

Hochfeld and Hidders evaluate the effect of phytoplankton adaptation to ecosystem functioning by using a 0-dimensional evolutionary ecosystem model. They used a previously implemented individual-based model from the same authors with the following components: one nutrient (nitrogen), three phytoplankton functional groups (cyanobacteria, dinoflagellates and diatoms), one generic zooplankton and a detritus pool. Phytoplankton adaptation was implemented as two 'flexible traits' as they called them, namely optimum temperature for growth and cell size, where the variation of the former is affected by a random mutation process and the latter by cell growth. They conclude by highlighting the importance of including phytoplankton adaptation in ecosystem models.

First, it is difficult to assess the scientific significance of their modelling approach. The model is briefly presented in this manuscript but is published in the supplementary material of a previous article by the same authors (Hochfeld and Hidders, 2024). The authors repeatedly refer to this work to describe the model, without explicitly explaining what they have 'slightly modified' or 'extended'. In particular, it is unclear what are the assumptions, processes, and parameters of the model, how they quantified them in their current model description and how these differ from their previous manuscript. Perhaps the individual-based modelling approach used by the authors is novel, albeit very hard to judge based on the current description.

Second, they used the same numerical experiments as in the previous work, which show the same results as in their previous ms (cf. figure 2 in this and their previous ms with biomass staked vs non stacked). Thus, the only new results seem to be the quantification of the ecosystem functions (later results in the current manuscript), but the conclusion between manuscripts is nearly the same. Overall, I would have appreciated a thorough presentation of the model, with its assumptions, and limitations, to better interpret how these impact the author's interpretations and how much their current analysis advances our understanding of adaptive response of phytoplankton and its impact to ecological functions. Unfortunately, I cannot see that in the current manuscript and less so in comparison to their previous work.

Third, competition for resources and phytoplankton adaptation based on functional traits related to size and to a lesser extent to temperature has been investigated in models with different complexity, covering various scales and with various modelling approaches (e.g.: Bruggeman and Kooijman, 2007; Follows et al., 2007; Hellweger and Kianirad, 2007; Pahlow et al., 2008; Merico et al., 2009; Banas, 2011; Clark et al., 2011; Norberg et al., 2012; Thomas et al., 2012; Ward et al., 2012; Toseland et al., 2013; Wirtz, 2013; Daines et al., 2014; Terseleer et al., 2014; Smith et al., 2015; Kerimoglu et al., 2017; Kremer et al., 2017a; Taherzadeh et al., 2017; Acevedo-Trejos et al., 2018; Chen et al., 2019; Dutkiewicz et al., 2020). Some of these eco-evolutionary trait-based modelling approaches have been reviewed over the past decades (Norberg, 2004; Anderson, 2005, 2010; Litchman and Klausmeier, 2008; Hellweger and Bucci, 2009; Smith et al., 2011; Follows and Dutkiewicz, 2011; Andersen et al., 2015; Bonachela et al., 2016; Hellweger et al., 2016; Kremer et al., 2017b; Ward et al., 2019; Zakharova et al., 2019; Kiørboe and Andersen, 2019; Klausmeier et al., 2020). However, the introduction only covers a few examples and gives the impression that not much work has been done in the past decades to capture the adaptive capacity of planktonic organisms in ecosystem models, which to my knowledge is not the case. Hence, I consider that the introduction needs to provide a better rationale for the study in the context of previous eco-

evolutionary trait-based models, what technical or knowledge gap is covered and to clearly present what is distinct in their modelling approach.

Last, in both manuscripts the authors suggest that their model aims to capture the dynamics of the Baltic Sea. However, no model calibration or validation against observations is provided. If the authors want to make such a claim, I would suggest having figures that clearly show model performance against observations.

Albeit the presentation quality of the manuscript is good, unfortunately, the various issues I have listed above do not allow me to recommend the manuscript for publication in its current state.

References

- Acevedo-Trejos, E., Marañón, E., and Merico, A. (2018). Phytoplankton size diversity and ecosystem function relationships across oceanic regions. *Proc. R. Soc. B Biol. Sci.* 285. doi:10.1098/rspb.2018.0621.
- Andersen, K. H., Berge, T., Gonçalves, R. J., Hartvig, M., Heuschele, J., Hylander, S., et al. (2015). Characteristic sizes of life in the oceans, from bacteria to whales. *Ann. Rev. Mar. Sci.* 8, 1–25. doi:10.1146/annurev-marine-122414-034144.
- Anderson, T. R. (2005). Plankton functional type modelling: running before we can walk? *J. Plankton Res.* 27. doi:10.1093/plankt/fbi076.
- Anderson, T. R. (2010). Progress in marine ecosystem modelling and the “unreasonable effectiveness of mathematics”. *J. Mar. Syst.* 81, 4–11. doi:10.1016/j.jmarsys.2009.12.015.
- Banas, N. S. (2011). Adding complex trophic interactions to a size-spectral plankton model: Emergent diversity patterns and limits on predictability. *Ecol. Modell.* 222, 2663–2675. doi:10.1016/j.ecolmodel.2011.05.018.
- Bonachela, J. A., Klausmeier, C. A., Edwards, K. F., Litchman, E., and Levin, S. A. (2016). The role of phytoplankton diversity in the emergent oceanic stoichiometry. *J. Plankton Res.* 38, 1021–1035. doi:10.1093/plankt/fbv087.
- Bruggeman, J., and Kooijman, S. A. L. M. (2007). A biodiversity-inspired approach to aquatic ecosystem modeling. *Limnol. Oceanogr.* 52, 1533–1544. doi:10.4319/lo.2007.52.4.1533.
- Chen, B., Smith, S. L., and Wirtz, K. W. (2019). Effect of phytoplankton size diversity on primary productivity in the North Pacific: trait distributions under environmental variability. *Ecol. Lett.* 22, 56–66. doi:10.1111/ele.13167.
- Clark, J. R., Daines, S. J., Lenton, T. M., Watson, A. J., and Williams, H. T. P. (2011). Individual-based modelling of adaptation in marine microbial populations using genetically defined physiological parameters. *Ecol. Modell.* 222, 3823–3837. doi:10.1016/j.ecolmodel.2011.10.001.
- Daines, S. J., Clark, J. R., and Lenton, T. M. (2014). Multiple environmental controls on phytoplankton growth strategies determine adaptive responses of the N:P ratio. *Ecol. Lett.* 17, 414–425. doi:10.1111/ele.12239.
- Dutkiewicz, S., Cermeno, P., Jahn, O., Follows, M. J., Hickman, A. E., Taniguchi, D. A. A., et al. (2020). Dimensions of marine phytoplankton diversity. *Biogeosciences* 17, 609–634. doi:10.5194/bg-17-609-2020.

- Follows, M. J., and Dutkiewicz, S. (2011). Modeling diverse communities of marine microbes. *Ann. Rev. Mar. Sci.* 3, 427–451. doi:10.1146/annurev-marine-120709-142848.
- Follows, M. J., Dutkiewicz, S., Grant, S., and Chisholm, S. W. (2007). Emergent biogeography of microbial communities in a model ocean. *Science*. 315, 1843–1846. doi:10.1126/science.1138544.
- Hellweger, F. L., and Bucci, V. (2009). A bunch of tiny individuals-Individual-based modeling for microbes. *Ecol. Modell.* 220, 8–22. doi:10.1016/j.ecolmodel.2008.09.004.
- Hellweger, F. L., Clegg, R. J., Clark, J. R., Plugge, C. M., and Kreft, J. U. (2016). Advancing microbial sciences by individual-based modelling. *Nat. Rev. Microbiol.* 14, 461–471. doi:10.1038/nrmicro.2016.62.
- Hellweger, F. L., and Kianirad, E. (2007). Individual-based modeling of phytoplankton: Evaluating approaches for applying the cell quota model. *J. Theor. Biol.* 249, 554–565. doi:10.1016/j.jtbi.2007.08.020.
- Hochfeld, I., and Hinnens, J. (2024). Evolutionary adaptation to steady or changing environments affects competitive outcomes in marine phytoplankton. *Limnol. Oceanogr.* 69, 1172–1186. doi:10.1002/lno.12559.
- Kerimoglu, O., Hofmeister, R., Maerz, J., Riethmüller, R., and Wirtz, K. W. (2017). The acclimative biogeochemical model of the southern North Sea. *Biogeosciences* 14, 4499–4531. doi:10.5194/bg-14-4499-2017.
- Kiørboe, T., and Andersen, K. H. (2019). Nutrient affinity, half-saturation constants and the cost of toxin production in dinoflagellates. *Ecol. Lett.* 22, 558–560. doi:10.1111/ele.13208.
- Klausmeier, C. A., Kremer, C. T., and Koffel, T. (2020). ‘Trait-based ecological and eco-evolutionary theory’, in *Theoretical Ecology: concepts and applications*, eds. K. S. McCann and G. Gellner (Oxford University Press).
- Kremer, C. T., Thomas, M. K., and Litchman, E. (2017a). Temperature- and size-scaling of phytoplankton population growth rates: reconciling the Eppley curve and the metabolic theory of ecology. *Limnol. Oceanogr.* doi:10.1002/lno.10523.
- Kremer, C. T., Williams, A. K., Finiguerra, M., Fong, A. A., Kellerman, A., Paver, S. F., et al. (2017b). Realizing the potential of trait-based aquatic ecology: New tools and collaborative approaches. *Limnol. Oceanogr.* 62, 253–271. doi:10.1002/lno.10392.
- Litchman, E., and Klausmeier, C. A. (2008). Trait-based community ecology of phytoplankton. *Annu. Rev. Ecol. Evol. Syst.* 39, 615–639. doi:10.1146/annurev.ecolsys.39.110707.173549.
- Meric, A., Bruggeman, J., and Wirtz, K. (2009). A trait-based approach for downscaling complexity in plankton ecosystem models. *Ecol. Modell.* 220, 3001–3010. doi:10.1016/j.ecolmodel.2009.05.005.
- Norberg, J. (2004). Biodiversity and ecosystem functioning: A complex adaptive systems approach. *Limnol. Oceanogr.* 49, 1269–1277. doi:10.4319/lo.2004.49.4_part_2.1269.
- Norberg, J., Urban, M. C., Vellend, M., Klausmeier, C. a., and Loeuille, N. (2012). Eco-evolutionary responses of biodiversity to climate change. *Nat. Clim. Chang.* 2, 747–751. doi:10.1038/nclimate1588.
- Pahlow, M., Vézina, A. F., Casault, B., Maass, H., Malloch, L., Wright, D. G., et al. (2008). Adaptive model of plankton dynamics for the North Atlantic. *Prog. Oceanogr.* 76, 151–191. doi:10.1016/j.pocean.2007.11.001.
- Smith, S. L., Pahlow, M., Merico, A., Acevedo-Trejos, E., Sasai, Y., Yoshikawa, C., et al. (2015). Flexible phytoplankton functional type (FlexPFT) model: size-scaling of traits and

- optimal growth. *J. Plankton Res.* 38, 977–992. doi:10.1093/plankt/fbv038.
- Smith, S. L., Pahlow, M., Merico, A., and Wirtz, K. W. (2011). Optimality-based modeling of planktonic organisms. *Limnol. Oceanogr.* 56, 2080–2094. doi:10.4319/lo.2011.56.6.2080.
- Taherzadeh, N., Kerimoglu, O., and Wirtz, K. W. (2017). Can we predict phytoplankton community size structure using size scalings of eco-physiological traits? *Ecol. Modell.* 360, 279–289. doi:10.1016/j.ecolmodel.2017.07.008.
- Terseleer, N., Bruggeman, J., Lancelot, C., and Gypens, N. (2014). Trait-based representation of diatom functional diversity in a plankton functional type model of the eutrophied Southern North Sea. *Limnol. Oceanogr.* 59, 1–16. doi:10.4319/lo.2014.59.6.0000.
- Thomas, M. K., Kremer, C. T., Klausmeier, C. A., and Litchman, E. (2012). A global pattern of thermal adaptation in marine phytoplankton. *Science*. 338, 1085–8. doi:10.1126/science.1224836.
- Toseland, A., Daines, S. J., Clark, J. R., Kirkham, A., Strauss, J., Uhlig, C., et al. (2013). The impact of temperature on marine phytoplankton resource allocation and metabolism. *Nat. Clim. Chang.* 3, 1–6. doi:10.1038/nclimate1989.
- Ward, B. A., Collins, S., Dutkiewicz, S., Gibbs, S., Bown, P., Ridgwell, A., et al. (2019). Considering the Role of Adaptive Evolution in Models of the Ocean and Climate System. *J. Adv. Model. Earth Syst.* 11, 3343–3361. doi:10.1029/2018MS001452.
- Ward, B. A., Dutkiewicz, S., Jahn, O., and Follows, M. J. (2012). A size-structured food-web model for the global ocean. *Limnol. Oceanogr.* 57, 1877–1891. doi:10.4319/lo.2012.57.6.1877.
- Wirtz, K. W. (2013). Mechanistic origins of variability in phytoplankton dynamics: Part I: niche formation revealed by a size-based model. *Mar. Biol.* 160, 2319–2335. doi:10.1007/s00227-012-2163-7.
- Zakharova, L., Meyer, K. M., and Seifan, M. (2019). Trait-based modelling in ecology: A review of two decades of research. *Ecol. Modell.* 407, 108703. doi:10.1016/j.ecolmodel.2019.05.008.