**Models’ bibliography**

(Jetz, Carbone, Fulford, & Brown, 2004)

(Wilson et al., 2015)

Mechanical model to define predator and prey speed and turn capacity in terrestrial species (based on muscular mass according to body size).

(Rizzuto, Carbone, & Pawar, 2018)

(C. Carbone, De Leeuw, & Houston, 1996)

(Chris Carbone, Pettorelli, & Stephens, 2011)

Relationship between predator and prey size and biomass (statistical).

(Chris Carbone, Mace, Roberts, & Macdonald, 1999)

Model that uses energetic constraints (energetic requirements) on feeding choice of terrestrial carnivores (maximal size that invertebrate diet can sustain).

(M. E. Baird & Suthers, 2007)

The model uses a 1D model of ocean mixed-layer, coupled with 3 classes of organisms (phytoplankton, zooplankton, metazoan). Each group is driven by specific allometric laws.

(M. Baird & Emsley, 1999)

Phytoplankton growth + sinking rates, and zooplankton encounter rate. Parameters from observed species (laboratory) and local fluid properties (turbulence and viscosity).

(M. E. Baird, Oke, Suthers, & Middleton, 2004)

Plankton model with a biomechanical oceanographic model.

(M. E. Baird, Timko, Suthers, & Middleton, 2006b)

The model is applied in a dynamic system (with advection, diffusion, nutrient and light uptake, growth, grazing, mortality, …).

(M. E. Baird, 2010)

Analysis of the size-resolve model and sensitivity.

(M. E. Baird, Timko, Suthers, & Middleton, 2006a)

Coupled mechanical nitrogen-phytoplankton-zooplankton model. Physical processes are diffusion of nitrogen and predator-prey encounter rate. Biological processes are maximum growth rates. The model captures the deep chlorophyll maximum during downwelling and bloom during upwelling.

Baird, M. E. (2010). Limits to prediction in a size-resolved pelagic ecosystem model. *Journal of Plankton Research*, *32*(8), 1131–1146. doi: 10.1093/plankt/fbq024

Baird, M. E., Oke, P. R., Suthers, I. M., & Middleton, J. H. (2004). A plankton population model with biomechanical descriptions of biological processes in an idealised 2D ocean basin. *Journal of Marine Systems*, *50*(3–4), 199–222. doi: 10.1016/j.jmarsys.2004.02.002

Baird, M. E., & Suthers, I. M. (2007). A size-resolved pelagic ecosystem model. *Ecological Modelling*, *203*(3–4), 185–203. doi: 10.1016/j.ecolmodel.2006.11.025

Baird, M. E., Timko, P. G., Suthers, I. M., & Middleton, J. H. (2006a). Coupled physical-biological modelling study of the East Australian Current with idealised wind forcing: Part II. Biological dynamical analysis. *Journal of Marine Systems*, *59*(3–4), 271–291. doi: 10.1016/j.jmarsys.2005.09.006

Baird, M. E., Timko, P. G., Suthers, I. M., & Middleton, J. H. (2006b). Coupled physical-biological modelling study of the East Australian Current with idealised wind forcing. Part I: Biological model intercomparison. *Journal of Marine Systems*, *59*(3–4), 249–270. doi: 10.1016/j.jmarsys.2005.09.005

Baird, M., & Emsley, S. M. (1999). Towards a mechanistic model of plankton population dynamics. *Journal of Plankton Research*, *21*(1), 85–126. doi: 10.1093/plankt/21.1.85

Carbone, C., De Leeuw, J. J., & Houston, A. I. (1996). Adjustments in the diving time budgets of tufted duck and pochard: Is there evidence for a mix of metabolic pathways? *Animal Behaviour*, *51*(6), 1257–1268. doi: 10.1006/anbe.1996.0130

Carbone, Chris, Mace, G. M., Roberts, S. C., & Macdonald, D. W. (1999). Energetic constraints on the diet of terrestrial carnivores. *Nature*, *402*(6759), 286–288. doi: 10.1038/46266

Carbone, Chris, Pettorelli, N., & Stephens, P. A. (2011). The bigger they come, the harder they fall: Body size and prey abundance influence predator-prey ratios. *Biology Letters*, *7*(2), 312–315. doi: 10.1098/rsbl.2010.0996

Jetz, W., Carbone, C., Fulford, J., & Brown, J. H. (2004). The scaling of animal space use. *Science*, *306*(5694), 266–268. doi: 10.1126/science.1102138

Rizzuto, M., Carbone, C., & Pawar, S. (2018). Foraging constraints reverse the scaling of activity time in carnivores. *Nature Ecology and Evolution*, *2*(2), 247–253. doi: 10.1038/s41559-017-0386-1

Wilson, R. P., Griffiths, I. W., Mills, M. G. L., Carbone, C., Wilson, J. W., & Scantlebury, D. M. (2015). Mass enhances speed but diminishes turn capacity in terrestrial pursuit predators. *ELife*, *4*(AUGUST2015). doi: 10.7554/eLife.06487.001

Hi Sébastien,

I had a quick look through the literature regarding first-principle models of handling time, or at least, the components of handling time beyond capture (which we have covered in the model):

- After capture, there is prey immobilisation/subjugation: I couldn’t find any theoretical paper that tries to model the immobilisation/subjugation mechanistically. Actually, the whole topic seems like quite a neglected topic, with the exception of some focus given to the case of dangerous prey (venomous prey…) . The only example of a systematic approach to this process is in a paper on an ant species, and is of hardly generalisable to there types of predators.

Mukherjee S, Heithaus MR. Dangerous prey and daring predators: a review: Daring predators. Biol Rev [Internet]. 2013 Aug [cited 2021 Jun 18];88(3):550–63. Available from: <http://doi.wiley.com/10.1111/brv.12014>

Schatz B, Lachaud J-P, Beugnon G. Graded recruitment and hunting strategies linked to prey weight and size in the ponerine ant Ectatomma ruidum. Behavioral Ecology and Sociobiology [Internet]. 1997 Jun 12 [cited 2021 Jun 18];40(6):337–49. Available from: <http://link.springer.com/10.1007/s002650050350>

- Ingestion: Here, there’s a little bit more meat to the topic. There is a tradition of modelling ingestion in terrestrial vertebrate herbivores in a mechanistic, even mechanical way (on which we partially based our own equations in the model). I found a paper that tries to generalise the approach to all consumers, over a broad range of body size. There are also traditions in the aquatic fields, that model more specifically filter-feeding, and suction feeding in fish. Notice though, that it’s only in aquatic systems that physical factors of the environment (eg, viscosity, density) are explicitly included.

Virot E, Ma G, Clanet C, Jung S. Physics of chewing in terrestrial mammals. Sci Rep [Internet]. 2017 Apr [cited 2021 Jan 28];7(1):43967. Available from: <http://www.nature.com/articles/srep43967>

Holzman R, Collar DC, Mehta RS, Wainwright PC. An integrative modeling approach to elucidate suction-feeding performance. Journal of Experimental Biology [Internet]. 2012 Jan 1 [cited 2021 Jun 16];215(1):1–13. Available from: <https://journals.biologists.com/jeb/article/215/1/1/10787/An-integrative-modeling-approach-to-elucidate>

- Digestion: A lot of mechanistic models of digestion (a classical one is Penry & Jumars’). But few that include physical factors (mostly prey size and the volume of the gut),  and none that consider the potential effect of external physical factors on the process. One promising model seems to me the surface gastric evacuation model, but it is unclear how applicable it is to organisms beyond fish. Notice that digestion is not only a chemical process: it involves mechanical processes to mix and move the food within the gut (gut motility). I couldn’t find any model that tries to estimate the quantitative effects of gut motility on digestion, and its sensitivity to external factors, such as t°, pressure…

Salvanes AGV, Aksnes DL, Giske J. A surface-dependent gastric evacuation model for fish. Journal of Fish Biology [Internet]. 1995 Oct [cited 2021 Jun 10];47(4):679–95. Available from: <http://doi.wiley.com/10.1111/j.1095-8649.1995.tb01934.x>

Olsson C, Holmgren S. The control of gut motility. Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology [Internet]. 2001 Mar [cited 2021 Jun 14];128(3):479–501. Available from: <https://linkinghub.elsevier.com/retrieve/pii/S1095643300003305>

- Actually, it is satiation level (or its mirror, hunger) that should be modelled, since it determines when the predator will start foraging again. Satiation is included in many functional response model as a factor, but seldom modelled mechanistically in any developed way. In most cases, it is modelled as ingestion rate minus digestion rate.

Jeschke JM, Kopp M, Tollrian R. PREDATOR FUNCTIONAL RESPONSES: DISCRIMINATING BETWEEN HANDLING AND DIGESTING PREY. Ecological Monographs [Internet]. 2002 Feb [cited 2021 Jun 14];72(1):95–112. Available from: [http://doi.wiley.com/10.1890/0012-9615(2002)072[0095:PFRDBH]2.0.CO;2](http://doi.wiley.com/10.1890/0012-9615(2002)072%5B0095:PFRDBH%5D2.0.CO;2)

So, in conclusion: large room for improvement; the few mechanistic models of the components of handling are often quite good  (Virot, Salvanes), but too specific. The question is: will it be possible to come with a simple, generic mechanistic model that will cover all the components of handling?

I hope that will help you in the discussion part!

Regards,

Mehdi