

The manuscript “Modelling survival and connectivity of *Mnemiopsis leidyi* in the southern North Sea and Scheldt estuaries” by van der Molen, van Beek, Augustine, Vansteenbrugge, van Walraven, Langenberg, van der Veer, Hostens, Pitois and Robbens focusses on coastal areas of the SW North Sea and compares by use of 3 different model approaches connectivity, drift and dispersal potential of an invasive comb jelly species. Drift models are conducted with and without considering biological components. Further, a dynamic energy budget model was included in the model comparison. This is an interesting study which is of large interest to a wide readership due to the documented impact of *M. leidyi* on ecosystem functioning and the long standing question about source sink dynamics in the North Sea. However, there are some drawbacks to the study, probably due to the ambitious character trying to combine diverse approaches and to put it into a coherent framework. Also a lot of short cuts with regard to previously published work are done with extensively citing review papers without acknowledging the original work. This is especially pronounced in the dynamic energy budget modelling part of the paper.

The authors should carefully check the current literature and all the references used in their manuscript. As outlined in the detailed comments, work has been wrongly cited which suggests that the authors are not familiar with the respective literature. This becomes a major critique since model assumptions for the drift model with biological component are based on the southern invasive population which are genetically different from the population present in the North Sea (Reusch *et al.*, 2010) and have known difference in physiological response to e.g. temperature. Not taking this into account leads to wrong model parameterizations. This is exemplified with the use of a lethal temperature threshold for the biological drift model of 2°C while *M. leidyi* present in northern Europe is known to be present throughout the entire year in the SW North Sea, more specifically Dutch Wadden Sea (Van Walraven *et al.*, 2013) and is also known to overwinter under the ice in its native habitat (Costello *et al.* 2006). Apart from this, credit is not given to the original work since summary, review and modelling papers are cited instead of the original, underlying literature. Another central issue is that a large body of the manuscript is based on temperature dependence on e.g. growth and egg production. However, temperature effects on physiological rates <10°C have seldom been tested in controlled laboratory investigations (but see Miller, 1970; Jaspers *et al.*, 2011). The authors cite Lehtiniemi *et al.* (Lehtiniemi *et al.*, 2011) but this paper contains no results about temperature effects but is instead using temperature effects published by other authors (Costello *et al.*, 2006). Costello *et al.* (2006) suggest, based on field observations, that temperatures <10°C have a dramatic impact on reproduction rates. However, they also report that reproduction was observed at 6°C. Therefore, the original literature is not correctly incorporated. This leads to the weakness that suggested temperature effects become cited as a fact, leaving uncertainty and discussion about possible limitations of the original data behind and leading to wrong assumptions for the models. I suggest appropriately citing the original work and conducting a sensitivity analysis of key parameters used in the analyses.

The paper seems stitched together from three independent, partly published models. For example: It remains unclear why the dynamic energy budget model and the ecological drift model used different model parameter values. To my understanding it is more relevant to test model outputs if they are fed with the same information. An example: Reproduction potential is based on two different egg carbon values of 0.22 µgC egg<sup>-1</sup> in the dynamic energy budget and 0.1 µgC egg<sup>-1</sup> in the ecological drift model. I suggest running the models again using the same parameter values to allow for comparisons. Otherwise the ecological application of these models remains speculative.

**Specific comments:**

**Title:** The authors investigate the SW North Sea, therefore I suggest changing the title from southern North Sea to south western North Sea.

**Abstract:** One model was abbreviated, while the others were not. I suggest giving abbreviations for all models used and consistently use these abbreviations throughout the manuscript. There was some confusion and model abbreviations were not consistently used.

**Introduction:** The introduction appears stitched together and could be improved. To my opinion, a bit more background on the observed source sink dynamics in other north European parts like the Baltic Sea could be a valuable addition (e.g. Schaber *et al.*, 2011; Haraldsson *et al.*, 2013).

For the outlined issue of problems with citations, three examples are indicated here but this flaw is manifold throughout the manuscript and should be carefully addressed:

Page 2 line 19-21: "The ctenophore *Mnemiopsis leidyi* originates from tropical to warmer temperate waters along the East coast of the American continent (Boersma *et al.*, 2007; Gesamp, 1997; Lehtiniemi *et al.*, 2012; Purcell *et al.*, 2001). Boersma *et al.* 2007 reported first sightings of *M. leidyi* in the German Bight. The work has nothing to do with occurrence of *M. leidyi* in its native habitat. Similarly, Lehtiniemi *et al.* 2012 did a drift model study in the Baltic Sea and their results have nothing to do with *M. leidyi* occurrence in its native habitat. Purcell *et al.* 2001 is a review paper comparing native and invasive *M. leidyi* populations.

Page 3 line 17-19: "The North Sea is the home of commercially important fish stocks and spawning and nursery grounds (Ellis *et al.*, 2011), and also shares the depleted state of fish stocks that characterized the Black Sea when *M. leidyi* was introduced (Boersma *et al.*, 2007; Fuentes *et al.*, 2010)." It is not clear what the citations of Boersma *et al.* and Fuentes *et al.* refer to since these papers only report the first occurrence of *M. leidyi* in the German Bight and NW Mediterranean Sea, respectively.

The following sentence: "Furthermore, recent work from Collingridge *et al.* (2014) found that large parts of the North Sea were suitable for *M. leidyi* reproduction in summer months, with some of the highest risk areas along the southern coastal and estuarine regions of the North Sea..." It would be more correct to cite this reference giving credit to their model, hence acknowledging that their model predictions suggested that... Direct experimental data to substantiate this model from the North Sea is lacking and temperature dependence on reproduction rates is experimentally not well understood.

Page 6 Line 9/10: "with limited adaptations" what do the authors mean with this? Please specify

#### **Materials and Methods:**

Page 8 Line 22: Diurnal vertical migration was incorporated in the model but it remains unclear how this has been done. Please specify this. Also I would advise taking published work on diel vertical behavior of *M. leidyi* into account as has recently been published for the Baltic Sea region (Haraldsson *et al.*, 2014).

Page 11 Line 2: "food stocks were assumed not to be impacted upon by *M. leidyi*." Can the authors explain why they assume this since dramatic impact on food stocks have been documented throughout its invasion range for an example from northern Europe, see (Riisgard *et al.*, 2012).

Page 11 Line 4 + Page 14 Line 1/2: "Constants were taken from Salihoglu *et al.* (2011) unless specified otherwise" The study cited is focusing on the southern invasion of *M. leidyi* in Europe. Animals are genetically distinct from northern Europe (Reusch *et al.*, 2010). Is it correct to assume that most model parameters are the same? There is a striking temperature difference between both populations. Therefore, later assumptions (page 14 line 1+2), where authors assume that temperatures <2°C are lethal, are not correct. The northern native *M. leidyi* population has been shown to be the source population present in the North Sea (Reusch *et al.*, 2010). They survive temperatures <2°C, see Costello *et al.* 2006. I suggest refining the model and making realistic assumptions based on eco-physiological experiments in the respective regions or at least with the same populations. Also it is strange that in the discussion section authors seem clear about the eco-physiological differences (e.g. page 24/25) so somehow model

assumptions and discussion of results do not match up. To my opinion it would be good to make realistic assumptions from the start.

Page 11 Line 12: Why is a different carbon content per egg used than in the dynamic energy budget model? Is it appropriate to compare model results if the carbon content per egg differs by a factor of 2.2?! I suggest to re-run the model using a coherent carbon value for eggs.

Page 13 Line 1: "empirical constants based on the graphs presented by Salihoglu et al. (2011)." To my knowledge the here cited paper is a modeling study without presenting empirical data. If empirical data are presented, they are likely to be from another original source. Please check this and give full credit to the original work.

Page 14 Line 3 and 4: "a daily starvation mortality rate of 13% for food concentrations less than 3mgCm<sup>-3</sup> (Oliveira, 2007)." The here cited manuscript only reports on first occurrences of *M. leidyi* in Norway. There are no data on starvation mortality shown!

### **Results:**

There are a lot of figures and the reader can easily lose track of which models are presented and what the difference is. Since the scope of this ms is to make a model comparison, I suggest to condense the Figures and make a key comparison figure where results of all 3 models can be easily assessed.

Page 20 Line 23 + Fig. 12: " Over a million eggs were produced per hour by the population ..." How can this happen in a species with synchronized spawning? Also in the Fig. 12d I could not find on which basis the egg production has been calculated. Please specify.

Page 23 Line 6: "the reproduction rates for adults of three size classes (2.8, 5 and 10mgC respectively) were computed." Please specify how these reproduction rates have been computed. It is not enough to refer to unpublished work (Augustine et al. submitted).

### **Discussion:**

The discussion should incorporate the above mentioned points. Also it is surprising, that the authors seem to know a lot of background information which is not incorporated into the models.

Page 25 Line 20: Here it would be valuable to discuss the findings in light of detailed population dynamic studies in the Baltic Sea where *M. leidyi* eggs and larvae have been quantified on an annual basis (Jaspers *et al.*, 2013).

### **Figures:**

The paper includes a large body of Figures. Can some of them be moved to an electronic supplement? This might include the figures describing the model grid.

Also, since 2 out of the 3 studies seem published, it would be good to indicate which Figures have already been published and which ones are based on new, original results. If figures are published and reproduced here, it should be indicated.

The lower panel in Fig. 8 reports up to 20 *M. leidyi* m<sup>-3</sup> densities on land ... Please check this.

Food dependent egg production rates presented in Fig. 14: I am surprised to see scaled food dependent egg production rates since, to my knowledge, these set of experiments have not been published. Where do these data come from, what is the experimental baseline for the model assumptions, hence for these figures? It should be clearly mentioned how certain model outputs were generated and what kind of data were used/what the underlying data was to generate such model assumptions.

- Costello, J. H., Sullivan, B. K., Gifford, D. J., Van Keuren, D. and Sullivan, L. J. (2006) Seasonal refugia, shoreward thermal amplification, and metapopulation dynamics of the ctenophore *Mnemiopsis leidyi* in Narragansett Bay, Rhode Island. *Limnol. Oceanogr.*, **51**, 1819-1831.
- Haraldsson, M., Bamstedt, U., Tiselius, P., Titelman, J. and Aksnes, D. L. (2014) Evidence of diel vertical migration in *Mnemiopsis leidyi*. *PLoS One*, **9**, 10.
- Haraldsson, M., Jaspers, C., Tiselius, P., Aksnes, D. L., Andersen, T. and Titelman, J. (2013) Environmental constraints of the invasive *Mnemiopsis leidyi* in Scandinavian waters. *Limnol. Oceanogr.*, **58**, 37-48.
- Jaspers, C., Haraldsson, M., Lombard, F., Bolte, S. and Kjørboe, T. (2013) Seasonal dynamics of early life stages of invasive and native ctenophores give clues to invasion and bloom potential in the Baltic Sea. *J. Plankton Res.*, **35**, 582-594.
- Lehtiniemi, M., Lehmann, A., Javidpour, J. and Myrberg, K. (2011) Spreading and physico-biological reproduction limitations of the invasive American comb jelly *Mnemiopsis leidyi* in the Baltic Sea. *Biol. Invasions*, **14**, 341-354.
- Miller, R. J. (1970) *Distribution and energetics of an estuarine population of the ctenophore, Mnemiopsis leidyi*. North Carolina State University at Raleigh, USA, pp.
- Reusch, T. B. H., Bolte, S., Sparwel, M., Moss, A. G. and Javidpour, J. (2010) Microsatellites reveal origin and genetic diversity of Eurasian invasions by one of the world's most notorious marine invader, *Mnemiopsis leidyi* (Ctenophora). *Mol. Ecol.*, **19**, 2690-9.
- Riisgard, H. U., Madsen, C. V., Barth-Jensen, C. and Purcell, J. E. (2012) Population dynamics and zooplankton-predation impact of the indigenous scyphozoan *Aurelia aurita* and the invasive ctenophore *Mnemiopsis leidyi* in Limfjorden (Denmark). *Aquat. Invasions*, **7**, 147-162.
- Schaber, M., Haslob, H., Huwer, B., Harjes, A., Hinrichsen, H. H., Koster, F. W., Storr-Paulsen, M., Schmidt, J. O. and Voss, R. (2011) The invasive ctenophore *Mnemiopsis leidyi* in the central Baltic Sea: seasonal phenology and hydrographic influence on spatio-temporal distribution patterns. *J. Plankton Res.*, **33**, 1053-1065.
- Van Walraven, L., Langenberg, V. T. and Van Der Veer, H. W. (2013) Seasonal occurrence of the invasive ctenophore *Mnemiopsis leidyi* in the western Dutch Wadden Sea. *J. Sea Res.*, **82**, 86-92.