COMMENTARY

A numerical model sheds new light on the effects of ocean acidification on an indicator species: A commentary on Hofmann Elizondo et al. (2024)

Martin Vodopivec[1]

[1]Marine Biology Station, National Institute of Biology , Fornače 41, 6330 Piran, Slovenia

Correspondence
Martin Vodopivec, Marine Biology Station, National Institute of Biology , Fornače 41, 6330 Piran, Slovenia
Email: martin.vodopivec@nib.si

Funding information
Slovenian Research Agency (research core funding No. P1-0237).

Ocean acidification (OA), a direct consequence of anthropogenic CO_2 emissions, significantly affects marine ecosystems, including the ocean carbon pump. It's most direct effect is felt by the marine calcifiers where acidity and low aragonite saturation (Ω) results in reduced calcification and shells dissolution (Bednaršek et al., 2023).

For those lacking a background in marine biology (myself included): Pteropods, or sea butterflies, are small planktonic marine snails, typically less than 1 cm in size, found in all the world's oceans. They serve as an important food source for many marine species and play a significant role in the biological carbon pump. Pteropods form thin aragonite shells, which is more soluble than calcite, making them highly sensitive to ocean acidification (OA). To avoid predation, pteropods dive into deeper, but also more acidic, layers during the day. These characteristics make pteropods a key indicator species for OA.

Laboratory experiments have shown that the shells of pteropods grow thinner in acidic environment (Bednaršek et al., 2019). Pteropods sampled in the California Current System, where deep, unsaturated waters rise closer to the surface, had significantly thinner shells than those sampled further offshore (Mekkes et al., 2021). These findings suggest that the pteropods are probably already experiencing the adverse effects of OA and could face significant threats under projected climate change. The observed response of pteropods to an acidic environment has been combined with observed and modelled trends in aragonite saturation in the world's oceans to assess and predict the impact of OA on pteropod populations (Bednaršek et al., 2023). However, none of these approaches is able to account for the complete life history of individual pteropods. As shown by Hofmann Elizondo et al. (2024), there is considerable spatial heterogeneity in Ω and the depth of diel vertical migrations of pteropods changes over their lifetime. The extent and intensity of time spent in a harmful acidic environment is thus difficult to estimate and varies drastically between individuals.

Hofmann Elizondo et al. (2024) approach this problem with a Lagrangian (trajectory-following) Individual Based Model (IBM, Grimm and Railsback (2013)). A large number of fictitious particles, representing individual pteropods, are released and tracked in hourly time steps in a numerical model. Such an approach is able to provide a complete life history of the individual pteropods. Results of the laboratory and *in situ* studies are incorporated into a comprehensive model which emulates the behaviour of each individual pteropod (diel vertical migrations), takes into account different life stages (stage-specific vertical migrations and sensitivity to acidic environment) and effects of environment (food- and temperature-dependent growth, aragonite saturation and temperature-dependent mortality, etc.). The basic assumptions and parameterisations used in the model are described in Hofmann Elizondo and Vogt (2022). In their new work, Hofmann Elizondo et al. (2024) apply new findings to improve the representation of individuals and develop a sophisticated attribution approach to infer the effects of natural variability in OA, its trend and extreme events on the development, reproduction and mortality of pteropods in the California Current System. This gives us unprecedented insight into the dynamics of OA influence on pteropod development. It also shows the wide range of possible life-history scenarios, which greatly differ between individuals. The results show that most damage is caused by naturally occurring exposure to low Ω conditions during diel vertical migrations. However, they also show that there have been increasing detrimental effects of anthorpogenically driven OA on pteropod populations in the California Current System since 1984 and these are expected to amplify in the future.

Hofmann Elizondo et al. (2024) exemplify how *in silico* experiments (Gentleman, 2002) can provide deeper and more holistic insights into marine ecosystem functioning. The study effectively addresses a number of very important issues, namely: What are the effects of OA on pteropods? Are these getting worse? What is the contribution of human-induced OA? Are pteropods already affected by increased OA? The study is very well thought out, with a clear set of research questions, a thorough model design that incorporates all available data in the model parameterisations, and an in-depth analysis of the model results. Due to the spatial heterogeneity of aragonite saturation, a Lagarangian approach is required to properly assess the exposure of pteropods to harmful environment and its consequences. The authors formulate their IBM according to the ODD (Overview, Design concepts, Details) protocol (Grimm et al., 2006) and adhere closely to the "as simple as possible, but as complicated as necessary" approach (Sun et al., 2016). Every model inherently differs from the system it is trying to emulate as the only way to eliminate all differences would be for the model to become the system itself. Therefore, it is important to know the limitations of the model in order to properly interpret its results and the authors transparently discuss the model's caveats and limitations. There is a known bias in the biogeochemical model used to provide Ω values (Desmet et al., 2022), and I find the re-seeding strategy that keeps the particles inside the California Current System somewhat questionable, but also necessary to keep the modelled pteropods in the area of interest. The authors also offer possibilities for future improvements of the model that would allow an assessment of the effects of combined stressors (e.g. OA in combination with temperature and food availability) on pteropod development. The model code is freely available and the principles and equations are thoroughly explained in the paper and the extensive Supplementary Information section.

The study provides a theoretical foundation for the future monitoring and management programmes that will enable the differentiation between the damages caused by natural variations and those caused by human influences. Moreover, it provides a modelling framework that could be used for many other marine calcifiers and an attribution scheme that could be used to assess the impact of environmental stressors on different marine organisms. Therefore, this work should prove to be an interesting read to marine biologists, ecologists and modellers alike.

conflict of interest

The author declares no conflict of interest.

references

Bednaršek, N., Feely, R. A., Howes, E. L., Hunt, B. P., Kessouri, F., León, P., Lischka, S., Maas, A. E., McLaughlin, K., Nezlin, N. P. et al. (2019) Systematic review and meta-analysis toward synthesis of thresholds of ocean acidification impacts on calcifying pteropods and interactions with warming. *Frontiers in Marine Science*, **6**, 227.

Bednaršek, N., Feely, R. A., Pelletier, G. and Desmet, F. (2023) Global synthesis of the status and trends of ocean acidification impacts on shelled pteropods. *Oceanography*, **36**, 130–137.

Desmet, F., Gruber, N., Köhn, E. E., Münnich, M. and Vogt, M. (2022) Tracking the space-time evolution of ocean acidification extremes in the california current system and northeast pacific. *Journal of Geophysical Research: Oceans*, **127**, e2021JC018159.

Gentleman, W. (2002) A chronology of plankton dynamics in silico: how computer models have been used to study marine ecosystems. *Hydrobiologia*, **480**, 69–85.

Grimm, V., Berger, U., Bastiansen, F., Eliassen, S., Ginot, V., Giske, J., Goss-Custard, J., Grand, T., Heinz, S. K., Huse, G. et al. (2006) A standard protocol for describing individual-based and agent-based models. *Ecological modelling*, **198**, 115–126.

Grimm, V. and Railsback, S. F. (2013) Individual-based modeling and ecology. In *Individual-based modeling and ecology*. Princeton university press.

Hofmann Elizondo, U. and Vogt, M. (2022) Individual-based modeling of shelled pteropods. *Ecological Modelling*, **468**, 109944.

Hofmann Elizondo, U., Vogt, M., Bednaršek, N., Munnich, M. and Gruber, N. (2024) The impact of aragonite saturation variability on shelled pteropods: An attribution study in the California Current System. *Global Change Biology*.

Mekkes, L., Renema, W., Bednaršek, N., Alin, S. R., Feely, R. A., Huisman, J., Roessingh, P. and Peijnenburg, K. T. (2021) Pteropods make thinner shells in the upwelling region of the California Current Ecosystem. *Scientific Reports*, **11**, 1731.

Sun, Z., Lorscheid, I., Millington, J. D., Lauf, S., Magliocca, N. R., Groeneveld, J., Balbi, S., Nolzen, H., Müller, B., Schulze, J. et al. (2016) Simple or complicated agent-based models? A complicated issue. *Environmental Modelling & Software*, **86**, 56–67.