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# Early engagement of stakeholders with individual-based modelling can inform research for improving invasive species management: the round goby as a case study.

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1. Conceptualization: ES, JMJT, SCFP, PEH, JWB .
2. Formal analysis: ES, SCFP
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4. Methodology: ES, SCFP
5. Project administration: ES, JMJT.
6. Resources: JMJT.
7. Supervision: JMJT.
8. Validation: ES, SCFP
9. Visualization: ES
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### *Abstract*

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Individual-based models (IBMs) incorporating realistic representations of key range-front processes such as dispersal can be used as tools to investigate the dynamics of invasive species. Managers can apply insights from these models to take effective action to prevent further spread and prioritize measures preventing establishment of invasive species. We highlight here how early-stage IBMs (constructed under constraints of time and data availability) can also play an important role in defining key research priorities for providing key information on the biology of an invasive species in order that subsequent models can provide robust insight into potential management interventions.

The round goby, *Neogobius melanostomus*, is currently spreading through the Baltic Sea, with major negative effects being reported in the wake of its invasion. Together with stakeholders, we parameterize an IBM to investigate the goby's potential spread pattern throughout the Gulf of Gdansk and the Baltic Sea. Model parameters were assigned by integrating information obtained through stakeholder interaction, from scientific literature, or estimated using an inverse modelling approach when not available.

IBMs can provide valuable direction to research on invasive species even when there is limited data and/or time available to parameterize/fit them to the degree to which we might aspire in an ideal world. Co-development of models with stakeholders can be used to recognize important invasion patterns, in addition to identifying and estimating unknown environmental parameters, thereby guiding the direction of future research. Well-parameterized and validated models are not required in the earlier stages of the modelling cycle where their main utility is as a tool for thought.

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3 **goby as a case study.**

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34 patterns, in addition to identifying and estimating unknown environmental parameters, thereby

35 guiding the direction of future research. Well-parameterized and validated models are not required in  
36 the earlier stages of the modelling cycle where their main utility is as a tool for thought.

## 37 **1 Introduction**

### 38 **1.1 Invasive species and the need for ecological modelling**

39 Invasive species are one of the driving forces behind biodiversity loss, and their persistence in non-  
40 native areas can result in substantial environmental and economic costs (Cardador et al., 2016;  
41 Molnar et al., 2008; Pimentel et al., 2005, 2000). Once established, invasive species have the  
42 potential to alter local habitat quality, increase competition for resources, prey on native populations  
43 and spread disease (Crowl et al., 2008; Gallardo et al., 2016; Karlson et al., 2007; Kwon et al., 2006;  
44 Salo et al., 2007). As a result, the management and control of invasive species has been a central  
45 research focus for many years, and a priority for biological conservation.

46 There is a continual need for the development and improvement of both new and existing  
47 conservation management strategies either to control the spread, reduce biomass or, if possible, to  
48 eradicate an invasive species from its non-native environment (Ojaveer et al., 2015). However,  
49 implementing management procedures can be costly, both economically and environmentally  
50 (Hulme, 2009). Therefore techniques for forecasting the spread of species and assessing the likely  
51 impact of alternative management strategies are desirable (Kotta et al., 2016; Uden et al., 2015). One  
52 such way to evaluate potential management strategies is through ecological modelling (Goldstein et  
53 al., 2016; Kotta et al., 2016; Uden et al., 2015). For example, being able to model the spatial  
54 distribution of a species accurately can potentially provide numerous facilities, such as predicting  
55 future distributions or furthering our understanding of the original invasion process (Adams et al.,  
56 2015).

### 57 **1.2 Forecasting dispersal in invasive species through spatially explicit models**

58 The accuracy and utility of process-based models for ecological forecasting has vastly improved over  
59 the past few years (Cuddington et al., 2013; Evans et al., 2013; Urban et al., 2016), particularly as the  
60 understanding surrounding ecological processes such as dispersal dynamics has increased (Bocedi et  
61 al., 2014b; Goldstein et al., 2016). As dispersal is one of the key determinants of species spatial  
62 dynamics, understanding and accurately simulating the dispersal process is central to predicting  
63 species spread (Bocedi et al., 2014b; Brown et al., 2014; Hastings et al., 2005). Numerous studies  
64 demonstrate that dispersal is key to species undergoing range expansion, and that there is selection  
65 for increased dispersal propensity at the range front (Brown et al., 2014; Huang et al., 2015; Myles-  
66 Gonzalez et al., 2015; Parry et al., 2015; Therry et al., 2015; Travis et al., 2010). For example, in the  
67 invasive Cane toad (*Rhinella marina* Linnaeus, 1758), individuals in the invasion front disperse  
68 further, more frequently and in straighter paths than those in established core populations (Brown et  
69 al., 2014; Hudson et al., 2015), and even possess physiology that facilitates their dispersal propensity  
70 (Phillips et al., 2006). As such, spatially explicit models that incorporate ecological and even  
71 evolutionary or physiological complexity can be vital tools in making predictions regarding range  
72 extent and the effectiveness of control regimes for invasive species (Goldstein et al., 2016; Higgins et  
73 al., 1996; Meekins and Mccarthy, 2002; Vuilleumier et al., 2011). Calibrating and validating such  
74 models with suitable data, if available, can provide an excellent opportunity to investigate species-  
75 specific invasions, assess invasion patterns and address concerns. However, very rarely (if ever) will  
76 all the data required to parameterize a model fully be readily available in the literature. One way of  
77 obtaining such information is through stakeholder interaction. Involving stakeholders in the

78 modelling process additionally allows for the continual evaluation of model utility, accuracy and the  
79 development of future model applications.

### 80 **1.3 Early engagement of stakeholders in the ecological modelling process**

81 Often stakeholders encounter a model only at the stage where it has been tightly parameterized and  
82 validated by ecological researchers. Traditional thinking tends to be that a model needs to be well-  
83 parameterized and validated before it can be useful in an applied context. Indeed, an often  
84 encountered view is that it can be dangerous for a modeller to demonstrate an ‘immature’ model to  
85 stakeholders due to risks of losing credibility or of providing unsound advice. However, developing a  
86 well-tested model can be a time consuming process, and this is problematic especially when early  
87 intervention is often critical for successful management outcomes. It has been repeatedly highlighted  
88 that early involvement of stakeholders into ecological management efforts increases chances for  
89 success (Bayliss et al., 2013, Seidl et al., 2013) and we consider that models can provide an important  
90 tool for thought at this early stage, well before they reach the level of maturity that we would expect  
91 them to have reached prior to providing robust management advice. In assessing the potential risks  
92 posed by an invasive species, and scoping out potential control options, scientists and stakeholders  
93 must first objectively assess where their knowledge might be incomplete (Krueger et al. 2012) and a  
94 prototype model can provide an excellent tool for formalizing the process of establishing what is  
95 already known, what is not known and, critically, identifying what it is that isn’t known that is likely  
96 to be most influential in determining the invasion dynamics. Understanding of where key knowledge  
97 gaps exist can inform future research and data collection (Voinov and Bousquet, 2010). Here, we put  
98 this into practice, and emphasize that it can be extremely valuable to engage stakeholders with an  
99 early prototype model and use their input to tailor the modelling process to practical needs. We  
100 additionally emphasise the value that an early stage model can provide a means for horizon scanning  
101 for potential threats due to the invasive species, and can be used to provide some initial risk  
102 assessments of particular threats (Parrott, 2017; Parrott et al., 2012; Reed et al., 2013).

### 103 **1.4 Case Study: The round goby in the Baltic**

104 As a case study, we use our experience of developing an early-stage model for the round goby’s  
105 spread through the Baltic Sea in order to facilitate stakeholder engagement. The round goby  
106 (*Neogobius melanostomus* Pallas, 1811). is a species, for which ecological modelling can be  
107 valuable, firstly for formalizing the process of establishing what we know and what we still need to  
108 know and, subsequently, for developing well-tested models that can be used to provide robust  
109 management recommendations. This species is native to the Ponto-Caspian region, and has invaded  
110 the Great Lakes in North America and multiple locations throughout Europe, most likely as a result  
111 of transport through shipping routes via ship ballast water (Kornis et al., 2012; Kotta et al, 2016). The  
112 species has been termed ‘one of Europe’s 100 worst invaders’ and has in a recent evaluation of 18  
113 taxa of non-indigenous species in the Baltic Sea region been found to be amongst those with the  
114 greatest impact (Hirsch et al., 2015; Kotta et al., 2016). For the past 25 years, the species has been in  
115 the process of spreading throughout the Baltic Sea (Sapota, 2004a; Schrandt et al., 2016). The first  
116 reported sighting was in 1990 in the Gulf of Gdansk, and since then, sightings of the species have  
117 been recorded in various areas of the Baltic (Kotta et al., 2016). Whilst some stages of the goby’s  
118 spread have been well documented, such as the introduction and invasion of the Gulf of Gdansk  
119 (Sapota 2004) and the inner Danish waters (Azour et al., 2015; Carl et al., 2016), there are other  
120 stages of the invasion that are substantially lacking in information.

121 Here, we highlight how a spatially explicit ecological simulation platform, RangeShifter (Bocedi et  
122 al. 2014) can rapidly be used to develop an initial prototype model for early engagement of  
123 stakeholders with the process, and subsequently calibrating using spatial data available from the  
124 literature and input from stakeholders. We then demonstrate how this intermediate-stage model can  
125 be applied to further research in order to identify key data gaps that would need to be filled before a  
126 well-tested model could be used to robustly inform management actions.

## 127 **2 Overview of the process**

128 The work described in this paper has been designed to be consistent with the adaptive modelling  
129 approach for ecological forecasting outlined in Urban et al. (2016). The overall process of developing  
130 the model is outlined in Figure 1. A prototype model of the goby's spread throughout the Baltic was  
131 developed and parameterized within a six week period through an iterative process (Grimm et al.,  
132 2005; Grimm and Railsback, 2012) to present to stakeholders in a symposium context. This period of  
133 initial model development was by necessity short in our case, as we had been invited to a round goby  
134 symposium to discuss the potential utility of the RangeShifter software in the context of managing  
135 the round goby. The description of this initial model development will be kept brief, as it was  
136 predominantly an iterative process of altering parameter values and comparing the model output to  
137 that of the HELCOM round goby distribution (Michalek et al. 2012). The rapid production of a  
138 prototype model allowed demonstration of the potential utility of the model to stakeholders,  
139 especially for use in the future after more rigorous assessment. Furthermore, it also provided an  
140 overview of what the model could do, which opened the way for suggestions on scenarios and  
141 improvements that the model can be used to explore.

### 142 **2.1 Stakeholder collaboration**

#### 143 **2.1.1 Overview of the symposium**

144 A symposium centred around the spread and impact of the round goby in the Baltic Sea was held in  
145 Kalmar, Sweden in June 2016. The organization of the symposium was headed by the Swedish  
146 Agency for Marine and Freshwater Management<sup>1</sup>, and there were an estimated 30 attendees. The  
147 main stakeholder groups consisted of representatives of different levels of local and regional  
148 environmental administration, people that participated in a private capacity, and representatives of  
149 other groups interested or affected by round goby spread, such as recreational and professional  
150 fishermen. The symposium was followed by a workshop focusing on solutions to manage and  
151 impede the spread of the round goby throughout the Baltic Sea. During the symposium the overall  
152 research project and the model was presented in a 30 minutes power point presentation  
153 (Supplementary Figure 1). The presentation had two main components. First, RangeShifter was  
154 presented to the participants along with examples of how the software had already been used to  
155 address conservation relevant questions, including invasive species. This was key as a means for  
156 establishing our credibility as modellers. Second, the prototype goby model, implemented using  
157 RangeShifter, was presented to the stakeholders to demonstrate the potential utility of the model  
158 within the Baltic Sea and hence within the geographical focus of the participants' interests.  
159 Throughout this second part, we repeatedly stressed both the prototype nature of the model and the  
160 fact that while we were in a room full of goby experts, the modellers who had rapidly developed a  
161 prototype for demonstration were certainly not.

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<sup>1</sup> <https://www.havochvatten.se/>

162 At the end of the presentation a specific call for input was issued: a slide stating “What we hope to get  
163 from you...” followed by six suggested inputs: Specific parameters (e.g. demographic and dispersal),  
164 The estimated introduction sites (and when), Patterns for comparing model outputs with spatial and  
165 temporal patterns of density and sediment type and habitat, Proposed management techniques.  
166 Following the presentation there was an open discussion with a call for feedback and input. In  
167 transdisciplinary projects it is important that both scientists and non-academic partners contribute at  
168 an equal footing (N’Guyen et al. 2016). This is especially relevant in the case when inputs are  
169 qualitative rather than quantitative. In our case, we were interested in qualitative inputs, and we  
170 therefore designed the interaction with stakeholders as open and did not follow a standardized  
171 procedure. We felt this would ensure an atmosphere that encouraged stakeholders to contribute even  
172 anecdotal but possibly relevant information which they might be less inclined to share when e.g.  
173 filling out a questionnaire.

### 174 **2.1.2 Outcomes of the symposium**

175 The interaction with stakeholders identified essential knowledge gaps, which would have gone  
176 unnoticed by us as scientists alone. Crucially the interactions also provided a clear focus in terms of  
177 what a useful model would need to include and would need to be able to predict in order that it was  
178 most useful to the stakeholders. Also, personal communications with multiple researchers and  
179 stakeholders present at the meeting provided an insight into the current understanding of the round  
180 goby’s spatial presence in the Baltic Sea that was not obvious from searching the literature, including  
181 information on new studies that will yield high quality data. Three essential qualitative outcomes of  
182 the symposium that were derived from the interactions between modelling team and stakeholders  
183 provided strong focus for future work. These related to model building such that key processes  
184 driving the spread dynamic are properly represented and parameterized and for developing the model  
185 to ensure its relevance for informing key management decisions:

186 First: A knowledge gap regarding the depth of goby dispersal was highlighted as potentially crucial.  
187 Prototype model results shown at the workshop included one suggesting that the invasion dynamic is  
188 likely to be very sensitive to the depth range over which gobies can disperse. At the workshop  
189 attendees noted that adult gobies are sometime caught in deeper water. However, it was suggested  
190 that this occurs during winter months and may reflect some adults exhibiting seasonal migration to  
191 deeper waters. It became obvious that whether gobies disperse through deep water or disperse solely  
192 in shallow areas is currently unknown. Understanding the depth range of goby dispersal may be of  
193 great importance to those involved with the round goby invasion for a number of reasons. Depth  
194 acting as a barrier to dispersal may be utilized in numerous management protocols to impede or  
195 inhibit goby spread into undesirable areas. Furthermore, understanding goby dispersal depth helps to  
196 predict future areas that may be under threat of round goby invasion, even without a human-mediated  
197 element to the dispersal. Identifying the potential importance of the depth sensitivity of dispersal for  
198 patterns of goby spread was a novel outcome of the workshop that will motivate new empirical work.

199 Second: Threats of the round goby’s invasion of the freshwater systems that connect to the Baltic  
200 Sea, particularly with regards to Salmonids were identified, as the round goby may devastate their  
201 populations through egg consumption (Chotkowski and Ellen Marsden, 1999; Ladago et al., 2016;  
202 Marentette et al., 2011). This potential impact of the round goby was a key issue for many of the  
203 stakeholders present and highlighted the importance that to be useful for management a model would  
204 need to be able to effectively operate into riverine systems and potentially also account for salinity  
205 gradients and tolerances.



206 Third; The threat that the round goby poses to the long-tailed duck (*Clangula hyemalis* Linnaeus,  
207 1758) was emphasized (Hearn et al., 2015). The Baltic Sea is the key wintering destination for the  
208 majority of the western Siberian and northern European populations of the long-tailed duck (Hearn et  
209 al., 2015), which currently faces a multitude of threats such as predation, competition, oil spills,  
210 gillnets, hunting, habitat destruction and water traffic (information available on the BirdLife  
211 International website<sup>2</sup>). The round goby and the long-tailed duck share a diet of mussels and  
212 crustaceans. Hence, the spread of the round goby to the overwintering habitats may result in  
213 competition for food. As the Baltic Sea is the main overwintering area, a reduction in food  
214 availability for the long-tailed duck in this area may prove devastating. Consequently, this area is  
215 recommended to be a crucial area to protect from invasion by the round goby (Hearn et al., 2015).  
216 Currently there are no effective means for estimating the risk that these areas will be invaded. Hence,  
217 estimations for whether, and if so when, the goby will reach the overwintering areas from their  
218 current distribution would be valuable, to estimate time-scales for conservation efforts for the long-  
219 tailed duck, and to design measures to protect the area from the spread of the round goby. We note  
220 here that while there was existing information in the literature highlighting the potential impact of  
221 round goby on long tailed duck in the duck's key overwintering sites (Hearn et al. 2015), it would  
222 have been unlikely that the modelling team would have easily found it. Thus, the stakeholder  
223 workshop provided a means for those fully familiar with the system to direct the modelling team to  
224 literature relating to the focal species and its potential impacts that isn't primarily about the focal  
225 species.

## 226 **2.2 The Modelling**

### 227 **2.2.1 Modelling population dynamics and dispersal in RangeShifter**

228 We used a spatially explicit, individual-based model, RangeShifter (Bocedi et al., 2014a) to simulate  
229 the spread of the round goby throughout the Baltic Sea. RangeShifter was developed in response to  
230 the demand for integrated dynamic models, and as such, provides a platform with which to model  
231 complex population dynamics and dispersal behaviors, at the individual scale (Franklin 2010;  
232 Huntley et al., 2010; Lurgi et al., 2014; Thuiller et al., 2013).

233 To represent the Baltic Sea, a gridded seascape was created in ArcGIS 10.3.1 using raster data  
234 extracted from the EMODnet Bathymetry portal<sup>3</sup>. Each cell was 2.5km by 2.5km and characterized  
235 by depth. Population dynamics were modelled at the cell scale. The numbers of individual fish in the  
236 Baltic, or even in a local area, at reported densities (Vélez-Espino et al., 2010) would be far too large  
237 to be represented in the model, and therefore we treated a modelled 'individual' as representing a  
238 localized established sub-population of unspecified size (hereafter 'individual' for consistency with  
239 RangeShifter terminology), which was regarded as female in a single-sex model. It was not necessary  
240 to represent the overlapping generations of the species, but sufficient to model the reproductive rate  
241 of such 'individuals', i.e. the rate at which 'daughter' sub-populations were produced, some of which  
242 would disperse to expand the range of the species.

243 At model initiation, individuals were assigned to cells within species introduction points at half  
244 carrying capacity. In each year, the overall dynamics consists of reproduction, death of adults and  
245 offspring dispersal. Reproduction by each individual is determined by a stochastic draw from a

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<sup>2</sup> <http://www.birdlife.org>

<sup>3</sup> <http://www.emodnet-bathymetry.eu/>

246 Poisson distribution having a mean set by the maximum growth rate at low density and subject to  
247 density-dependent reduction following Maynard-Smith and Slatkin (1973). Carrying capacity,  $K$ , was  
248 set to 10 individuals/ha for all cells. However, this limitation is unlikely to be critical for the pattern  
249 of range expansion on which we were focused, given that densities at the range front are expected to  
250 be much lower than in long-established areas (Azour et al., 2015; Brownscombe et al., 2012; Groen  
251 et al., 2012).

252 Once reproduction has taken place, individuals could emigrate away from their natal cell, an action  
253 dependent on the local density within the cell. If an individual left the cell, its trajectory was  
254 modelled using the Stochastic Movement Simulator (SMS; Palmer et al., 2011). SMS simulates an  
255 individual's path throughout the landscape, in which the direction of movement between cells is  
256 based on the relative cell 'costs' to movement and on a tendency to follow a correlated path  
257 (directional persistence). The perceptual range, in which costs were evaluated, was set at 1 cell (i.e.  
258 no more than 2.5km).

### 259 **2.2.2 Incorporating the stakeholder input into the model**

260 A key issue that emerged from the stakeholder workshop was a lack of knowledge relating to the  
261 depths of water through which gobies can disperse. This issue was, in part, highlighted by some of  
262 the runs of the prototype model, demonstrated at the workshop, in which it was clear that including a  
263 depth threshold resulted in very different spread patterns than omitting one. Accordingly, cell cost  
264 was set in relation to a threshold depth for movement: the cost of traversing a cell of the depth  
265 threshold and deeper was set to a very high value, and the cost of traversing a cell above the depth  
266 threshold was set to a very low value. In doing so, individuals were much less likely to travel into  
267 deeper water than that set by the threshold. For all depths, each step an individual took had an  
268 associated spatially and temporally constant mortality risk.

269 Upon reaching a new cell, an individual had the opportunity to settle or continue movement to a  
270 different cell. The decision to settle was density-dependent. If the population density was too high in  
271 a cell, then the individual would not settle but continue to disperse to a neighboring cell (Bocedi et  
272 al., 2014a).

### 273 **2.2.3 Parameter calibration and assessing model performance**

274 The majority of the parameters required for the model were not widely available in the literature or  
275 through online resources. Consequently, in order to calibrate the model parameters, the Gulf of  
276 Gdansk was chosen, as detailed spatial information regarding the goby's spread through the area was  
277 available. This spatial information was primarily obtained from the NOBANIS fact sheet, produced  
278 by Sapota (2012). NOBANIS is the European Network on Invasive Alien Species, and the project  
279 produces information and fact sheets on invasive alien species. The fact sheet, written and referenced  
280 by experts, provides a range of information including recommendations for management, species  
281 ecology and information regarding its historical introduction and spread. This temporal spatial  
282 presence information available in the NOBANIS fact sheet was used as a baseline to calibrate the  
283 model.

284 Parameter values were calibrated using a pattern-oriented modelling approach (POM) (Bauduin et al.,  
285 2016; Grimm et al., 2005; Grimm and Railsback, 2012), in which simulations were run for a variety  
286 of values for four key parameters, namely the maximum growth rate, the depth threshold, the per-step  
287 mortality risk and the maximum settlement probability (Table 1), in order to find a combination  
288 which most precisely matched that of the historical round goby spread throughout the Gulf of

289 Gdansk. For each simulation, the final model distribution was compared to the actual distribution  
290 reported in Sapota (2012). Other more minor parameter values, such as the depth threshold cost, were  
291 assigned during the creation of the prototype model, using an iterative process. During this process,  
292 the values chosen were arbitrary, and altered until the model output started to match the goby  
293 distribution seen in the NOBANIS fact sheet. Therefore, these parameters were used more as values  
294 to tune the initial model, rather than parameters that were important to investigate. The models  
295 predicted output was compared to the observed output for each year that data were available, in order  
296 to obtain the most accurate dispersal pattern throughout the Gulf of Gdansk.

#### 297 **2.2.4 Accuracy of model calibration**

298 To assess the accuracy of the model for each parameter combination, four metrics were used, in  
299 addition to visually inspecting the model output. Model *specificity* (in which both the observed  
300 distribution and the models predicted distribution do not have individuals present in a cell),  
301 *sensitivity* (in which both the actual distribution and the model have individuals present in a cell), the  
302 receiver operator characteristic (ROC) curve with the associated area under the curve (AUC), and  
303 Cohen's Kappa,  $\kappa$ . The  $\kappa$  statistic represents a way to measure reliability, or precision, and compares  
304 the model prediction accuracy with the accuracy expected to occur by chance (Allouche, Tsoar &  
305 Kadmon, 2006). Sensitivity and specificity both vary from -1 to +1, in which a score of 0 represents  
306 no better than chance, and +1 would represent a perfect score.  $\kappa$  can vary between 0 and 1, where 0  
307 represents an agreement no better than chance, and 1 represents a perfect agreement. An accurate  
308 model with an AUC score of an ROC plot would be close to 1. A score close to 0.5 would represent a  
309 poor model. Whilst the AUC is threshold independent, the other measurements are threshold  
310 dependent. The threshold during analysis is the cut-off value used to translate predicted probabilities  
311 into a presence or an absence. Consequently, for a predicted probability to be classed as a presence  
312 under a high threshold (such as 0.9), a cell would need to be colonized by individuals in 90% or more  
313 of replicated model runs given the specified combination of model parameters.

314 In order to calculate the sensitivity, specificity, AUC and  $\kappa$  for each parameter combination, each  
315 combination was repeated over 100 simulations. These metrics were calculated using the  
316 PresenceAbsence package in RStudio 3.3.1 (Freeman and Moisen, 2008).

#### 317 **2.2.5 Ports of introduction and modelled population initiation in the Gulf of Gdansk and the** 318 **Baltic Sea**

319 The species introduction points of the Baltic Sea, where populations were initiated, were estimated  
320 using information available in the literature (Kotta et al., 2016), species presence information from  
321 the symposium and shipping port and traffic information available on Baltic Transport Maps<sup>4</sup>. Ports  
322 of introduction were assumed to be the closest shipping port to a current goby distribution. The  
323 initiation of a population at the entry points was staggered in an attempt to replicate the introduction  
324 of the goby throughout the Baltic at various points in time. For example, populations were initiated in  
325 the Gulf of Gdansk entry points at year 0 (representing the year 1990), but populations initiated  
326 around Kalmar were not initiated until year 20 (2010). The timing of the staggered introductions at  
327 various points on the map were based on estimates from the literature (reviewed by Kotta et al.,  
328 2016). The staggered introductions were carried out using a customized version of RangeShifter that  
329 allowed populations to be initialized in individual cells at specified times. Parameter values applied  
330 were informed by the results from fitting the model to the Gulf of Gdansk (Table 1).

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<sup>4</sup> <http://www.baltictransportmaps.com>

### 331 **3 Model Results**

#### 332 **3.1 Model calibration: role of depth threshold in the Gulf of Gdansk**

333 Model accuracy was most strongly influenced by the depth threshold: 76% of the variance in  $\kappa$  was  
334 explained by depth, as compared with 11% by the maximum settlement probability, 4.6% by the per-  
335 step mortality risk, 3.3% by the maximum growth rate and negligible amounts by interactions. The  
336 model was most accurate for a depth threshold between 10 and 25m, and accuracy increased slightly  
337 with decreasing settlement probability and mortality risk and with increasing growth rate (Figure 2).  
338 Similar conclusions regarding the importance of the depth threshold were drawn from the other  
339 accuracy metrics (Table 2; Supplementary Table 1). Examples of various outputs can be seen in  
340 Figure 3, ranging from good (AUC and  $\kappa$  scores close to 1) to poor (AUC and  $\kappa$  scores close to 0.5  
341 and 0, respectively). Through the process, a number of models with high accuracy were produced,  
342 with some models obtaining accuracy values of 0.8 for all four accuracy metrics, even when the  
343 model threshold was high (0.8) (Figure 4).

#### 344 **3.2 Model output: projections based on the role of depth threshold, across the entire Baltic** 345 **Sea**

346 Despite obtaining a range of accurate parameter combinations for the Gulf of Gdansk, when they  
347 were applied to the entire Baltic, the overall model output was poor when compared to the extensive  
348 observed distribution spanning a substantial proportion of the Baltic coastline as reported in the  
349 literature (Figure 5). The accuracy scores calculated for The Baltic suggest that the model was not  
350 much better at predicting the goby distribution than chance (AUC scores close to 0.5, and other  
351 scores close to 0.1).

### 352 **4 Discussion**

353 In this study, we rapidly developed a prototype model of round goby spatial dynamics that was used  
354 to facilitate early engagement with stakeholders. We subsequently combined data available in the  
355 literature and stakeholder input in order to calibrate the individual-based model such that it simulated  
356 the round goby's spread throughout the Gulf of Gdansk to a high level of accuracy. We then used the  
357 calibrated model to simulate its spread through the Baltic Sea, despite the limitation of imprecise and  
358 potentially inaccurate presence data. Our experience demonstrates the value of involving  
359 stakeholders early in the modelling process. Prototype model results had indicated that predicted  
360 spread was highly sensitive to the inclusion of a depth threshold for dispersal, and the subsequent  
361 stakeholder communication highlighted how little is currently understood about goby dispersal at  
362 various depths. Consequently, various depth thresholds were incorporated into the modelling, in  
363 order to assess the impact of depth on model accuracy and therefore goby dispersal. We  
364 demonstrated how, by using known spread patterns, it can be possible to use the model to infer  
365 details of the dispersal process, in this case related to the depth threshold of goby dispersal. In detail,  
366 we could show that that the limit to dispersal depth of the round goby lies between 10 and 25m.  
367 Empirical data are now required on the depth sensitivity of dispersal such that a robustly  
368 parameterized model can be used by the stakeholder/modeler grouping in further steps towards  
369 identifying management options. The involvement of stakeholders as early as possible in the process  
370 and their regular inclusion throughout as co-developers of the modelling will facilitate a cooperation  
371 between scientists and stakeholders in putting possible management measures into practice.

#### 372 **4.1 Stakeholder collaboration – putting theory to practice**

373 Research has identified that the long lag time between research and its publication hinders managers  
374 of biological invasions to make use of such important results as our models generated (Matzek et al.,  
375 2015). In addition, theory predicts that the success rate of management should be higher if  
376 stakeholders and scientists engage early on in the transdisciplinary process of managing an invasive  
377 species (Hirsch et al., 2016a, N'Guyen et al., 2016). The main reason behind this is that scientific  
378 results that were co-produced by relevant parties in a transdisciplinary process should have better  
379 social acceptance and higher compliance by decision makers (Pohl et al., 2008).

380 In our study, we put these theoretical predictions into practice and engaged in a modelling process  
381 that used stakeholder input as an essential component. Stakeholders provided two essential inputs  
382 regarding future model optimization: providing information on where higher quality distribution data  
383 would be available in the near future and on the priority of including depth in the model.  
384 Stakeholders contributed their knowledge and understanding on an equal footing. In an excellent  
385 recent contribution on how to co-develop models with stakeholders effectively to address pressing  
386 ecological problems, Parrott (2017) argues that it is important for the modelers to get to know the  
387 study system well before meeting with stakeholders. Parrot (2017) writes, “Knowing the system well  
388 is a key to gaining the trust and confidence of stakeholders in the ability of the modeler and the entire  
389 research team to contribute meaningfully to the issue. If the researchers are not from the area, they  
390 should spend time visiting and getting to know the region before initial meetings with stakeholders.”  
391 Indeed, we had been approached by stakeholders and asked to present the modeling software at a  
392 meeting on the threat posed by round gobies to illustrate what might be possible in terms of using  
393 RangeShifter to inform management of the species. We only had a few weeks ahead of the meeting  
394 in which we were able to build a prototype model for the goby. However, at the meeting we were  
395 able to demonstrate our credibility as ecological modelers by first providing examples of how the  
396 RangeShifter was being used to address a range of other applied issues, including landscape  
397 management to conserve African forest birds (Aben et al., 2016), assisted colonization of butterflies  
398 in Finland (Heikkinen et al., 2014) and the invasion of American mink (*Neovison vison*) in Scotland  
399 (Fraser et al., 2015).

#### 400 **4.2 Acknowledging the different roles of scientists and stakeholders**

401 A potential advantage of the approach we took in this study is that the stakeholders naturally take the  
402 role as the species/system experts, and the potential risk whereby stakeholders perceive that the  
403 researchers assume the role of experts and tell them how their system works is reduced. One potential  
404 disadvantage of such an approach is that researchers cannot glean data from stakeholders in the form  
405 of quantitative assessments through e.g. specifically designed questionnaires. This disadvantage,  
406 however, is compensated by the fact that stakeholders can contribute their knowledge freely through  
407 unstructured interactions with researchers. For that, it is clearly critical that the modeling team gain  
408 the confidence of the stakeholders, but that need not be by having acquired detailed understanding of  
409 the particular study system in advance of a first meeting. Indeed, we suggest that the effective  
410 establishment of a model co-development group may be facilitated if this is actually not the case and  
411 at the start of the process there is a clear division of expertise between modelers and stakeholders. As  
412 the process of co-development of a model proceeds, both researchers and stakeholders can build upon  
413 this first interaction on an equal footing albeit with quite different expertise. Our study provides a  
414 practical example for future model building efforts on how to rapidly initiate transdisciplinary  
415 projects, which is absolutely vital if models are to be successfully used to inform early intervention  
416 against invasive species.

### 417 **4.3 Model calibration**

418 Calibrating the model with precise spatial data produced a highly accurate model that simulated the  
419 spread of the goby throughout the Gulf of Gdansk over an 11 year period. The model outputs  
420 obtained from the calibration process highlighted the key role of the depth threshold to movement.  
421 However, when scaled up through space and applied to the whole of Baltic Sea, the model failed to  
422 predict a distribution similar to that observed in the literature. The failure to produce a model for the  
423 Baltic Sea with a high degree of accuracy has several implications.

424 One of the main downfalls of the Baltic model seems to occur from uncertainty regarding  
425 introduction points. In order to obtain a predicted presence from the model that was similar to that of  
426 the observed presence, further introduction points would need to be added, if the parameters obtained  
427 from Gdansk were to be used. Although short-distance (~30km/year) active migration appears to  
428 occur in some local areas (Azour et al., 2015), this suggests that, at the scale of the Baltic sea, the  
429 goby did not disperse over long distances as a primary mode of invasion, but that human-mediated  
430 transport, for example via ships or other means, was the primary cause of invasion. As large ports  
431 were used in the model as the introduction points, this may also suggest that the goby was introduced  
432 to various areas that were not necessarily large commercial ports, but also small recreational ports.  
433 Subsequently, future efforts to manage the spread of the goby may benefit from focusing preventative  
434 measures on human-mediated transport, such as the cleaning of recreational boats (Hirsch et al.,  
435 2016). This will be particularly important in protecting regions that would otherwise be likely to be  
436 out of the range of goby colonization due to their being effectively isolated by channels of deeper  
437 water.

438 Furthermore, the presence data used to produce the observed map for model calibration was at a  
439 coarse spatial scale. It may be that the goby's presence at various depths in the Baltic was not  
440 represented in the observed distribution at a fine enough resolution for accurate model assessment.  
441 Given more precise presence data, at a finer resolution, the accuracy of the models predicted goby  
442 presence in the Baltic Sea could improve substantially. One of the benefits of such models is the  
443 ability to identify on which future data collection efforts should be focused. This is in agreement with  
444 the recent call for mandatory catch records and citizen science programs in order to collect data on  
445 the round goby (Ojaveer et al., 2015). In the case of this modeling exercise, presence data over  
446 various depth distributions, and the identification and incorporation of the correct introduction points,  
447 have been identified as being critical for accurate model calibration.

### 448 **4.4 Depth sensitivity**

449 In order to replicate the observed goby distribution throughout the Gulf of Gdansk, a dispersal depth  
450 limit of approximately  $20 \pm 5$ m produced the most accurate model. It is nevertheless important to note  
451 that this was calibrated using one area of the Baltic Sea. Thus, to obtain more accurate results,  
452 presence data spanning various depths over more locations in the Baltic Sea are required. Hitherto  
453 there have however not been any studies dedicated to investigating this aspect of the biology of the  
454 species. Furthermore, as round goby is not a commercial species, no catch-related depth information  
455 is available from the fishery. The sparse information that exists is from a Polish young fish surveys  
456 program, showing that, although generally considered a shallow water inhabitant, high catch rates  
457 occur at 50-60m depth during winter months (November and January–March) (Grygiel 2007). This  
458 suggests that during the cold season, the fish is wintering in deeper sea areas, but whether dispersal  
459 occurs during this period or when the fish resides in more shallow, coastal waters remains  
460 speculative. The present modelling exercise thus indicates that future research efforts should  
461 prioritize obtaining presence and absence data for round goby at various depths throughout the

462 Baltic, and investigate whether dispersal to novel areas occurs during the warm or cold season.  
463 Although often expensive and time consuming to collect, this type of information has been achieved  
464 for several species through tagging studies (e.g. Boje et al. 2014). Furthermore, compilation of  
465 existing data from various national and international surveys and monitoring programs (e.g. the  
466 biannual Baltic International Trawl Surveys, BITS) could prove to be a cost-efficient way to obtain  
467 essential information. The depth threshold of round goby dispersal is an essential parameter not only  
468 for calibrating models, but also for incorporating into risk assessments of the species spread, both  
469 generally and for areas of special interest.

#### 470 **4.5 Salinity tolerance and ecological parameters influencing spread**

471 Although not identified by the stakeholders in the present study, parameters besides depth should be  
472 evaluated for their potential relevance for dispersal tendency. Charlebois et al. (2001) highlighted the  
473 need for research determining ‘dispersal mechanisms and environmental characteristics that limit  
474 dispersal’. Round goby is considered a euryhaline species, which is able to adapt to salinities ranging  
475 from freshwater to brackish conditions. Previous studies have suggested that round goby will not  
476 endure oceanic conditions (i.e. high salinity) (Ellis and MacIsaac 2009; Karsiotis et al 2012). A  
477 recent study acclimating round goby to salinities spanning from fresh to seawater has shown that  
478 slow increases in salinity (5 PSU per week) to salinities approaching oceanic conditions (30 PSU)  
479 severely affected the osmoregulatory capacity of round goby. Although survival was also reduced at  
480 oceanic salinities, still 61% of the fish survived at 30 PSU. So while salinity will likely not act as an  
481 effective barrier, it might still impede the ongoing dispersal of round goby through the salinity  
482 gradient from the brackish Baltic Sea and into the oceanic North Sea and this warrants its inclusion  
483 into dispersal models (Behrens et al. 2017). Further parameters which could turn out to be relevant  
484 depend on the study system and could include temperature (thermal limits in round goby are between  
485 0.5 and 26°C (Chekunova 1974 cited in Charlesbois et al. 2001) and, in running waters, flow velocity  
486 (round goby show a critical swimming speed of 35.5 cm s<sup>-1</sup>; Tierney et al 2011). Recent research  
487 suggests that population niche modelling in combination with climatic parameters might benefit from  
488 the introduction of thresholds for certain environmental parameters (Almpanidou et al. 2016).  
489 Incorporating a minimum of climatic suitability might allow coupling of dispersal models with  
490 models of population establishment (Almpanidou et al. 2016). Understanding the interplay of  
491 population dynamics and dispersal is relevant for selecting population management options in newly  
492 identified populations (N’Guyen et al. 2017).

#### 493 **4.6 Personality-dependent behavior as a model parameter and management options**

494 Not only the abiotic environment, but also personality-dependent behaviors can be important at the  
495 invasion front, where local sub-populations consists mostly of bigger/older asocial individuals  
496 (Thorlacius et al. 2015). Recent research has found that personality traits can inform models of  
497 dispersal such that only individuals showing trait values above a certain threshold are predicted to  
498 disperse (Hirsch et al. 2017). In combination with the depth thresholds, such an approach can  
499 complement future models to achieve an even higher accuracy in predicting dispersal.

500 Until further information is available, our modeled depth trial results may be used as a preliminary  
501 guide to assess management regimes and prioritize management areas for vulnerable species. For  
502 example, from an applied perspective, the model results raise the prospect that artificial deep  
503 channels may stymie the spread of the species. Telemetry-based data on the spread of invasive  
504 crayfish in a Central European large lake has also suggested a spread along the shoreline down  
505 towards a certain depth isocline. This might make it plausible to slow the natural spread by barriers  
506 (Hirsch et al., 2016b). In Lake Tahoe, USA, invasive bivalves have been successfully controlled by

507 the installation of gas impermeable benthic barriers (Wittmann et al., 2012). These examples  
508 demonstrate how knowledge of the spatial spread of an invasive species can directly inform its  
509 management.

#### 510 **4.7 Practical model application for protecting the long-tailed duck**

511 In a practical application of this transdisciplinary approach, we designed a preliminary modeling  
512 experiment as an example of how detailed models developed with stakeholders can inform risk  
513 assessment of invasive species and help to identify priority areas for management. A key issue that  
514 emerged through the stakeholder interaction is the implication of the goby's invasion of the over-  
515 wintering habitat of the western Siberian and northern European wintering populations of the  
516 endangered long-tailed duck. The populations of the duck may be threatened by the round goby  
517 through exploitative competition for food (BirdLife International website<sup>5</sup>; Hearn et al., 2015;  
518 Skabeikis and Lesutienė, 2015). In a preliminary trial, we used the calibrated model to demonstrate  
519 how an effectively parameterized model could be used to assess whether the long-tailed duck  
520 overwintering habitat was at risk of colonization from the round goby in the future. Again, we did  
521 this by running the model over a number of years and a number of depth thresholds. This produced a  
522 number of scenarios in which the overwintering habitat of the long-tailed duck was invaded, but the  
523 time it took for the invasion depended greatly on the depth threshold at which the round goby was  
524 able to disperse. Given the current uncertainty surrounding the results of these initial trials or the risk  
525 to long-tailed duck populations, and the potential influence results from them might have, we decided  
526 that it was premature to publish the results at this stage. However, whilst only being a preliminary  
527 experiment, this example reinforces generally (and very effectively reinforced to our co-development  
528 team of modelers and stakeholders) the importance of obtaining accurate spatial data regarding the  
529 presence of the round goby at various depths.

#### 530 **4.8 Future modelling perspectives**

531 In this study, we made use of an individual-based model to simulate the spread of the invasive  
532 species. However, it is important to recognize that alternative approaches exist that could equally  
533 well be used in transdisciplinary work where models are co-developed to inform understanding and  
534 management of invasive species. Indeed, in future studies one valuable approach will be to utilize  
535 more than one of these modelling approaches in concert. For example, there can be considerable  
536 benefits of jointly developing a stochastic individual-based model and a typically deterministic  
537 integrodifference model to estimate rates of spread (e.g. Travis et al. 2011; Santini et al. 2016).  
538 Notably, while until recently integrodifference models have almost exclusively been used to project  
539 spread rates across homogenous landscapes, recent developments are enabling rapid simulation of  
540 integrodifference equations across spatially complex landscapes (e.g. Synes et al. 2016; Gilbert et al.  
541 2017). One major potential advantage of the integrodifference approach is that the much faster speed  
542 of individual simulations will make inverse fitting of parameters through Bayesian approaches  
543 including approximate Bayesian computation much more readily achievable. A further important  
544 development will be to integrate environmental niche modelling with the population dynamic  
545 modelling approaches available.

546 A key challenge is to move beyond the approach most often taken in what are often termed hybrid  
547 species distribution models and to relate the environmental variables directly to the key demographic  
548 traits (e.g. reproduction, survival and dispersal), rather than simply using the environmental niche

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<sup>5</sup> <http://www.birdlife.org>



549 model to demark suitable and unsuitable environments for a focal species. However, many such  
550 relationships have yet to be established in detail (see Zurell et al. 2016 for excellent discussion of key  
551 issues). We note here that regardless of the modelling approach taken, in order to engage with  
552 stakeholders effectively, it is extremely useful to have clear spatially realistic model output that  
553 enables individuals of different backgrounds to relate to the modelling process and its potential.  
554 Thus, as we develop more sophisticated and complex models for predicting and managing spread, we  
555 need also to focus on how we develop effective approaches for presenting the results of these models  
556 (including associated uncertainties) in an accessible form for those stakeholders with whom we are  
557 jointly developing the models, and for others who are likely to find the models useful.

#### 558 **4.9 Concluding remark**

559 We calibrated an IBM for the round goby, using spatial presence information from the invasion of  
560 the Gulf of Gdansk. Stakeholder involvement with question design provided both a preliminary  
561 answer and future research directions for the most important information. It is important that we  
562 encourage a culture of publishing work on the process of co-development of models, such that we  
563 can learn from one another's successes and failures. This will require more papers, such as this one,  
564 that are published at potentially earlier stages of model development and before models are  
565 necessarily ready for use to inform management action. In this instance, while short of being ready to  
566 inform management action, the model has helped to emphasize the requirement for investment in  
567 gathering greater empirical understanding of the depth at which round goby disperse. In the next part  
568 of the co-development modelling spiral (Parrot 2017) this will be gathered, and models will be built  
569 using this information, together with higher quality information on human-mediated dispersal  
570 pathways, to improve our ability to capture Baltic-wide patterns of invasion and to enable improved  
571 forecasts of future distribution under alternative management options to be developed. In general, we  
572 promote the increased use of models as a heuristic device for horizon scanning and risk assessment of  
573 invasive species and suggest that this utility may be at least as influential as their more traditional  
574 usage for informing management at the stage when they are well validated.

575

576

577 **5 Author Contributions**

- 578 1. **Conceptualization:** ES, JMJT, SCFP, PEH, JWB.  
579 2. **Formal analysis:** ES, SCFP  
580 3. **Investigation:** ES, SCFP, JMJT, PEH, JWB  
581 4. **Methodology:** ES, SCFP  
582 5. **Project administration:** ES, JMJT.  
583 6. **Resources:** JMJT.  
584 7. **Supervision:** JMJT.  
585 8. **Validation:** ES, SCFP  
586 9. **Visualization:** .ES  
587 10. **Writing – original draft:** ES, SCFP, JMJT, PEH, JWB  
588 11. **Writing – review & editing:** ES, SCFP, PEH, JWB, JMJT  
589

In review

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861

In review

862 Table 1 RangeShifter settings and parameter values for Gulf of Gdansk and Baltic Sea models

Parameter	Description	Gdansk	Baltic
	Cell-based landscape, cell size	2500m	2500m
	Rows x Columns	48 x 43	625 x 717
	Habitat codes (representing depth classes)	1 - 12	1 - 12
	Female-only model, no stage structure		
<i>K</i>	Carrying capacity (per ha) (all habitats)	10.0	10.0
<i>Rmax</i> **	Mean growth rate at low density	1.2, 1.4, 1.6	1.2, 1.4, 1.6
<i>bc</i>	Competition coefficient	1.0	1.0
<i>d</i>	Density-independent emigration rate	0.7	0.7
	Transfer model - SMS		
	Cost for depth layers above threshold	1	1
	Cost for depth layers below threshold	100000	100000
<i>PR</i>	Perceptual range (cells)	1	1
<i>PRmethod</i>	Perceptual range method	1	1
<i>DP</i>	Directional persistence	1.0	1.0
<i>SMconst</i> **	Per-step mortality risk	0.1, 0.2, 0.3, 0.4	0.1, 0.2, 0.3, 0.4
	Density-dependent settlement:		
<i>SO</i> **	maximum probability	0.4, 0.5, 0.6, 0.7, 0.8, 0.9	0.4, 0.5, 0.6, 0.7, 0.8
<i>alphaS</i>	slope	-10.0	-10.0
<i>betaS</i>	inflection point	1.1	1.1

863

864 \*\* For the Gulf of Gdansk, three levels of *Rmax*, four levels of *SMconst*, six levels of *SO* and eleven  
865 depth thresholds were applied in a fully factorial design yielding 792 simulations, each of which  
866 was replicated 100 times. For the Baltic Sea, a partially factorial set of 48 combinations of *Rmax*,  
867 *SMconst*, *SO* and four depth thresholds (selected from the Gulf of Gdansk model) were each  
868 replicated 100 times.

869

870 Table 2. An example of the effect of varying the depth threshold of dispersal on the accuracy of the  
 871 predicted population distribution, all other parameters being held constant. For all three model  
 872 assessment parameters, values over 0.8 represent a highly accurate model fit. The model threshold for  
 873 the cut-off (i.e. above which the predicted probability was regarded as presence, and below which as  
 874 absence) was 0.8. The three most accurate models are shaded in grey, with the best model text in  
 875 bold.

Depth Threshold (m)	Sensitivity	Specificity	Kappa	AUC
0-5	0.587	0.876	0.432	0.843
5-10	0.471	0.997	0.588	0.803
10-15	0.740	0.993	0.807	0.906
<b>15-20</b>	<b>0.888</b>	<b>0.976</b>	<b>0.862</b>	<b>0.959</b>
<b>20-25</b>	<b>0.915</b>	<b>0.964</b>	<b>0.848</b>	<b>0.970</b>
25-30	0.897	0.930	0.757	0.957
30-35	0.892	0.904	0.699	0.944
35-40	0.888	0.889	0.666	0.935
40-45	0.883	0.881	0.647	0.932
45-50	0.883	0.871	0.628	0.924
Below 50	0.901	0.689	0.379	0.836

876

877 **Figure Legends**

878 Figure 1. A schematic representation of the modelling process, from initial literature search to the  
879 proposed next steps. Model refinement and evaluation is iterative, reflecting the alterations that are  
880 constantly made to the model during the calibration process. Once refined, this model should then be  
881 reintroduced to stakeholders for further co-development.

882

883 Figure 2. Fit of the RangeShifter model for the Gulf of Gdansk: marginal mean values of  $\kappa$  (kappa) in  
884 relation to (A) the depth threshold class, (B) the maximum settlement probability, (C) the risk of  
885 mortality at each step taken during dispersal and (D) the maximum population growth rate.

886

887 Figure 3. Example model outputs from four different parameter combinations in the Gulf of Gdansk.  
888 Green cells represent a cell that was colonized by populations in each of the 100 repetitions (i.e. 1.0  
889 refers to 100% of repetitions). Model (A) represents the actual goby distribution, and therefore a  
890 perfect model output. Model (B) represents an example of an accurate model, whereas (C) represents  
891 model over dispersion and (D) under dispersion combined with dispersion into the wrong depths.

892

893 Figure 4. An example of the plots used to assess the accuracy of parameter combinations, using  
894 kappa, specificity and sensitivity measures. The accuracy measures vary from zero to one, in which a  
895 value of one represents a perfect accuracy measure and zero a poor one. The cutoff threshold  
896 represents the number of repeat simulations a cell was required to have been colonized, in order to be  
897 characterized as a presence in the final model evaluation, with 1.0 being 100% and 0.0 being 0% of  
898 repeats. (A) represents a set of parameter combinations that predict a goby presence close to that of  
899 the observed presence from the literature. In comparison, plots (B), (C) and (D) demonstrate a  
900 decrease in model accuracy.

901

902 Figure 5. Comparison between (A), the observed goby distribution available from the literature, and  
903 (B), an example predicted distribution obtained from the model. The color of the cell represents the  
904 presence of a population in a cell, and therefore its colonisation in a repetition. The presence varies  
905 from one to zero, with a value of one meaning the cell was colonized in every repetition and a value  
906 of zero meaning the cell was never colonized. The values along the axis represent the cell numbers of  
907 the landscape grid used in the modelling exercise, in which each cell size was 2.5km

Figure 1.JPEG

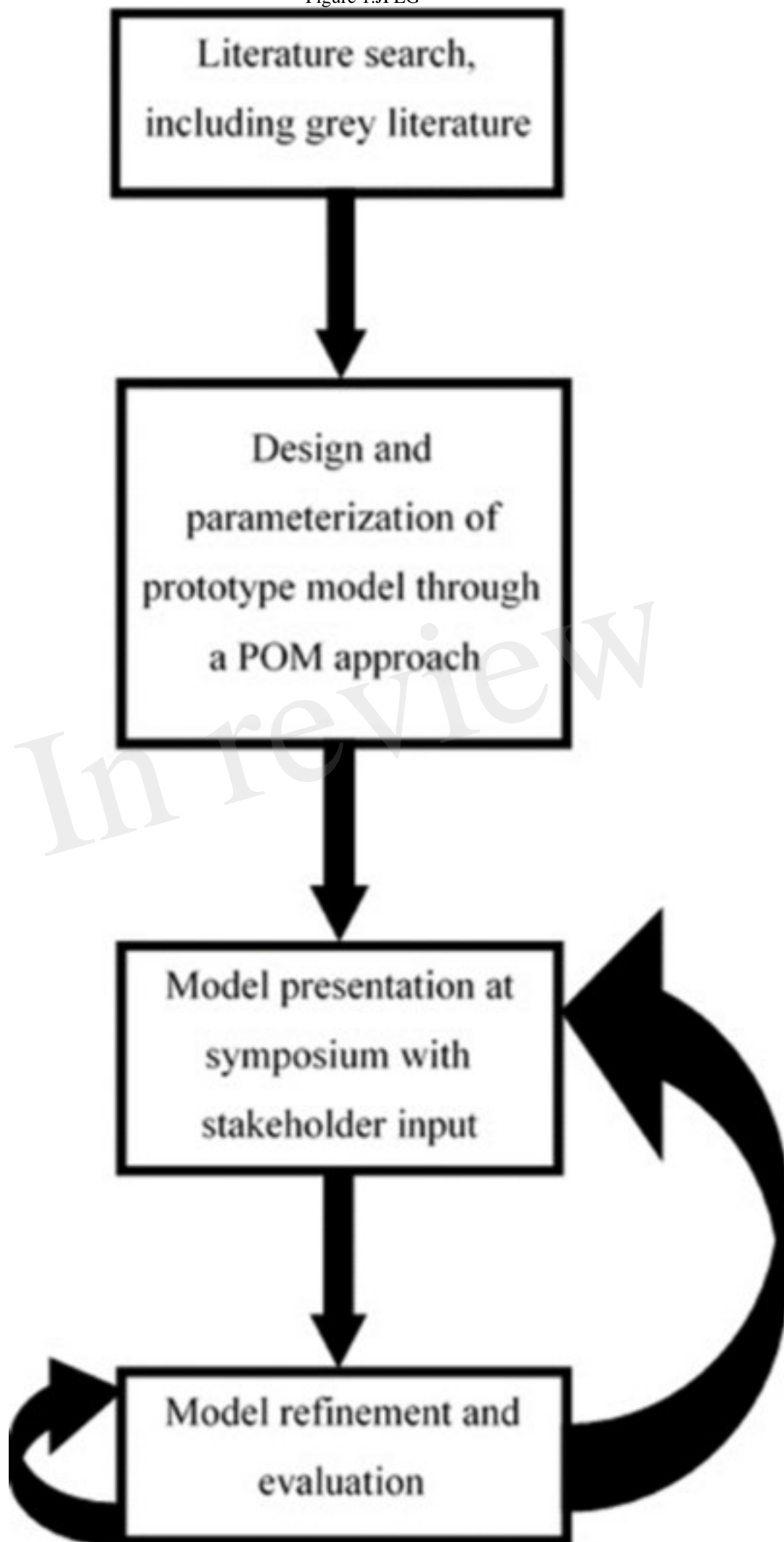


Figure 2.JPEG

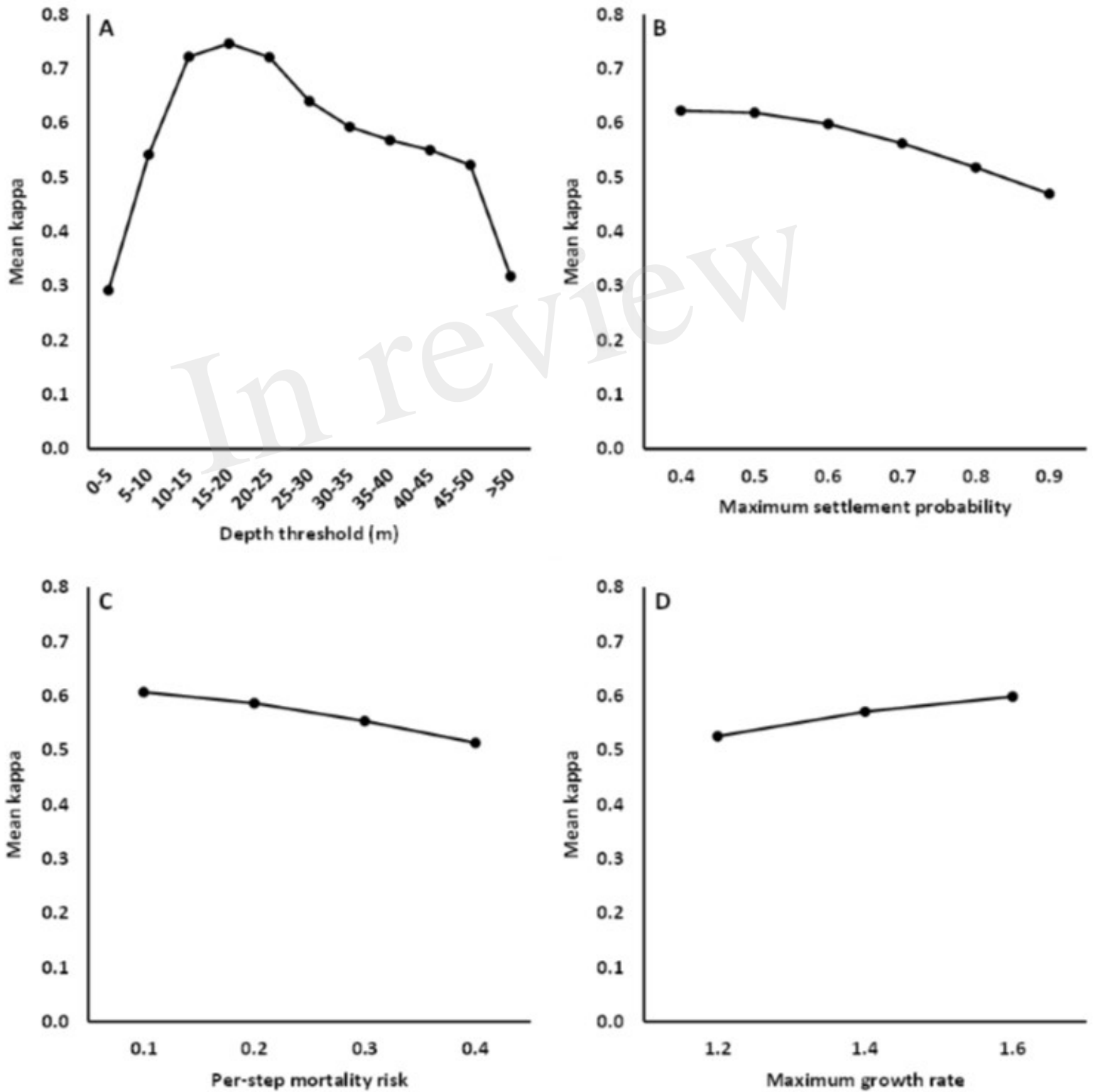
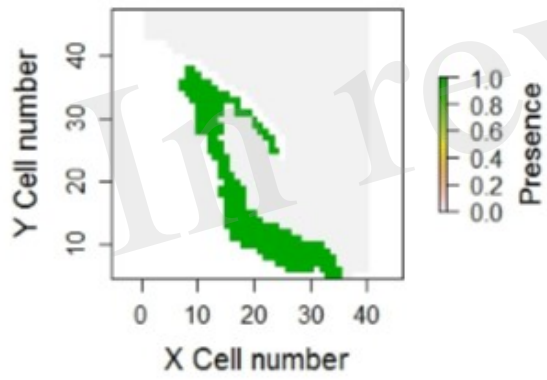
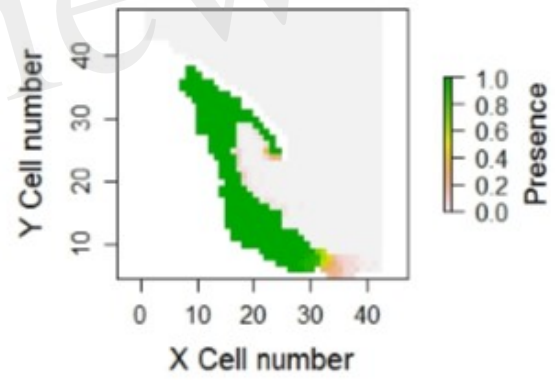


Figure 3.JPEG

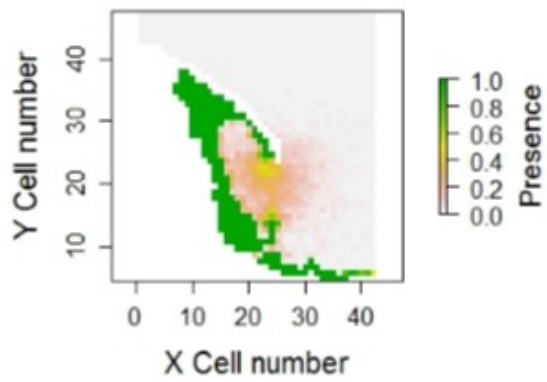
A



B



C



D

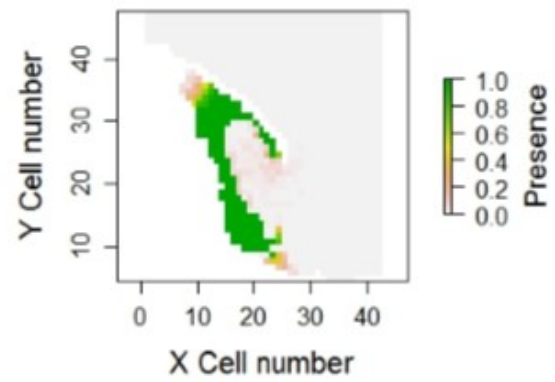
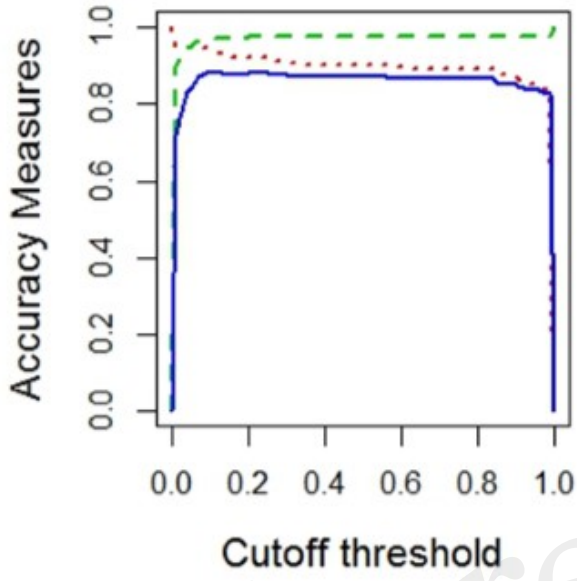


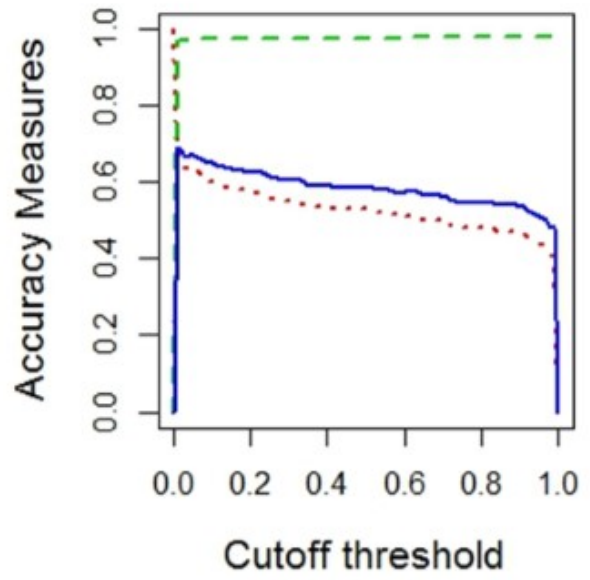
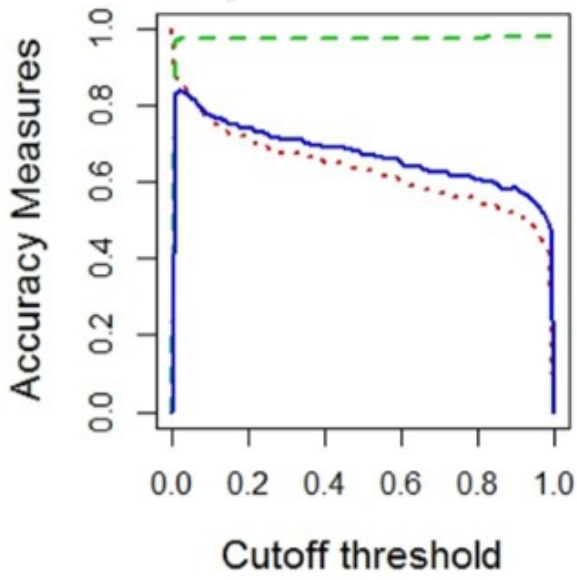
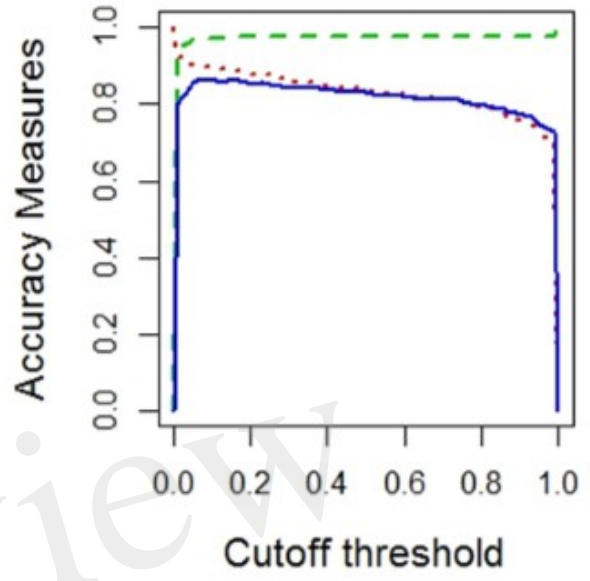


Figure 4.JPEG

A



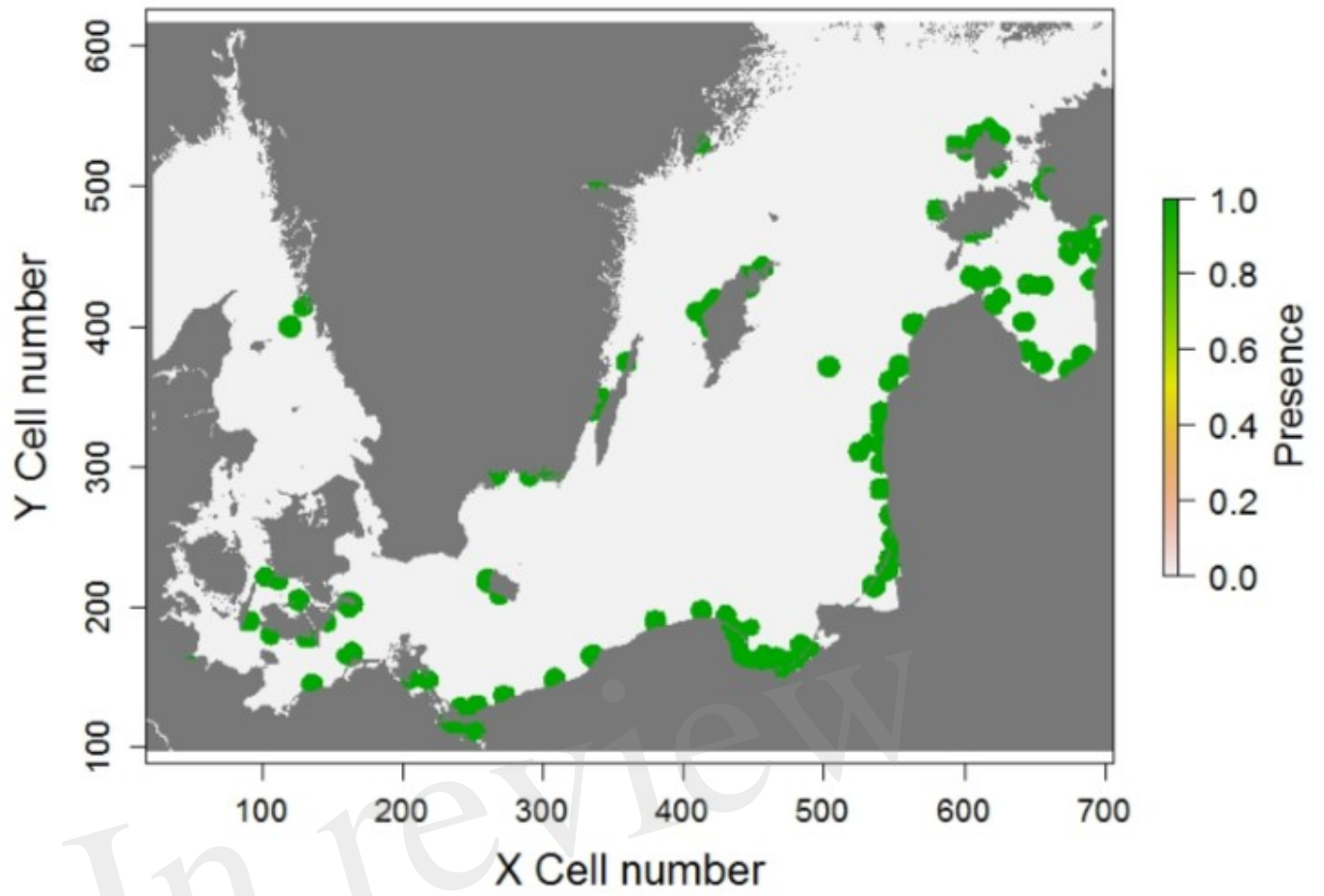
B



C

D

A



B

