Author comments in red. (only included where suggested changes require additional comments) Changes to document in blue.

General response.

We thank the referees for their very positive and constructive comments.
We recognise three main points that run through the comments:

Introduction and references
Model names and connection with results
Description/details DEB model

Below, we suggest substantial changes to the text associated with these three points, in addition to numerous minor changes.
We think that these changes will improve the overall legibility of the paper.

Referee #1

General comments

Introduction

In this paper is van der Molen with co-authors modeling the reproduction, survival and dispersal of the invasive ctenophore Mnemiopsis leidyi in the Scheldt estuaries and the southern North Sea. By taking use of three different models with varying resolution and complexity, they are able to estimate the potential dispersal patterns of Mnemiopsis in the southern North Sea and surrounding estuaries, and perhaps more importantly, to explore potential factors effecting the dispersal patterns. In their hand, except for the models, they have field observations from several field campaigns in Dutch waters, and they are partly using model parameters previously defined in published work.

Merits

It is a highly relevant topic within its research field. Since the introduction of Mnemiopsis in European waters, the scientific community has questioned if, how and where Mnemiopsis may be transported and if this will result in further spreading through European waters. Since Mnemiopsis have the potential of affecting the whole ecosystem, this is of high relevance not only for "jellyfish researchers". The authors' use of different models to explore different aspect of the dispersal potential, it allows them to draw conclusions about potential important factors influencing Mnemiopsis spread. This is certainly one of the better drift-modeling papers involving this species. The paper is well structured and written, and understanding the limitations of the models, the authors have managed to write a nicely balanced discussion.

Critique

Because it is a very ambitious work with several models it demands a long and technical method section, and the result section contains a lot of figures. To make the manuscript slightly less heavy, it would be to their advantage to at least reduce the total number of figures. I have included some suggestions below. The manuscript is generally well structured and written, but certain sections will need clarifications. For example, the authors are using different names (or parts of the full name) for the same model throughout the text. Because there are many models used in this study it is particularly important to simplify it for the reader by consistently using the same name. Suggestively, after writing out the full model name once (e.g. here in abbreviation, GETM-ERSEM-BFM model with particle tracking GITM), a short-name can be used (e.g. the GETM-model or similar). The DEB model is the least well written part, and the method and result section are sometimes difficult to follow, sometimes due to lack of information. In the method and discussion section the authors are also referring to the original article (Augustine et al. 2014/in press) for details. At this stage it is problematic, since as far as I know, it is not publicly available yet. The authors must therefore make sure all parts are clearly explained independent on Augustine et al. Several comments on this can be found below.

Model names:

We agree that the substantial number of model names can be confusing. However, these are official names and abbreviations that are essential to specify and identify the models used, so we cannot completely eliminate and simplify them. We have chosen to retain the original names in the Materials and Methods section to reflect this, and to refer to the models in the remainder of the paper as GETM model, Delft model, and DEB model.

p. 1566, l. 8: Change into:

Three existing models were used: i) Delft 3D (in the results and discussion referred to as Delft model), ii) GETM-ERSEM-BFM model with particle tracking (GITM) (in the results and discussion referred to as GETM model) and iii) the Dynamic Energy Budget (DEB) model (in the results and discussion referred to as DEB model).

- p. 1566, l. 15: The Delft model implementation at high spatial resolution provided insight into...
- p. 1566, l. 19: The GETM model was developed to include...
- p. 1566, l. 26: ...reproduction model in the GETM model and to...
- p. 1578, title section 3.1: change into: Estuaries (Delft model)
- p. 1578, l. 18: ...model runs with the Delft model are presented...
- p. 1580, title section 3.2: change into: North Sea (GETM model)
- p. 1580, l. 2: The particles in the GETM model dispersed as...
- p. 1582, l. 28: ...particle in the GETM model.
- p. 1583, l. 2: The GETM model predicted that...
- p. 1583, l. 16: ...in the Delft model...
- p. 1584, l. 19: The GETM model suggested...
- p. 1585, title 4.2: Comparison DEB model and GETM model *M. leidyi* implementation
- p. 1586, l. 10: ...extracted from the biogeochemical module of the GETM model in line...
- p. 1586, l. 19: ...by the biogeochemical module of the GETM model. Running...
- p. 1587, l. 19: The simulations with the GETM model indicated...
- p. 1588, l. 2: ...assumed in the GETM model. Further...

Augustine et al.: this has now been published, so should no longer be a problem

p. 1589, l.1. Change reference to:

Augustine, S., Jaspers, C., Kooijman, S. A. L. M., Carlotti, F., Poggiale, J.-C., Freitas, V., van der Veer, H. and van Walraven. L.: Mechanisms behind the metabolic flexibility of an invasive comb jelly, Journal of Sea Research, 94: 156-165, DOI:10.1016/j.seares.2014.09.005, 2014.

Specific and technical comments

Page 1562 Line 20: Change "East" to "east" Make change.

Line 20: Only Purcell et al. 2001 is a paper concerning the American Mnemiopsis pop-

ulation. I would suggest the authors to go back to the original articles, since Boersma et al. 2007, Gesamp et al. 1997, and Lehtiniemi et al. 2011 only cite papers from the US (see for example Costello, Kremer, Reeve, etc.).

We have reviewed and followed through the references in the Introduction, also following comments by Referee #3. This has led to a re-written introduction (see below). Boersma and Lehtimiemi references were removed.

Replace p.1562, l. 19 to p. 1563 with:

The comb jelly *Mnemiopsis leidyi* originates from temperate to sub-tropical waters along the East coast of the American continent (Purcell et al. 2001, Costello et al. 2012). *M. leidyi* is notorious for its highly adaptive life traits: A fast growth rate combined with high fecundity, early reproduction, the ability of self-fertilization and a euryoecious lifestyle tolerating a wide range of environmental parameters (temperature, salinity, water quality) are characteristics which favour its establishment and fast expansion in invaded areas (Purcell et al. 2001, Fuentes et al. 2010, Jaspers et al. 2011, Salihoglu et al. 2011).

M. leidyi was introduced in the Black Sea in the early 80s (See also the comprehensive review by Costello et al., 2012), probably through ballast water (Vinogradov et al., 1989). The presence of *M. leidyi* together with eutrophication and overfishing caused a deterioration of the ecosystem, which finally degraded to a low biodiversified 'dead-end' gelatinous food web (Shiganova, 1998). This led to an economic loss/collapse of the pelagic fish population, in particular anchovies and sprat fisheries (Kideys, 1994; Kideys, 2002). *M. leidyi* then spread further into the Sea of Azov (Studenikina et al. 1991), the Sea of Marmara (Shiganova 1993), the Aegean Sea (Kideys and Niermann 1994), and the Levantine Sea (Kideys and Niermann 1993). In 1999, *M. leidyi* was transported from the Black Sea to the Caspian Sea (Ivanov et al., 2000). *M. leidyi* spread from the eastern Mediterranean to other regions of the Mediterranean: it was recorded in 2005 in the northern Adriatic Sea (Shiganova and Malej, 2009) and in 2009, blooms were reported in waters of Israel (Galil et al., 2009), Italy (Boero et al., 2009), and Spain (Fuentes et al., 2010).

M. leidyi was also transported from the northwestern Atlantic to northern European waters (Reusch et al., 2010); first records date back to 2005 and originates from Le Havre harbour in northern France (Antajan et al., 2014), Danish territorial waters (Tendal et al. 2007) and Norwegian fjords (Oliveira 2007). By 2006 *M. leidyi* had been reported in the western Baltic Sea (Javidpour et al. 2006), in the Skagerrak (Hansson, 2006), in the Scheldt estuaries and Wadden Sea (Faasse and Bayha 2006) and the German Bight (Boersma et al. 2007). In 2007, the species was found in Limfjorden (Riisgård et al. 2007) and in Belgian waters in the harbour of Zeebrugge (Dumoulin, 2007; Van Ginderdeuren, 2012). In the following years the species remained present in the western and central Baltic Sea (Javidpour et al 2009, Jaspers et al. 2013), Kattegat, Skagerrak and inshore Danish waters (Tendal et al 2007, Riisgard et al 2012) and Wadden Sea (Kellnreitner et al. 2013, van Walraven et al. 2013). In most of these areas the highest densities are observed in summer, although in the Wadden Sea as well as in the Baltic the species has been observed in all seasons. In the Scheldt area *M. leidyi* is observed in Lake Veere, Lake Grevelingen, the Eastern Scheldt and Western Scheldt. In this area, *M. leidyi* is observed, every year, with highest densities in summer as well (Gittenberger 2008, L. van Walraven, et al. in prep).

Since 2009 *M. leidyi* has been observed frequently along the French coast of the North Sea (Antajan et al., 2014). This is particularly worrying because the North Sea is the home of commercially important fish stocks, including 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 (Kideys, 1994; Daskalov, 2002; Mutlu, 2009). Furthermore, model predictions from recent work from Collingridge et al. (2014) suggest that large parts of the North Sea are 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, due to a combination of high temperatures and high food concentrations. The presence and potential establishment of *M. leidyi* in the southern North Sea is

therefore cause for concern, and there is a need to further expand our understanding on the mechanisms involved in the dynamics of *M. leidyi* populations and its potential spread from source locations where it is established.

In this paper we apply three different models to simulate aspects of transport, survival and reproduction of *M. leidyi* in the Scheldt estuaries and the North Sea. We use the combined results to provide insight into the potential spreading and population dynamics of *M. leidyi* at a range of spatial and temporal scales in the area, which could not have been obtained with each model individually.

p. 1588 and further: include the following additional references:

- Costello, J. H., Bayha, K. M., Mianzan, H. W., Shiganova, T. A., and Purcell, J. E.: Transitions of *Mnemiopsis leidyi* (Ctenophora: Lobata) from a native to an exotic species: a review, Hydrobiologia, 690, 21-46, 2012.
- Boero, F., Putti, M., Trainito, E., Prontera, E., Piraino, S., and Shiganova, T. A.: First records of *Mnemiopsis leidyi* (Ctenophora) from the Ligurian, Thyrrhenian and Ionian Seas (Western Mediterranean) and first record of *Phyllorhiza punctata* (Cnidaria) from the Western Mediterranean, Aquatic Invasions, 4, 675-680, 2009.
- Daskalov, G. M.: Overfishing drives a trophic cascade in the Black Sea, Mar. Ecol. Progress Ser., 225, 53-63, 2002.
- Galil, B. S., Kress, N., and Shiganova, T. A.: First record of *Mnemiopsis leidyi* A. Agassiz, 1865 (Ctenophora; Lobata; Mnemiidae) off the Mediterranean coast of Israel, Aquatic Invasions, 4, 357-360, 2009.
- Gittenberger, A.: Risicoanalyse van de Amerikaanse langlob-ribkwal *Mnemiopsis leidyi* A. Agassiz, 1865, GiMaRIS Rapport Nr. 2008.13, GiMaRIS, Leiden, 2008.
- Hansson, H. G.: Ctenophores of the Baltic and adjacent Seas the invader *Mnemiopsis* is here!, Aquatic Invasions, 1, 295-298, 2006.
- Javidpour, J., Sommer, U., and Shiganova, T.: First record of *Mnemiopsis leidyi* A. Agassiz 1865 in the Baltic Sea, Aquatic Invasions, 1, 299-302, 2006.
- Jaspers, C.; Haraldsson, M.; Lombard, F.; Bolte, S. & Kiørboe, T.: 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, 2013.
- Javidpour, J.; Molinero, J. C.; Peschutter, J. & Sommer, U.: Seasonal changes and population dynamics of the ctenophore *Mnemiopsis leidyi* after its first year of invasion in the Kiel Fjord, Western Baltic Sea, Biol. Invasions, 11, 873-882, 2009.
- Kellnreitner, F.; Pockberger, M.; Asmus, R. & Asmus, H.: Feeding interactions between the introduced ctenophore *Mnemiopsis leidyi* and juvenile herring *Clupea harengus* in the Wadden Sea, Biol. Invasions Springer, 15, 871-884, 2013.
- Kideys, A.E., Niermann, U.: Intrusion of *Mnemiopsis mccradyi* (Ctenophora; Lobata) into the Mediterranean Sea. Senckenbergiana Maritima 23, 43-47, 1993.
- Kideys, A.E., Niermann, U.: Occurrence of *Mnemiopsis* along the Turkish coasts (from northeastern Mediterranean to Istanbul), ICES Journal of Marine Science 51, 423-427, 1994.
- Kideys, A.E.: Recent dramatic changes in the Black Sea ecosystem: the reason for the sharp decline in Turkish anchovy fisheries, Journal of Marine Systems 5, 171-181, 1994.
- Kideys, A.E.: Fall and rise of the Black Sea ecosystem, Science 297, 1482-1484, 2002.
- Mutlu, E.: Recent distribution and size structure of gelatinous organisms in the southern Black Sea and their interactions with fish catches, Marine Biology 156(5), 935-957, 2009.
- Oliveira, O. M. P.: The presence of the ctenophore *Mnemiopsis leidyi* in the Oslofjorden and considerations on the initial invasion pathways to the North and Baltic Seas, Aquatic Invasions, 2, 185-189, 2007.

Reusch, T. B. H., Bolte, S., Sparwel, M., Moss, A. G., and Javidpour, J.: Microsatellites reveal origin and genetic diversity of Eurasian invasions by one of the world's most notorious marine invader, *Mnemiopsis leidyi* (Ctenophora), Molecular Ecology, 19, 2690-2699, 2010.

Riisgård, H.U., Bøttiger, L., Madsen, C.V., Purcell, J.E.: Invasive ctenophore *Mnemiopsis leidyi* in Limfjorden (Denmark) in late summer 2007 - assessment of abundance and predation effects, Aquatic Invasions 2, 395-401, <u>http://dx.doi.org/10.3391/ai.2007.2.4.8</u>, 2007.

- Riisgård, H. U.; Madsen, C. V.; Barth-Jensen, C., Purcell, J. E.: Population dynamics and zooplanktonpredation impact of the indigenous scyphozoan *Aurelia aurita* and the invasive ctenophore *Mnemiopsis leidyi* in Limfjorden (Denmark), Aquatic Invasions 7, 147-162, 2012.
- Shiganova, T.A.: Ctenophore *Mnemiopsis leidyi* and ichthyoplankton in the Sea of Marmara in October of 1992, Oceanology 33, 900-903, 1993.
- Shiganova, T. A., Malej, A.: Native and non-native ctenophores in the Gulf of Trieste, Northern Adriatic Sea, Journal of Plankton Research 31, 61–71, 2009.
- Studenikina, E. I., Volovik, S. P., Miryozan, I.A., Luts, G.I.: The ctenophore *Mnemiopsis leidyi* in the Sea of Azov, Oceanology 3, 722–725, 1991.
- Tendal, O. S., Jensen, K. R., Riisgård, H. U, Invasive ctenophore *Mnemiopsis leidyi* widely distributed in Danish waters, Aquatic Invasions, 2, 455-460, 2007.
- van Walraven, L.; Langenberg, V. T. & van der Veer, H. W.: Seasonal occurrence of the invasive ctenophore *Mnemiopsis leidyi* in the western Dutch Wadden Sea, J. Sea Res. 82, 86-92, 2013.

Line 21: The full species name is sometimes fully spelled out (Mnemiopsis leidyi) in the beginning of a sentence, and sometimes not (see for example pp. 1563 line 1 vs. line 9, page 1576: line 14 and 17). Maybe the journal has a standard way for this, if so follow this. Either way, be consistent throughout the manuscript.

Change to *M. leidyi* throughout (except the first occurrence in abstract and in introduction) Change in these locations:

p. 1562, l. 21 p. 1563, l.1 p. 1563, l. 18 p. 1576, l. 14 and l. 16

Page 1563 Introduction section generally: If the ambition is to shortly review the distribution and spread of Mnemiopsis in new habitats, they should also include the Baltic Sea are with surrounding waters (see for example Javidpour et al. 2006, Tendal et al. 2007 or Riisgård et al. 2012 etc.). I would also like to see some more background information about Mnemiopsis in the Scheldt estuaries and close surrounding. When where they first observed, have they been observed year after year etc.?

The introduction has been rewritten to expand on the spread of *Mnemiopsis* in European waters, including the Baltic Sea. The background information on the Scheldt estuaries suggested by the reviewer has also been added. See new introduction text above.

Line 18: Change "M. Leidyi" to "M. leidyi"

See more general comment above

Line 18-19: Again, these are not the primary references. I find it more suitable to refer to for example Daskalov 2002, Kidey 2002, or Mutlu 2009.

Done, see response to first comment on this topic above.

Line 27-28: Just a note. In previous description of the study you mention "Transport, survival and reproduction", while only "transport and reproduction" here.

Change into: transport, survival and reproduction

Page 1566 Line 8: The names used for the models: Make sure the same name is used for the same model through the whole manuscript.

See response to first comment on this topic above.

Line 8 and onwards: I would suggest numbering the models mentioned here. For a reader unfamiliar with these models, and/or when reading the paper for the first time, I suspect it may be hard to separate the different models, particularly since some consists of several coupled models.

See response to first comment on this topic above.

Line 9-10: "with limited adaptations", the authors can be more direct with what they mean.

This was a mistake in the manuscript: there were no adaptions to the DEB model; we used the same model and parameters to perform original simulation experiments

Please remove "with limited adaptions"

Line 11-12: Logically, it seems like "deploying the strengths of the individual models" should be written out before "intercomparison of the results"?

Rewrite as:

By deploying the strengths of the individual models, and through intercomparison of the results...

Line 16..: Although the language flow is very nice here, I still believe enumerating the different models will make it "crystal clear" also for the first time reader.

See response to first comment on this topic above.

Line 24: "(dramatically)", this is an interpretation and should not be included here.

Delete.

Page 1568

Particle tracking: I would appreciate more information about the vertical movement, and information about what parameterization was used for the vertical movement: Is there a vertical movement, and what decides it (behavior, random walk, turbulence)? Also, are the final outputs summed over all depth intervals?

The presented output is averaged over the vertical, page 1578 line 22 and further describes the procedure.

Page 1568 line 12 change to:

The depth varying vertical diffusion as calculated by the hydrodynamic turbulence model is incorporated by a stochastic bouncing-algorithm to move the particles in the vertical. The algorithm closely approximates the analytical solution.

P 1569, line 7 change to: The horizontal dispersion coefficient was set to 1.0 (m² s⁻¹) and no behaviour was included (neutral buoyancy).

p. 1578, l. 22: change to: The final depth-averaged concentration pattern...

p. 1578, l.24: change to: ..the volume, averaging over all cells in the vertical, and scaling...

Page 1571 Line 26: Is the temperature taken from the GETM-ERSEM-BFM model? (the same on page 1572 Line 27)

Insert on p.1570, line22:

...development stages, using physical and biological information from the GETM-ERSEM-BFM model (e.g. temperature and food fields).

Page 1574 Line 1: Does mortality below 2 degrees C apply only to the adults, and not to the juveniles? This could be written out.

P 1570, line 1, after 1st sentence, add:

For such low temperatures, there is no reproduction in the model. As the maturation in the model is artificially compacted into a single time step, this means that there are then no juveniles, so a similar rule for juvenile mortality is not relevant.

Page 1575 Line 10: Write out the previously used model name here (particle tracking IBM), particularly since a particle tracking unit were used also in the Delft3D model.

Change into: The particle tracking IBM GITM was run...

Line 11: It is not clear from which depth the particles were released (random depth, specified depth), please precise.

Change into: ...October near the surface in each...

Line 20: Perhaps shortly clarify why the sensitivity of juvenile mortality in particular are tested (and not other parameters).

At line 17, add:

...standard run. The standard run did not produce bloom conditions, because very few juveniles survived due to a combination of a long juvenile duration and the imposed daily juvenile mortality.

Hence, additional runs were carried out to, specifically targeting these factors, to investigate how blooms might occur. To...

Page 1576 DEB model generally This is the least well explained part in the manuscript, and since the original article (Augustine et al. 2014) is not accessible yet, it is extra important that the description of the model is clear. I have made some comments and I further recommend the authors to carefully work through this part again.

The original article Augustine et al 2014 is now published and accessible online via the Elsevier website.

We have clarified the description of the DEB model (subsection 2.3.1) and it's setup for the present study (subsection 2.3.2) as well as corrected a few typo's which were in 2.3.2.

We further substantially re-organised the results section 3.3 where the results of both simulation studies are provided.

Figure 13 and its caption which comprises the results of the first simulation has been revised to increase the clarity of presentation.

Finally the discussion concerning the DEB model (4.2) was also revised to include discussion elements which were previously found in 3.3.

Please see the response to the specific comments for details.

Line 4-5: This sentence sounds a bit strange to me, particularly "all organisms" and later "applies to all animals" (which organisms and animals). Do the authors mean "any organism", or "all organisms under conditions in which food densities and temperatures vary"? Please clarify the sentence.

p. 1576, I.3: Please change sentence to:

Dynamic Energy Budget (DEB) theory (Kooijman, 2010) describes the uptake and use of food for all organisms under conditions in which food densities and temperatures vary.

Line 8: The article is referred to as both (in press, the reference list and table 1) and (2014, all the text), please be consistent.

The paper is now published, see response to previous comments.

p. 1595, caption Table 1:

change: Augustine et al. in prep. into: Augustine et al. (2014).

Line 10: Here EH is defined as "maturity level", and in Fig. 3 as the "cumulated energy invested in maturation". If these can be considered the same (maturity level = cumulated energy invested in maturation), I would advice to specify this at the same place in the text. I would also include the definition of ER here.

p. 1576, l. 11-16: replace with:

The model closes the full life-cycle from egg to adult. Stage transitions are assumed to occur at fixed maturity levels, quantified by the cumulated amount of energy invested in maturity. The model encompasses three life-stages: embryos (does not feed, and allocates energy to maturation), juveniles (feeds, and allocates energy to maturation) and adults (feeds, and allocates energy to reproduction). Birth is defined as the moment when feeding is switched on ($E_H = E_H^b$) while puberty ($E_H = E_H^p$) is defined as the moment juveniles start allocating energy to reproduction (E_R) instead of maturation. The different life-stages are defined in Fig. 13a.

M. leidyi is characterized, along with a variety of other species, by a so-called metabolic acceleration during ontogeny, which means that the embryo and early juvenile stages develop more slowly than later stages (Kooijman, 2014).

Line 12: The definitions of the life stages are not very clear, this can be improved. (Maybe include egg, juvenile, adult etc.). Section starting on line 25: Puberty (maturation?) seems to be an important moment described by the model where the allocation of energy is significantly changed. I would suggest explaining with one or two lines what the "puberty" refers to in the model.

Please see response to previous comment.

Page 1577 Line 4: Since I cannot access Augustine et al., it is not clear to me how the analyses in this manuscript are differing from the once about to be published in the original article. I would like the authors to be more precise about this.

The article is now available. The article dealt with analyzing *Mnemiopsis* data and estimating the parameters. Here we use the parameters to "simulate effects of food and temperature on key life history traits" – these simulations (found in fig. 13 and 14) are not included in Augustine et al. 2014. In response to comments below, we have suggested changes that specify the additional work that was done.

Line 8-10: Which is the second simulations experiment: If you write out "the first", write out "the second" as well.

p. 1577, l. 8-11, replace with:

We performed two original simulation experiments. In the first experiment we simulated juvenile stage duration and reproduction rates as function of temperature for three different levels of constant food availability. In the second experiment we simulated the change in reproduction rates for organisms of three different size classes subject to time varying temperature and food availability. We extracted the temperature and the (juvenile and adult) food densities experienced by a particle in the GETM model. Note that food density from the GETM model was converted from mgC m⁻³ to molC L⁻¹ for input into the DEB model.

Food availability for an individual is quantified by the scaled functional response f which relates ingestion to food density in the environment, X:

p. 1577, l.15:

remove: "X is the density of food in the environement (gC L^{-1})" change: and K (gC L^{-1}) into: and K (mol C L^{-1})

Line 16: Should it be "L d-1 cm-2", with capital L, perhaps?

Change I to L

Typo corrections in addition to comments by referee: p. 1577, L. 16: correct typo in equation:

$$K = \frac{\{\dot{J}_{XAm}\}}{\{\dot{F}_m\}}$$

p. 1578, l. 16: remove decimal point: μ_E = 550 kJ mol⁻¹

Equation 13: What food concentration (X) is used?

See response to previous comment.

Page 1578 Line 18: For clarity, perhaps specify which of the model runs from the Eastern Scheldt you refer to, e.g. "the results of the Eastern Scheldt model runs using a uniform initial distribution of particles are presented in...".

We have removed figure 4 and 6 to avoid duplication with the tables.

Page 1578, line 18 please change: The results of all of the monthly Eastern Scheldt model runs using a uniform initial condition are presented in Table 2.

Page 1579, line 1 please change: The results of all of the monthly Western Scheldt model runs using a uniform initial condition are presented in Table 3.

Line 10: Which sensitivity test: as far as I can see, this has not been explained in the method section.

Page 1569, line 17 please insert:

To test the sensitivity of the results for the release moment, the July runs for both estuaries were also performed from low tide towards low tide over a period of 30 days.

Line 14: Perhaps introduce this name, the "realistic run", already in the method section (just as the authors have done with the "standard run" for the GETM-ERSEM-BFM model)

Page 1570, line 6 please add: The runs with non-uniform initial condition will be referred to as the realistic runs.

Line 14: I suggest changing to: "... of the realistic runs for the Western and Eastern Scheldt are presented...", then the authors don't need to repeat this again on line 23. Later, delete sentence 22-23 and go straight to the results.

Page 1579, line 14-26 please replace:

The initial conditions and results of the realistic runs for the Western and Eastern Scheldt are presented in Fig. 8 as contour plots of *M. leidyi* densities (ind. m^{-3}) as calculated by the model together with the observed values as coloured circles using the same scale.

For the Western Scheldt there is a good match in the middle of the estuary. At the innermost station there is overestimation of the concentration. The relative high measurement outside the estuary is not met by the model. The correlation coefficient r between the model and observations excluding the station outside the estuary is 0.28.

For the Eastern Scheldt run the model represented the conditions in the inner estuary reasonably well with some underestimation in the northern branch and some overestimation in the south eastern branch. There is an overestimation of the concentration in the outer part of the estuary. The correlation coefficient r between the model and observations is 0.72.

Line 16: Change to "observational measurements" or similar.

See above.

Line 16: Make sure to consistently use "Figure" or "Fig." throughout the manuscript.

Copernicus, please do a search and replace to conform with the journals' standard.

Page 1580 Line 11-12: "West" and "North" don't need to be spelled with capital letters

Please change.

Line 21: Take away one "in", in front of "in December. . ."

Please change.

Page 1581 Line 6: Fig. 12, red lines are in the figure referring to the run assuming 10% temperature increase, not the 2/3 juvenile mortality. The legend does not seem to agree with the text (see also line 10). Check this carefully.

Change into:

green lines

Line 9: Where is the value 8.6 coming from (I assume it is the same value/factor given in table 1)? Please clarify this information.

p. 1582, l. 9, Please change into: ... but not so much on the value of the acceleration factor which stays around 8.6 (see table 1).

Line 10-12: It is not clear from Fig. 13a where these values comes from. Please clarify.

p. 1582, l.10-12: change into:

The predicted carbon mass at the different stage transitions for f = 1 (*ad libitum*) are also shown in Fig 13a (grey text). Overall, the mass at the different stage transitions is less sensitive to the prior feeding history than age. The predicted mass at the end of the acceleration phase varies from 0.11 to 0.16 mg C for f = 0.3 and 1 respectively. Carbon mass at puberty goes from 1.8 mg C for f = 1 to 0.8 mg C at f = 0.3.

Line 12: Change "at libitum" to "ad libitum".

See above.

Line 13-15: As far as I can see, it is only Fig 13a which is showing the carbon weight of Mnemiopsis at different transition stages. Therefore, it is not clear to me where the authors get these other carbon masses from? Please clarify.

p. 1581, l. 24 to p. 1582, l. 6: replace with:

From the DEB model simulations, the age at the start and the end of metabolic acceleration as well as the age at puberty for f = 1, 0.45 and 0.3 at 22 °C are provided in Fig. 13A (three bottom rows). These simulations show that the timing of stage transitions is extremely sensitive to the food level experienced by an individual. Indeed, f can be interpreted as the actual ingestion relative to the maximum possible one for an individual of that size. So f is a dimensionless quantifier for food level. The duration of metabolic acceleration ranges from approximately 2 weeks to a little over 1.5 months at 22 °C depending on the food history. Furthermore, the model predicted that an individual would mature even when experiencing food levels only 30 % of the maximum, but that it would take 4 times longer at that low food level than for ad libitum feeding.

p. 1582, l.13-15: change into:

The DEB model predicts that growth after puberty is extremely sensitive to food level: the predicted maximum carbon mass goes from ca. 80 mg C (f= 1) to 2 mg C at f = 0.3.

p. 1582, l. 16: add at end of sentence: ...food history (compare values in fig. 13 C and D).

Line 21: At the end of the sentence "...reach puberty", I would suggest including a reference to the figure (Fig. 13b).

Please implement.

Line 23: This reference does not belong in the result section (also, the authors are returning to this in the discussion), please delete.

Please delete: in accordance to ... (1974)

Line 24-26: This is also more of a discussion point and can be moved.

p. 1582, l.24-26: please delete.

p. 1582, l. 27-29: please change into: The results of the second simulation experiment are summarized in fig. 14 (A-C).

p. 1583, l. 2-4: Please delete The GETM ... as juveniles.

Page 1583 Line 12: "... response to changes in reproduction as function of food level." - and temperature?

p. 1583, l. 12: please add: and temperature.

Line 8-11: This is a very long and a bit confusing sentence and should suggestively be split up, at least with some commas.

p. 1583, l. 8-11: Change into:

Assuming that the organism stops reproducing when f decreases below the minimum f to pay its maintenance, it follows that larger individuals are more sensitive to drops in food availability. However, they also reproduce more when food is abundant enough.

First two paragraphs: Something that may be worth considering in this section of the discussion is that the model is not including potential influence of behavior of Mnemiopsis. This can for example involve predator avoidance (e.g. Titelman et al. 2012), or prey search including diel vertical migration (e.g. Haraldsson et al. 2014). Both behaviors often result in a vertical movement, and the vertical position may in turn have a significant influence on the transportation. This potential discussion point may be more or less relevant depending on how the vertical movement was accounted for in the models (see previous comment in method section).

p. 1584, l. 17: add:

At the start of this work, we did not have firm evidence of vertical migration behaviour by *M. leidyi*. Hence, we implemented *M. leidyi* as passive particles in the models. Since then, new evidence has emerged suggesting vertical migration behaviours (Haraldsson et al., 2014). As such behaviour may influence particle dispersal pathways, this should be considered in further work.

p.1590: add reference:

Haraldsson, M., Båmstedt, U., Tiselius, P., Titelman, J., Aksnes, D.L.: Evidence of Diel Vertical Migration in *Mnemiopsis leidyi*, PLoS ONE 9(1), e86595, doi:10.1371/journal.pone.0086595, 2014

Page 1584 Line 15: Perhaps indicate what the salinity levels are.

Change into:

Salinities in this area are often at or below the values for which *M. leidyi* reproduction appears to be limited (salinities <15, Jaspers et al 2011) and larval mortality is increased (salinities <10, Lehtiniemi et al., 2012). This might explain why observed *M. leidyi* densities are one to two orders of magnitude lower in the western Scheldt than in the eastern Scheldt.

Page 1585 Line 3: Delete "in the chain", or reformulate this part.

Please delete.

Line 9-13: This is a very long sentence, and the last part, "should it be able to establish itself in East Anglia", seems out of place. Delete or reformulate.

Change into:

If such colonisation were to happen, *M. leidyi* is not expected to be able to colonise much further along the UK coast through natural transport processes, because the general residual coastal flow converges from north and south in this area, and then moves offshore across the North Sea towards Scandinavia.

Line 15: Change "M. Leidyi" to "M. leidyi"

Please change.

Line 17: I suggest to change "But it also becomes difficult to assess. . ." to "At this stage it is difficult to assess. . .", or similar.

p.1585, l. 17: please make the suggested change.

Page 1586 Line 5: "mass as function of length", I haven't seen these results?

Please change the paragraph (I.3 - 9) into:

In previous work, Augustine et al (2014) parameterised and validated the DEB model for *M. leidyi* based on an extensive literature review of eco-physiological data. They showed, among others, that the predictions for reproduction rates and mass as function of length are in accordance with reproduction rates against length and wet mass reported in Baker and Reeve (1974), Jaspers (2012) and Kremer (1976) respectively. The new simulations presented here in Fig. 13 and 14 thus represent the best possible estimate of the metabolism of *M. leidyi* that we can achieve to date.

Line 7: Again I wonder how this study is differing in the analyses using the DEB model compared to the original article. If the same analyses were done in this manuscript as in Augustine et al., it would be more appropriate to only discuss their results rather than reporting them again. Please make this clearer.

See changes suggested with previous comment.

Line 10-12: I am not sure what the authors want to say here. Maybe change the order on the last part of the sentence, "... BFM model, based on observations and physiology, in line with the model proposed by Salihoglu (2011)", or only write "Separate juvenile and adult food densities were extracted from the GETM-... model".

We agree that the last suggestion is preferable.

p. 1586, l. 10-16: replace as follows:

Separate juvenile and adult food densities were extracted from the GETM model. It is difficult...

Line 16: Maybe it is appropriate to include the "discussion points" raced in the result on page 1582 here (see previous comment).

We suggest to move and reformulate this as below. Because of the change above, it can now not go exactly to where the referee suggests.

p. 1586, l. 22: add:

...(Fig. 14b). Moreover, the model results indicated that juveniles can maintain themselves at very low environmental food levels and can wait out the bleak season especially if temperatures are low until conditions are favorable for rapid growth and reproduction. We see...

Line 17-21: I do not fully understand what the authors want to say here. Please try to rephrase and clarify.

p. 1586: change l. 17-19 into:

The GETM model provided the density (in carbon) of two size classes of zooplankton experienced by the particles. Subject to a few additional assumptions to translate this information into carbon ingested per individual per unit time (see Section 2.3.2), the DEB model allowed us

Line 22: Perhaps change "high" to "higher"!?

Please implement.

Line 26: Why was this value used, a reference perhaps?

p. 1586, l. 26: please change into:

... the organism. We found that $\{\dot{F}_m\} = 4 L d^{-1} cm^{-2}$ provided theoretical ingestion rates within the range of those recorded by Sullivan & Gifford (2004) [table 4], and have hence assumed this value.

Page 1587 Line 4-5: All readers are not familiar with the fisheries literature. Please be more specific and include references.

We think that this would be beyond the purpose of the paper, and suggest deleting this sentence. Please delete: Are the processes ... recruitment?

Line 6: Delete ", as far as possible with the current results,". This is given.

Please delete.

Line 16: Delete ", however,".

Please delete.

Line 24: This is an abbreviation not defined previously. Please write out.

Please change to International Bottom Trawl Survey (IBTS; ocean.ices.dk/Project/IBTS)

Line 25: Change "These results" to "Our results".

Please change into Our results, however, are subject ...

Page 1588 Line 11: Include a "than" after temperatures.

Please insert

Tables Table 1: I assume you mean Fig. 3?

Please change.

Table 2 and 3: I suggest including "connectivity matrix" in the table text.

A connectivity matrix describes the connectivity between areas, in a format where both the lines and the columns list the areas for which connectivity is presented. Our tables are not in this format. They might be cast into such a format, by combining both tables, and creating a separate table for each month of the year. However this would take up much more space in the document. So to avoid confusion, we have not followed this suggestion. No change.

Figures Figure 1 and 2: What unit is the x and y coordinate (and in all other maps)?

These are in metres in the Dutch Rijksdriehoeksstelsel coordinate system (RD epsg:28992), text added to the figures. For Fig 9 and 10 it should be evident that these are latitude and longitude; no change included.

Also, figure 1 and 2 can be combined into one figure with two panels.

We have combined the two figures to one figure with the caption below:

Figure 1: change caption:

Figure 1. Model grid of the Delft3D model in blue and definition of the areas in red. (a) Eastern Scheldt estuary, (b) Western Scheldt estuary, (c) Eastern Scheldt mouth, (d) Western Scheldt mouth, (e) Zeebrugge harbour area and (f) southern North Sea.

Remove Figure 2, renumber figures and update figure references in text.

Figure 3: Where are Ex and Ep included? I cannot find them either in equations, table 1 or in the text.

Please remove Ex : food (J), Ep :faeces(J) from the caption

Figure 4, 5, 6, 7: These figures can with advantage be combined into one figure with four panels (like in Fig. 8). As it is now, these results take a "lot of space" (compared to the rest of the results) by being presented one by one. It will also be easier to compare the connectivity between the two regions if they are plotted together.

This is a good suggestion. We suggest removing Figs 4 and 6, which duplicate with Tables 2 and 3. We have combined the new versions of Fig 5 and 7 (see bottom of this reply).

Remove Figs 4 and 6, renumber figures and update figure references in text. Combine caption of Figs 5 and 7, renumber figures and update figure references in text. Caption: change:

Figure 5. **a** Final concentration (N. m^{-3}) relative to an assumed initial concentration of 1.0 (N. m^{-3}) for the Eastern Scheldt July simulation; **b** similar for the Western Scheldt.

Figure 8: Change to "Observed density of M. leidyi". The lower left panel: There are indicated observation (density circles) along the river north of the eastern estuary, was this river also covered by the model? If not, I suggest including information about this in the figure text.

Some observation available for the Grevelingen estuary were plotted for the sake of completeness. This estuary was not included in the modelling.

We have deleted the observations from the figure.

Figure 8, 9, 10, 11, 12: Write out a-d/i on the respective panels.

This is a good suggestion. Can this be done by Copernicus in the final editing?

Figure 12: Axes title is missing on the upper left panel. Check the figure legend, the figure text and the result section carefully as they do not seem to agree (see previous comment in the result section). In some of the panels all 5 simulation results are not visible (e.g. panel c). I assume this is because they are masked by the last added line. If so, mention this in the figure text.

It's not an axis title, but units. The number of individuals is a non-dimensional number, and hence has no units. This is indicated by a - character. We agree that this is easy to miss, but don't see an obvious alternative.

The reference to colours is correct in the caption text; changes have been suggested with the previous comment to the main text.

Please add:

for (b): (missing lines coincide with light blue line)

for (c): (missing lines coincide with light blue line)

for (f): (missing lines coincide with x-axis)

for (g): (missing lines coincide with x-axis)

for (h): (missing lines coincide with green line)

for (i): (missing lines coincide with light blue line)

Figure 13: It took me time to fully understand panel a. I would suggest including curled brackets on the left hand side indicating the "stage transitions", "carbon mass" and "duration". Why is the "puberty node" on the vertical line and not along the horizontal line? The functional response seems to have been applied at 22 degrees, while in table 1 the reference temperature seems to have been 20 degrees. Is this correct? In the figure text is says "Reproduction rate at puberty and at ultimate mass and respectively as function of temperature". The sentence is incomplete, and, I cannot see any figure with masses? It is not clear to me why panel (C-B) and (A-C) are combined?

Thank you for the helpful suggestions. The figure has been revised accordingly: puberty node on the horizontal line, curly brackets on the left indicating what the information on each row corresponds to. Furthermore the caption is revised to increase the clarity of the figure.

Please change caption to:

Results of the first DEB model simulation – (A) Carbon mass and age at each stage transition (modified from Augustine et al 2014). The different stage transitions occur at fixed maturity levels (black horizontal line). At puberty (grey circle) the organism no longer invests in maturity and starts investing in reproduction (red horizontal line). Below, the carbon masses at each stage transition are computed for f = 1 (grey text). The three bottom rows show the predicted ages at the start and end of metabolic acceleration as well as the age at puberty for ingestion levels ranging from 1 to 0.3. The ages are all temperature corrected to T = 22 °C using Eqn 14. (B) Age at puberty as function of temperature. (C–D) show the predicted reproduction rates at puberty (1.8 mg C) and at maximum size (80 mg C) respectively as function of temperature. (B-D) Values are computed for three different ingestion levels: f = 1 (solid line), f = 0.45 (dashed line) and f = 0.3 (dotted line).

Given references: Daskalov (2002) Overfishing drives a trophic cascade in the Black Sea. Mar Ecol Prog Ser 225: 53-63

Haraldsson, Bamstedt, Tiselius, Titelman, Aksnes (2014) Evidence of diel vertical migration in Mnemiopsis leidyi. Plos one e86595

Javidpour, Sommer, Shiganova (2006) First record of Mnemiopsis leidyi A. Agassiz 1865 in the Baltic Sea. Aquat Inv 1: 299-302

Kidey (2002) Fall and rise of the Black Sea ecosystem. Science 297: 1482-1484

Mutlu (2009) Recent distribution and size structure of gelatinous organisms in the southern Black Sea and their interactions with fish catches. Mar Biol 156: 935-957

Riisgård, Madsen, Barth-Jensen, Purcell (2012) Population dynamics and zooplankton-redation imact of the indigenous scyphozoan Aurelia aurita and the invasive ctenophore Mnemiopsis leidyi in Limfjorden (Denmark). Aquat Inv 7: 147-162

Tendal, Jensen, Riisgård (2007) Invasive ctenophore Mnemiopsis leidyi widely distributed in Danish waters. Aquat Inv 2: 455-460

Titelman, Hansson, Nilsen, Colin, Costello (2012) Predator-induced vertical behavior of a ctenophore. Hydrobiologia 690: 181-187

Referee #2

The manuscript by van der Molen et al focuses on understanding the spread dynamics of M. Leidyi in the North Sea from source locations. The manuscript has potential to relate to a broad, international readership, and the content is appropriate for the journal. Manuscript presents concrete conclusions and suggestions. I suggest publication in Ocean Science after minor revision.

General comments:

Some parts of the manuscript are hard to follow mainly because the reader loses track of details of different models. For example application of particle tracking model and particle tracking IBM (one without and one with biology) gets mixed up. It can be useful to have a table illustrating the models that are applied to each region and which physical models are used with which biological model. It should be justified/explained why both Delfth 3D and GETM are used as hydrodynamics models.

We have followed the similar comments made by Referee #1, please see responses there. We don't think that including an additional table would help: we did not mix hydrodynamics models, particle tracking models and regions, so it would be rather boring. This should be clear from Materials and Methods. It does seem useful though to specifically mention the models in the figure and table captions.

Please add to the captions:

- Fig 1: Definition of the areas, Delft model.
- Fig 2: Model grid of the Delft model.
- Fig 4: ...days, Delft model.
- Fig 5: ...simulation, Delft model.
- Fig 6: ...days, Delft model.
- Fig 7: ...simulation, Delft model.
- Fig 8: ...for 2011, Delft model.
- Fig 9: ...cell), GETM model.
- Fig 10: ...cell), GETM model.
- Fig 11: ...Somme, GETM model.
- Fig 12: Cumulative results (GETM model) over all...
- Fig 14: ...one particle from the GETM model.
- Fig 14: Scaled functional response f (-) of the DEB model, assuming...
- Fig 14: (C) The combined ... individual of the DEB model.

Specific comments:

Page 1565: why Southern North Sea is not defined in Fig 1?

Please change: other North Sea into: southern North Sea

Page 1566: which model (Delft 3D and or only Getm ERSEM) is run with GITM and DEB?

Delft3D has its own particle tracking module. GETM-ERSEM runs with GITM. The DEB model is an individual-based model not associated with a hydrodynamics model. If the changes associated with

previous comments are implemented, this should be much clearer. In addition, we suggest the following changes to clarify this further:

Please change:

p. 1566, l.8: ...used (the three-dimensional Delft3D with particle tracking module, the three-dimensional GETM-ERSEM-BFM model with and the zero-dimensional Dynamic Energy ...
p. 1566, l. 16: ...estuaries, and with its native particle tracking module using passive particles...
p. 1566, l.21: The DEB model was then used for fixed hypothetical locations using prescribed temperatures to simulate...

p. 1568, section title: Particle tracking in Delft3D

p. 1568, l. 9: The particle tracking module of Delft3D uses...

Page 1568: what is the justification that the particle tracking model is run without any biology (IBM)?

Please add:

I. 25. At the start of this study, we had no information suggesting migration behaviour for *M. leidyi*. Hence, use of passive particles was assumed to be sufficient to study the potential exchange between the estuaries and offshore waters.

Page 1575, line 10: particle tracking model or particle tracking with IBM?

Please change into: The particle tracking IBM GITM was run...

Page 1578 (part 3.1): these are the results of a simulation from which time period?

The year 2008 (described in the Methods section). I. 18, please change: ...model runs with the Delft model...

Page 1578 (line 18): I don't think both Table 2 and Fi. 4 are necessary as Fig 4 repeats the information form Table 2.

We have decided to delete the figure, for changes see corresponding comment by Referee #1.

Page 1579 (line 1): Same comment as above about Table 3 and Fig. 6

We have decided to delete the figure, for changes see corresponding comment by Referee #1.

Page 1579 (line 24): some statistical analyses (this can be a simple mismatch percentile, RMSD etc) should be given, what is reasonably well?

We have chosen to give the correlation coefficient between the model and the observations. We think that an RMSD does not give much information because the gradient in the estuary is very high which makes the separate points incomparable to each other since the RMSD is scale-dependent. For the adjusted text see response to comments on this paragraph by referee #1.

Page 1580: which model is used here?

See response to comment by Referee #1 on model names.

Page 1584 (lines 12-17): if these are the models results the exact reason should be know, if salinity is the reason of low production this can be easily verified with a model sensitivity test.

These are observations; alternative text is suggested below to clarify. Please replace I. 12-17 with:

The landward (eastern side) of the Western and Eastern Scheldt, where retention of *M. leidyi* was highest in the Delft model, have very different environmental characteristics. The Eastern Scheldt is an enclosed tidal bay with salinities equal to those in the nearby North Sea in the whole area (Smaal & Nienhuis 1993), while the Western Scheldt estuary includes river inflow, resulting in a west-east salinity gradient. The area in the Western Scheldt where *M. leidyi* retention is highest in the Delft model is a mesohaline area (Meire et al 2005). Salinities in this area are often at or below the values for which *M. leidyi* reproduction appears to be limited (salinities <15, Jaspers et al 2011) and larval mortality is increased (salinities <10, Lehtiniemi et al., 2012). This might explain why observed *M. leidyi* densities are one to two orders of magnitude lower in the western Scheldt than in the eastern Scheldt.

Figures Fig 8: which figs correspond to a, b, c,d?

See corresponding comment Referee #1.

Fig 12: Hard to follow, which fig corresponds to a, b,c d?

See corresponding comment Referee #1.

Referee #3

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 introduction was re-written (see response to comments of Referee #1).

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.

Lethal temperature: this does not normally occur in offshore waters in the study area. We suggest adding a sentence to explain this (see below).

Difference northern/southern populations: we have not found firm evidence in the literature to suggest differences in physical responses to temperature as the referee suggests.

Temperature of reproduction: we have traced this down, and have established the following: -Lehtiniemi refer to Purcell (2001) and to Sarpe et al. (2007, see below) for the 12 °C threshold -Purcell report 12 °C (based on their own observations). However the lowest temperature that they observed was 12 °C, and hence this cannot be considered to be a threshold -The abstract of Sarpe et al. (2007) does not mention a threshold for reproduction

We thus conclude that the referee is correct, and that Lehtiniemi et al. have mis-interpreted the earlier investigations.

Looking at our own results (Fig. 12), the total egg production goes down to very low levels several weeks before the average temperature experienced by the population falls to the -incorrect- threshold of 12 °C; this must be in response to reduced food availability and temperature-related feeding activity and metabolism. Hence, we do not think that this threshold for reproduction has had a significant effect on the model results.

So we have two options to deal with this point:

1. remove the threshold (from the model and the paper), re-run the model without the reproduction threshold (and the lethal temperature), and essentially produce the same results

2. retain the threshold, discuss Lehtiniemi etal.'s mis-interpretation, expose the false threshold and ensure that this is captured in the written literature (so that others may not use it in the future), and argue that it has not had a significant effect on the current results.

We prefer option 2, and suggest the changes below.

Sarpe D, Grosskopf T, Javidpour J (2007) *Mnemiopsis leidyi*—analysis of an invader in the Kiel Fjord with focus on respiration and reproduction rate, 42nd European marine biology symposium, 27–32 August 2007, Kiel, Germany

p. 1574, l. 3: add/change:

...was imposed for completeness following Salihoglu et al. (2011). There is evidence to suggest that *M. leidyi* can survive lower temperatures (Costello et al., 2006), so this element of the model may be refined. As offshore water temperatures in the south western North Sea only very rarely fall to such low levels, however, the results presented here are not expected to change if such a refinement was implemented. Also, a daily...

p. 1571, l.5. Add:

Genetic evidence suggests differences between northern and southern populations (Reusch et al., 2010). However we have not found corresponding evidence for differences in physiological response to temperature, hence it is assumed that the parameter values suggested by Salihoglu et al. (2011) are a reasonable first approximation for populations in the North Sea.

p. 1571, l. 7:

...(Lehtiniemi et al., 2012; see, however, Section 4.3). The ...

p. 1588, l. 3: add the following paragraph:

Two thresholds were included in the model that, on closer inspection, are not in agreement with field observations, and that should not be used in future modelling: the lethal temperature of 2 °C for adults, and the reproduction threshold of 12 °C. The lethal temperature should not be used because *M. Leidyi* is known to overwinter under the ice in its native habitat (Costello et al. 2006). The reproduction threshold of 12 °C that can be inferred from Lehtiniemi et al. (2012) was based on field data presented by Purcell et al. (2001) that did not include temperatures lower than 12 °C, and is thus artificial. Lehtiniemi et al. (2012) also refer to Sarpe et al. (2007) in connection with reproduction above 12 °C, but this abstract does not contain such a threshold. We do not think that either of these two thresholds has had a significant effect on the model results, however, because i) offshore sea-water temperatures below 2 °C are very rare in the area of interest, and ii) Figure 14 shows that the egg production in the model falls to very low levels (in response to reductions in food-availability and temperature-driven reductions in feeding and egg-production efficiency; eq. (1)-(5)) before the average temperature experienced by the particles drops to 12 °C.

p. 1588, l. 20: add:

The authors thank the three anonymous referees for their constructive comments, which led to significant improvements.

p. 1593, add reference:

Sarpe, D., Grosskopf, T., Javidpour, J.: *Mnemiopsis leidyi*—analysis of an invader in the Kiel Fjord with focus on respiration and reproduction rate, 42nd European Marine Biology Symposium, 27–32 August 2007, Kiel, Germany, www.embs42.meeresbiologie.at., 2007.

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 0.22µgC egg-1 in the dynamic energy budget and 0.1 µgC egg-1 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.

We reject the suggestion that this paper was stitched together. The work with the different models was designed to fit together from the start, and extensive discussions and exchanges have taken place to ensure that the work fits together as well as possible. As this is collaborative work by three different groups, it is inevitable that there are differences in style throughout the paper.

Egg carbon values: the referee has made a mistake:

in Figure 13 it is stated that the biomass at conception is 0.12 μ g C egg⁻¹, which is close enough to the value used in the GETM model to be of minor influence (and probably within the natural variability and/or measurement error).

It is not clear to us which other parameter values the referee is referring to. Please note that these two models use very different approaches to describe development, and that differences are inevitable. These differences (and associated differences in results) are dominated more by inclusion/exclusion of specific processes (e.g. the GETM model includes mortality, the DEB model doesn't; the DEB model describes development in detail, the GETM model uses a coarse parameterisation, etc.) than by individual parameter settings. But this is not the point of the paper, which is rather to use the combined results to get an impression of the viability of offshore populations of *M. leidyi* (see last sentence of section 1.1).

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.

Please change.

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.

For the naming of the models, please see response to the similar comments by Referee #1. p. 1562, l. 5, please remove abbreviation.

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.

For all of the above: we have revised the introduction, including references, based on the comments of the three referees, see new introduction text in response to the corresponding comment by Referee #1. The original sentence "recent work from Collingridge et al. (2014) found that large parts of the North Sea were suitable for *M. leidyi* reproduction in summer months" has been modified to: "model predictions from recent work from Collingridge et al. (2014) suggest that large parts of the North Sea are suitable for *M. leidyi* reproduction in summer months".

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

See response to corresponding comment by Referee #1.

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).

See response to corresponding comments by Referee #1.

p. 1568, l. 25, please add: For the purpose of this study, passive particles were used.

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).

p. 1571, l. 3, add:

...*leidyi*. Including the latter would require either inclusion of a comb jelly functional type in ERSEM-BFM, or development of full, on-the-fly coupling and feedback between ERSEM-BFM and GITM. These options were considered beyond the scope of this study. As a result, the survival and reproductive success of individuals simulated by the present model implementation should be considered an over-estimate. The reproduction... p. 1587, l. 21, add:

...large numbers. Further work is required to assess to which extent this result would hold if feedback of *M*. *leidyi* on food stocks were included. However as the current results suggest negligible offshore reproductive success, we expect numbers to remain low and such feedback to be limited. The present...

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.

See suggested changes in response to general comments above.

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.

The referee has made a mistake: see response to the general comment above.

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.

p. 1573, l. 1: change into: ...= 12.4 constants based on graphs with model results presented...

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

p. 1574, l. 4, Change into:

... 3 mg C m⁻³, based on the observation that *M. leidyi* can survive without food for up to 17 days (Oliveira, 2007), and observations of the lowest concentrations of zooplankton at which *M. leidyi* has been found in the field (Kremer, 1994).

p. 1591: add reference:

Kremer, P.: Patterns of abundance for *Mnemiopsis* in US coastal waters: a comparative overview, ICES J. of Mar. Sci. 51, 347-354, 1994.

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.

We have reduced the number of figures (see response to comments of Referee #1 and #2 above). It should be noted, however, that the purpose of the paper is not model intercomparison, but rather to combine the results of very different models to assess scientific and management questions. This is very clearly stated in the last sentence of section 1.1 (p. 1563, I. 27-29). We think that all the remaining figures are essential to convey this message. We also don't see how the results could be usefully combined in a 'key comparison figure', as the three different models do not have significant spatial overlap.

p. 1566, l. 11, change:

Through combining and intercomparison of the results...individual models, this study provides insight into...

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.

Synchronised spawning: see changes suggested below.

Fig 12d: following a comment from Referee #2, the updated caption will state that these results are from the GETM model; the reader can then follow this back to the model description where this calculation is described explicitly.

p. 1571, l. 7: insert:

... 2012). *M. leidyi* exhibits synchronised spawning (Pang and Martindale, 2008). In the model, this behaviour was not included, and egg production was spread over time. As in the model eggs were not released as separate particles, and predation processes were not explicitly included, the influence of this simplification on the modelled adult population is expected to be small. The number... p. 1592: add reference:

Pang, K., Martindale, M.: *Mnemiopsis leidyi* spawning and embryo collection, Cold Spring Harbor Protocols 2008, doi:10.1101/pdb.prot5085, 2008.

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).

This work has now been published, so this should no longer be an issue.

p. 1578, l. 15, please add:

Reproduction rates *R* are given by $R = \kappa_R \dot{p}_R / E_0$ where E_0 is the initial energy content of an egg. \dot{p}_R is specified in fig. 3 (row 8) and κ_R is the reproduction efficiency (see table 1).

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.

See the changes suggested by us associated with previous comments.

Apart from the specific points addressed above, it is not clear to us which background information the referee is referring to. Moreover, a model is an abstraction of reality - not every bit of information can be incorporated into any model. So without more specific directions, we can't make useful changes over those specified so far in this reply to the document in response to this comment.

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).

p. 1585, between l.19 and l.20, add the following paragraph:

Given the predicted plasticity in growth and juvenile stage duration, future studies should consider incorporating these processes into models designed to analyze observations that include the size structure of populations in the field. Simulation studies using ambient temperature and zooplankton biomass could be performed, where one starts with hatched eggs, to study how juvenile stage duration and condition would vary (in the absence of predation). Such results could be compared to data of the type presented by Jaspers et al. (2013) who recorded the size structure and abundance of early life stages of *M. leidyi* in the Baltic Sea. Mismatches between data and model might guide research aiming to understand natural mortality and food availability.

p.1591, l.8: add reference:

Jaspers, C., Haraldsson, M., Lombard, F., Bolte, S., Kiørboe, T.: Seasonal dynamics of early life stages of invasive and native ctenophores gives clues to invasion and bloom potential in the Baltic Sea, Journal of Plankton Research, 35, 582-594, 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.

As stated before, we don't think that the number of figures is excessive for a paper of this kind. We will take guidance from the editor.

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.

All model results presented here are original and have not been published elsewhere.

Please replace the first sentence of the caption of Figure 3 with:

Energy flux scheme of the standard DEB model and model equations (modified from Kooijman, 2010).

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

We think the referee is referring to the observations in the Grevelingen estuary; these have now been removed: see response to related comment by Referee #1 and suggested changes.

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.

These are all model predictions and not data; we agree that the text in subsection 2.3.2 should be clearer. We re-wrote part of subsection 2.3.3 and specify that we are performing original simulation experiments (see also responses to comments by referee 1).

In addition, at the end of subsection 2.3.2 (p1578, l.15)) we specify how ages and mass at stage transitions as well as reproduction rates are computed (see response to a previous comment)

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 Kiørboe, 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.

p. 1951, l. 17: update reference: Kooijman, S. A. L. M.: The evolution of metabolic acceleration in animals, J. Sea Res., 94: 128-137, 2014.

New versions of figures:



Fig 1







Fig 8





Fig 13