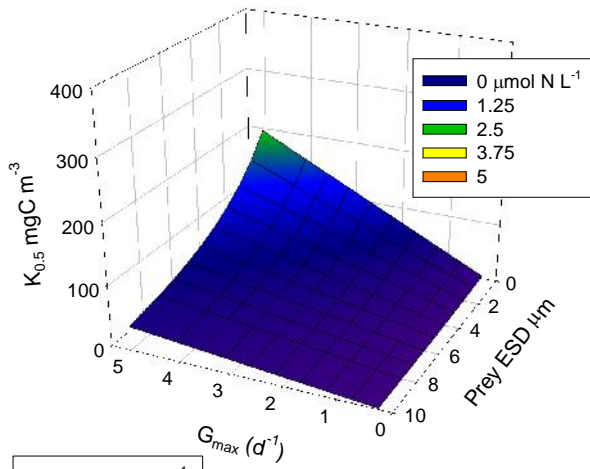
Predator ESD 2.5-m



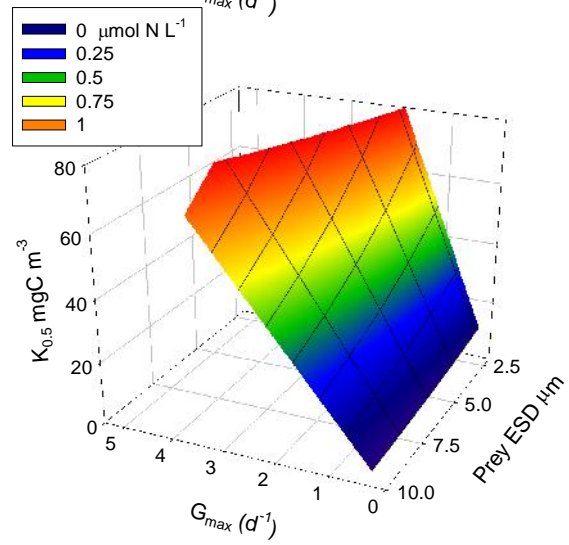
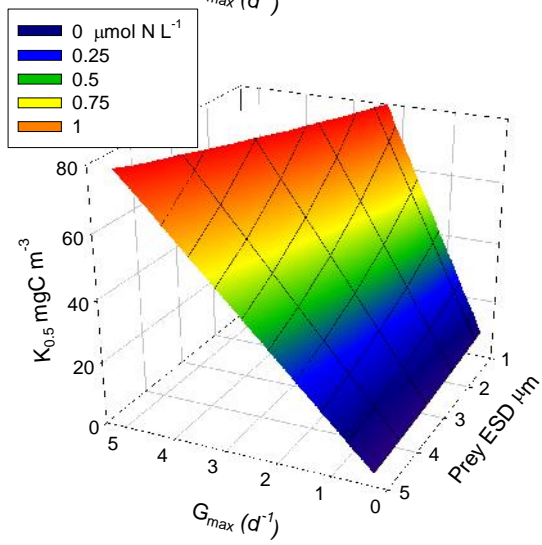
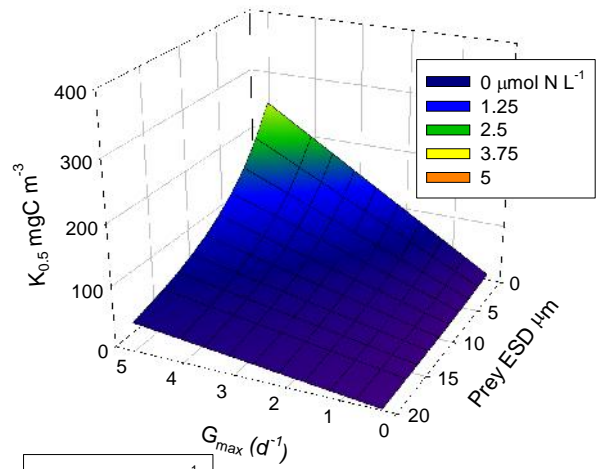
Predator ESD 5-m



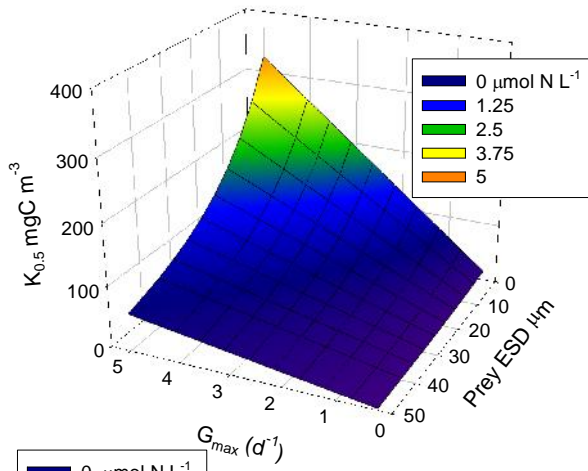
Predator ESD 10~m



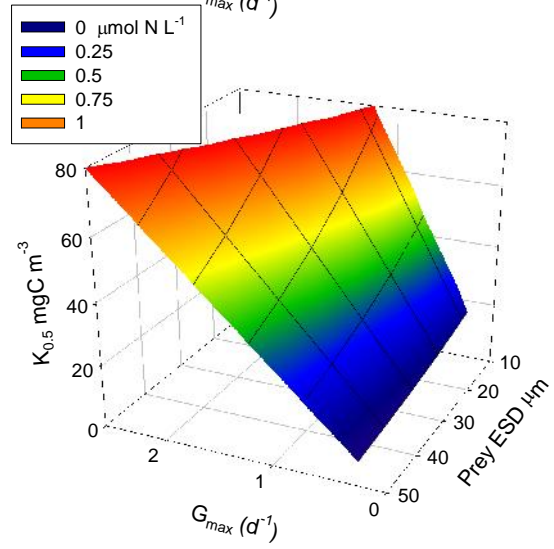
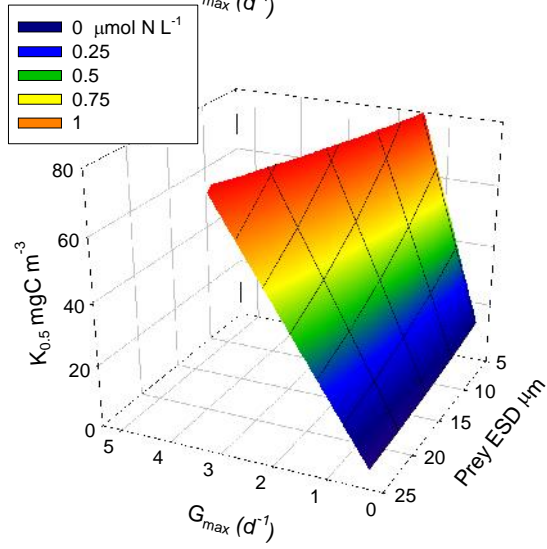
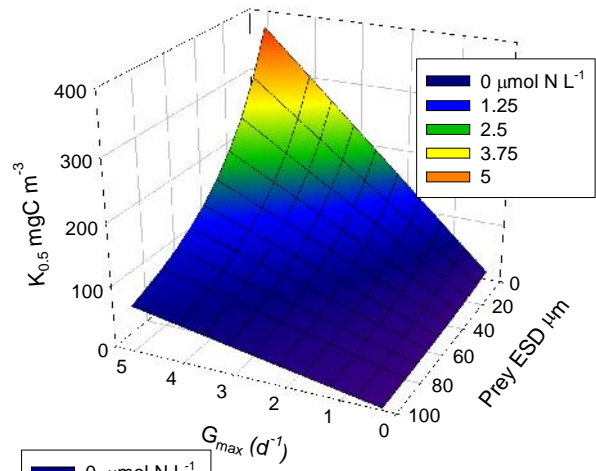
Predator ESD 20~m



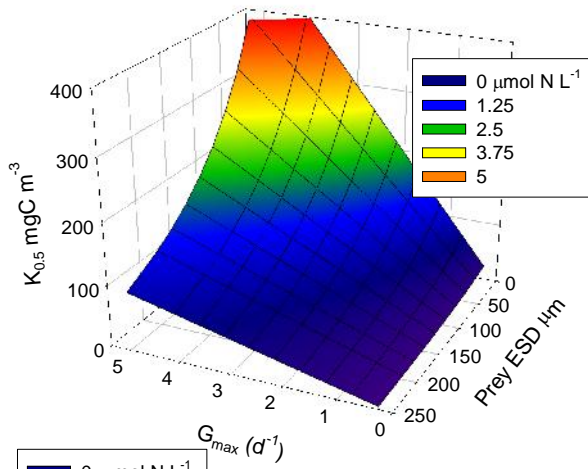
Predator ESD 50~m



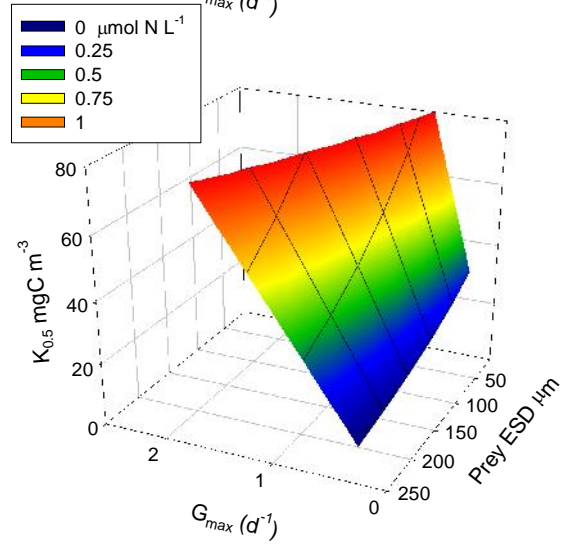
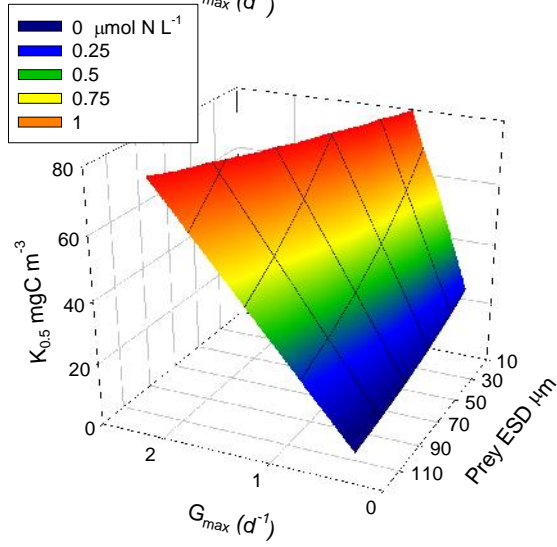
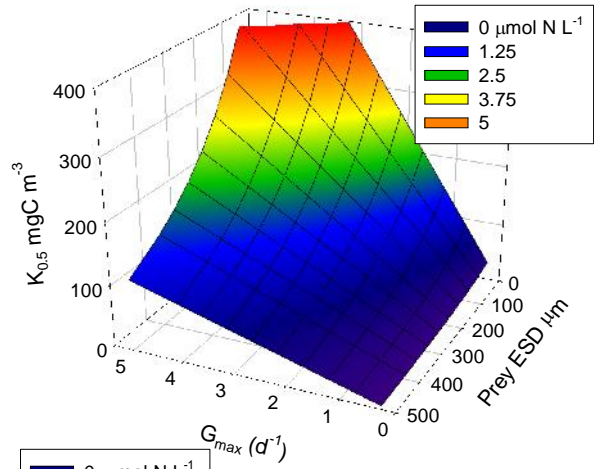
Predator ESD 100~m



Predator ESD 250~m



Predator ESD 500~m



Predator ESD 1000-m

