Improving confidence in complex ecosystem models: The sensitivity analysis of an Atlantis ecosystem model

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Abstract :

There is growing interest in using mechanistic ecosystem models for ecosystem-based management, as they have the advantage of capturing both bottom-up and top-down processes as well as system interactions from food web structure, spatial constraints, and human activities. However, they have the disadvantage of requiring many parameters, many of which are unknown and must be estimated or calibrated to available data. Sensitivity analysis (SA) is an important part of simulation model development in order to understand model uncertainty and which parameters are more or less influential, but has been relatively neglected with Atlantis models due to the large number of parameters and long simulation run time. The Atlantis Eastern English Channel (Atlantis-EEC) model has been applied to investigate ecosystem dynamics and processes as well as fishery management scenarios. Here we present the results of a SA of growth, mortality, and recruitment parameters, which are parameters particularly difficult to measure and thus commonly tuned through model calibration. To manage the large number of parameters in the model, we used a Morris screening approach. This method can efficiently provide information on parameter main effects and interactions/non-linear effects with relatively few simulations. We performed an initial SA including all groups on 90 parameters, where we found that the most important drivers of system dynamics and biomass across groups were: (1) plankton growth and mortality rates and (2) top predator's fixed recruitment and juvenile mortality rates. We then performed a follow-up SA on a subset of 61 parameters, excluding top predators and plankton groups from the analysis. We found that all parameters were important for system stability, while individual groups' biomass were generally most influenced by their own parameters and a subset of benthic invertebrates. Nonlinear/interaction effects were widespread, demonstrating the prevalence of feedback loops in the trophic structure, and the importance of bottom-up effects and, to a lesser extent, top-down effects. The information gained from this SA provided a better understanding of the model structure. It also allowed us to make recommendations on the general Atlantis model calibration process as well as suggesting which parameters may be most important for propagation of uncertainty in model scenarios.

Highlights

► Sensitivity analysis of an end-to-end Atlantis model of the Eastern English Channel. ► Morris screening analysis with growth, mortality, and reproduction parameters. ► All parameters important for system stability. ► Bottom-up effects (plankton and some invertebrate parameters) stronger role than top-down.

Keywords : Sensitivity analysis, Morris screening, Atlantis, Eastern English Channel, Ecosystem model, Marine, Food-web

1   Introduction

Ecosystem models are growing in popularity in fisheries management in tandem with the rise of ecosystem-based management (EBM), in recognition of the complex ecosystem interactions that are rarely or only partially incorporated into traditional single-species models (Curtin & Prellezo 2010, Garcia et al. 2003, Pikitch et al. 2004, Skern-Mauritzen et al. 2016). In particular, end-to-end ecosystem models strive to include all major relevant processes ranging from mechanistic processes like hydrodynamics and nutrient cycling to food web interactions to human activity in one modeling framework (Fulton 2010). One particular end-to-end ecosystem model is Atlantis (Fulton et al. 2011, Audzijonyte et al. 2019), which has been implemented across at least 25 ecosystems around the globe with more in development (Weijerman et al. 2016). Atlantis models have been used to investigate different management strategies (Fulton et al. 2014, Kaplan et al. 2012, Weijerman et al. 2016), potential impacts of climate change on ecosystems (Griffith et al. 2012, Marshall et al. 2017, Nye et al. 2013, Ortega-Cisneros et al. 2018), and impacts of extreme events such as oil spills (Ainsworth et al. 2018, Morzaria-Luna et al. 2018). However, a drawback of end-to-end ecosystem models in general and Atlantis models in particular, is the sheer number of parameters combined with the long running time which makes robust calibration and evaluation of the model difficult (Arhonditsis and Brett 2004, Fulton 2010, Rose et al. 2010).

Due to these challenges, sensitivity analyses (SAs) of Atlantis models are rare and have tended to be local rather than global, meaning they explore small changes around the nominal values of parameters, e.g. the calibrated model, rather than a more complete exploration of the parameters space (Iooss & Lemaître, 2015). For example, Ortega-Cisnerosa et al. (2017) utilized a full factorial design but changed only the growth rate parameter for three plankton groups to three different values. Sturludottir et al. (2018) likewise examined parameters for plankton growth, as well as vertebrate recruitment, and oceanographic regime. Kaplan et al.

74 (2012) modified the fishing mortalities across all fleets and all species by five values as well

75 as tested removing spatial management. A more comprehensive SA was undertaken by

76 Hansen et al. (2019) involving four parameters for nine different groups, utilizing primarily a

77 one-at-a-time (OAT) design centered on baseline values. However, problems with a simple

78 OAT approach of varying one parameter while holding the rest constant at baseline values are

79 that is a local approach, thus it presumes model linearity and has also been shown to

80 inadequately explore the parameter space, particularly as the number of parameters increases

81 (Saltelli and Annoni, 2010). Additionally, a simple OAT SA cannot identify interactions

82 among parameters. On the other hand, the full factorial designs used for few parameters and

83 groups are not scalable to a comprehensive SA of an Atlantis model. Pantus (2007) used a

84 precursor to Atlantis to examine adaptive screening, where the experimental design is not pre-

85 specified, rather information from each experiment is used to design the next, thus adaptively

86 exploring the parameter space. However, adaptive screening generally assumes relatively few

87 parameters (i.e. 10-20% of the total) are responsible for most of the response variance and that

88 the effects of parameter interactions are small, which are increasingly violated the longer the

89 model is run for, and thus was not successful when running the model beyond 10 years.

90   In this paper, we take a global, screening approach to perform a more comprehensive SA

91 of an Atlantis model for growth, recruitment, and mortality parameters. We chose a Morris

92 analysis (Morris, 1991), the most complete screening method (Iooss and Lemaître, 2015) and

93 a recommended alternative to a simple OAT SA for models with long run times that preclude

94 more expensive variance based methods (Saltelli and Annoni, 2010). We propose that this

95 approach could be used for existing Atlantis models as well as facilitate performing a SA as

96 part of model development for new Atlantis implementations.

97   We performed the SA on the Atlantis Eastern English Channel (Atlantis-EEC) model,

98 which was developed to investigate the ecosystem dynamics and effects of fisheries in that

99 system (Girardin et al. 2018). Located between England and France, the eastern English

100 Channel is a shallow temperate continental shelf sea characterized by strong megatidal

101 hydrodynamics, vertical mixing present throughout the year, resuspension of particulate

102 matter, and significant freshwater and nutrient inputs from rivers, particularly the Seine River

103 (Bailly du Bois and Dumas 2005, Korotenko et al. 2013). Ecologically the system is

104 characterized by both high benthic productivity and a strong bentho-pelagic coupling. (Desroy

105 et al. 2003, Giraldo et al. 2017, Kopp et al. 2015). The species assemblages are structured by

106 the abiotic habitat and constitute a diversity of species (pelagic, flatfish, gadoids, skates,

107 catsharks, crustaceans, and cephalopods) exploited by different fishing fleets (Vaz et al. 2007,

108 Carpentier et al. 2009).

109   Our goals for the SA are 1) to better understand the internal structure and dynamics of the

110 Atlantis-EEC model, in particular, the effect on Atlantis model outputs of a change in

111 parameter inputs, 2) to provide information to aid calibration of new Atlantis models and

112 potential future automatic calibration efforts (e.g. Fennel et al. 2001), and 3) to determine

113 which parameters are most influential on Atlantis model output. However, a set of non-

114 influential parameters that can be fixed to nominal values is unlikely to be found for two

115 reasons: we evaluate parameters frequently tuned during calibration and thus already known

116 to be sensitive, and models with feedback loops, such as the trophic network in complex

117 ecological models, have high levels of interactions and thus all parameters can potentially

118 influence outputs (Pantus 2007). We hypothesize that the strong bentho-pelagic coupling in

119 the EEC may be reflected in the SA through bottom-up effects of parameters for benthic

120 producers influencing benthic and pelagic consumers.

2   Methods

2.1   Model

We performed the SA on the Atlantis-EEC model (Girardin et al. 2018), an implementation of the Atlantis framework (Audzijonyte et al. 2019, Fulton et al. 2011). Atlantis is an end-to-end ecosystem model comprising of biophysical, trophic food web, and fisheries components which uses a set of deterministic, mechanistic equations to represent the underlying processes of ecosystem dynamics and tracks nitrogen through the system (Fig. 1). The Atlantis-EEC model covers approximately 35,000 km^2 and is spatially structured by 35 polygons. Hydrodynamic forcing is from the integrated output of the MARS3D (Model for Applications at Regional Scales) numerical coastal hydrodynamic model (Baily du Bois and Dumas 2005), and freshwater and nutrient inputs from rivers were also included. The trophic network is represented by 40 functional groups: 21 vertebrate groups, 16 invertebrate groups (including 4 plankton groups), and 3 detrital groups (Table A.1). Vertebrate groups are each subdivided into 10 age classes, while invertebrate groups are considered as biomass pools, with the exception of cephalopods that have juvenile and adult stages. While the original model considered multiple fishing fleets organized by fishing activities or métiers, we opted to simplify this portion of the model by utilizing a single fishing fleet with constant fishing mortality per functional group.

2.2   Selected parameters

From the thousands of possible Atlantis parameters, we focused our efforts on the parameters most frequently tuned during the model calibration process (Audzijonyte et al. 2019): those governing growth (*C, mum*), mortality (*mL, mQ*), and recruitment (*BHalpha*, *BHbeta*, *KDENR*) applied across the vertebrate and invertebrate/plankton groups (Table 1). Even with this restricted list of parameters, the total number was still over 500 parameters across functional groups and age classes. Due to the long simulation running time (~4 hours

146 with an Intel i5-6440HQ 2.60 GHz processor), we thus examined ways to further reduce the

147 number of parameters examined. We now briefly describe how the parameters we selected

148 function in the Atlantis model, and we direct the interested reader to Audzijonyte et al.

149 (2019), particularly Supplement 1, for a more complete description of Atlantis model

150 equations, to Girardin et al. (2018) for how baseline parameter values were determined, and to

151 Appendix A for more details on the parameters in the SA.

152 *2.2.1*   *Growth/consumption parameters*

153 The parameters *C* and *mum* are used in the model to describe how much prey biomass is

154 consumed by each predator relative to what is available. Atlantis-EEC uses a modified

155 Holling type II functional response (Murray & Parslow 1997) to describe predation, and the

156 amount of biomass for each prey group (*i*) consumed by a predator (*j*) is expressed as a

157 consumption term, CR_{ij}:

158 $$CR_{ij} = \frac{C_j a_{ij} B_i}{1 + \frac{C_j}{mum_j} \sum_k (a_{kj} B_k E_{kj})} \tag{1}$$

159 where B_i is the biomass of prey *i*, a_{ij} is the availability of prey *i* to predator *j*, and E_{kj} is the

160 assimilation efficiency of prey *k* for predator *j*. Specifically, for predator *j*, C_j is the clearance

161 rate, or volume of water searched by an active predator or filtered by a filter feeder, and mum_j

162 is the maximum consumption rate or growth rate, which can be thought of as the inverse of

163 the handling time. The values for the parameters *C* and *mum* are strongly correlated as a

164 consequence of model construction, where an initial relationship between *C* and *mum* was

165 assumed and only adjusted slightly for some groups as necessary during the model calibration

166 process (Audzijonyte et al. 2019). We therefore opted to move these parameters together,

167 using the linear relationship *mum* = 3 * *C* for vertebrate groups and the baseline *mum* value

168 for invertebrate groups (Appendix A). This means that we are running SA on the "growth"

169 parameter, i.e. the combined effects of *C* and *mum*. For phytoplankton the growth equation is

170 different; *mum* is the maximum specific growth rate and is multiplied by the biomass and a

171 light limitation factor, thus we varied *mum* directly in this case (Appendix A).

172   For vertebrate groups with growth parameters defined per age classes, changing them

173 independently would result in ecologically unrealistic values and require many parameters.

174 Instead, for each vertebrate group i, we used a function of a single hyperparameter a_i based on

175 allometric relationships between the clearance rate at age x, $C_i(x)$, and the nitrogen dry

176 weight-at-age of an average individual, $W_i(x)$, as suggested by Audzijonyte et al. (2019):

177      $C_i(x) = a_i W_i(x)^{0.7}$, where the age x is $\mathbb{N} \in [1, 10]$.   (2)

178 We estimated a_i by fitting the function to the existing baseline values for C using least squares

179 (Fig. B.1, Table A.2) and manipulated a_i in the SA, thereby reducing 20 parameters per group

180 (10 age-class values for C and 10 age-class values for *mum*) parameters per group to 1.

181   *2.2.2   Asymptotic recruitment*

182   Two stock recruitment relations are used in Atlantis-EEC, Beverton-Holt (BH) for all the

183 fish functional groups and fixed recruitment (a fixed number of pups per adult) for mammals

184 and birds. The BH stock-recruit relationship is given by

185      $R = \frac{Sp \cdot BHalpha}{B + BHbeta}$ (3)

186 where Sp is the spawn produced, B is the group's total biomass, and *BHalpha* and *BHbeta* are

187 the BH α and β parameters. To examine its sensitivity, we chose to constrain the SA to the

188 asymptotic part of the equation (see Appendix A) and investigate only the asymptotic

189 recruitment parameter, *BHalpha*, leaving *BHbeta* fixed. For mammals and birds, recruitment

190 is defined as

191      $R = KDENR \cdot \rho \cdot N$ (4)

192 where *KDENR* specifies the number of pups per adult, ρ is the proportion of mature

193 individuals, and N is the total number of individuals. In this case, recruits are calculated as a

194 number of individuals and an initial size is specified to convert into biomass.

195   *2.2.3   Natural mortalities*

196   Most Atlantis model are calibrated to capture mortality through fishing and predation

197   mortality, however for some functional groups additional mortality can be used to mimic

198   other processes not explicitly modeled. For vertebrate groups this additional mortality is

199   represented as

200   $M = (mL + mQ\ N)\ N$ (5)

201   based on their numbers, N, and uses stage-specific (juvenile and adult) values, while for

202   invertebrate groups it is instead based on biomass, B,

203   $M = (mL + mQ\ B)\ B,$ (6)

204   where in both cases mL represents linear additional mortality and mQ represents quadratic

205   additional mortality. Non-zero mortality is classically used for invertebrate groups to enforce

206   density dependence due to space limitation. Therefore a quadratic mortality term suitable for

207   density-dependent processes is defined for invertebrates groups, while the linear mortality is

208   set to zero. Conversely, for top predators (e.g., large fish, marine mammals, sea birds) and a

209   few other fish groups with sources of mortality that are not included in the model through

210   predation and fishing, non-zero linear mortality, and rarely quadratic mortality, are used

211   (Table 1, Appendix A). For the 13 groups that have a value of zero for mortality in the

212   calibrated model, meaning all mortality is already accounted for by fishing and predation, the

213   outcome of changing the value to a non-zero value would be testing the effect of the

214   parameter outside the range of meaningful values, or, in effect, testing the impact of

215   decreasing the biomass of that group on the ecosystem. Thus, we did not include mortality

216   parameters with a baseline value of zero in the SA, and left their value fixed at zero.

217   ## 2.3   Defining parameter bounds

218   The approach described above thus allowed us to reduce the number of parameters to

219   examine in the SA to 90. To determine upper and lower bounds for each parameter in the SA,

220 we first considered if there were any data available to inform our choice of parameter bounds.

221 For the *BHalpha* parameter, we compiled 2018 ICES (International Council for the

222 Exploration of the Sea) stock assessment data for all species in the model for which stock

223 distributions in the assessment encompassed the EEC (Table A.3) and assembled the time

224 series of estimated recruitment and spawning stock biomass (SSB) for each species. For each

225 species, only the years with SSB above B_{lim}, were retained (as we focused on the asymptotic

226 part of the stock recruitment relationship). Then, for each year, we calculated the recruitment

227 error, or the percentage difference in recruitment relative to the average recruitment, over the

228 entire time series. The 5th and 95th percentiles across all the years were used as the upper and

229 lower bounds for the percent change from the baseline *BHalpha* value in the calibrated

230 Atlantis-EEC model. For functional groups with no assessment available, the same method

231 was applied using the ICES data for all species combined.

232   For other parameters (i.e., growth, mortality, and non-Beverton-Holt recruitment), data to

233 set parameter bounds was unavailable, and we used the upper and lower bounds of -50% and

234 +100% around the baseline parameter value (Girardin et al. 2018, Table A.4). These bounds

235 were based on an examination of parameter ranges used in the small number of existing SAs

236 for Atlantis models (Hansen et al. 2019, Kaplan et al. 2012, Ortega-Cisnerosa et al. 2017,

237 Sturludottir et al. 2018), as well as a small series of test simulations on key groups identified

238 by Girardin et al. (2018) to explore model outcomes of different magnitudes of parameter

239 value changes. In particular, we wanted to avoid parameter values that would frequently lead

240 to group extinctions which was a problem with larger decreases from parameter baseline

241 values like -75%.. The doubling and halving of these values allows us to account for the

242 asymmetric nature of increasing and decreasing by a fixed percentage and was verified in

243 some preliminary simulations.

2.4   Sensitivity analysis plan

244

245   We used a Morris screening analysis (Morris, 1991) as a feasible approach given the

246 number of parameters we had to analyze, the long-running time of the simulation, and our

247 access to Datarmor, Ifremer's supercomputer. The advantage of the Morris method is that one

248 obtains information for both the main effects/linear effects and the non-linear effects and/or

249 interactions, although one is not able to distinguish between non-linear effects and

250 interactions like more comprehensive decomposition-of-variance methods. With the Morris

251 method, the parameter space is turned into a grid by discretizing the space into a user-defined

252 number of subintervals. The more subintervals, the finer the evaluation of non-linearities will

253 be, though possibly at the cost of a thorough exploration of the space. One follows a set of

254 trajectories through parameter space. Each trajectory starts with a random point in parameter

255 space, and then each step consists of moving one parameter in turn. From a set of trajectories,

256 the elementary effects (EE) can be calculated, that is, the changes in the output measure for a

257 relative change in the input parameter. The standard set of metrics calculated from the

258 elementary effects (Morris, 1991) are μ_i, the mean of the EE (the average change in output

259 across all changes to the parameter i) which gives the sensitivity of output to input i due to all

260 first- and higher-order effects, and σ_i, the standard deviation of EE (the variance in how much

261 the output changes in response to changes in the parameter i) which indicates interactions

262 and/or non-linearities. In addition, the metric μ_i^* is similar to μ_i, except the absolute value is

263 first applied to the EE before the mean is taken (i.e., the average absolute value of change in

264 output across all changes to parameter i), which is useful for the sensitivity of the parameter

265 independent of cancelling out effects if the direction of the change in output is not always

266 consistent (Campolongo et al., 2007). Furthermore, we used the intervals of σ/μ^* established

267 by Sanchez et al. (2014) to classify parameter effects into different zones: almost linear (σ/μ^*

268 < 0.1), monotonic (0.1 < σ/μ^* < 0.5), almost-monotonic (0.5 < σ/μ^* < 1), and markedly non-

269 monotonic or with interactions (σ/μ^* > 1), and these zones are demarcated in the figures.

270   We performed two Morris SAs, both of which used 50 trajectories (at the high end of

271 recommended ranges for the number of trajectories; Saltelli et al. 2004, Campolongo et al.

272 2007), 8 levels for each parameter (including upper and lower bounds with values uniformly

273 distributed between them), and the recommended grid jump of 4 (how many levels the

274 parameter changes for a step in the trajectory). The 50 trajectories were selected from a

275 candidate set of 200 trajectories as the most orthogonal and thereby best spanning the

276 parameter space (Campolongo et al., 2007). Because computing resources are often limited

277 and other models have even longer running times, we also considered the impact of using

278 fewer trajectories (10, 20, 30, and 40 trajectories) by performing a bootstrap test with 100

279 sampled trajectory sets for each size to compare with the results from all 50 trajectories. We

280 compared the estimation of μ^* and σ for the top five parameters for as well as the agreement

281 in order of the top ten parameters between each subset and the full trajectory set.

282   We created the SA plan and calculated the resulting EE using the `morris` method in the

283 'sensitivity' R package (Iooss et al. 2019). We ran the full set of simulations on the Datarmor

284 supercomputer. We performed an initial SA (SA1) with the full parameter set of 90

285 parameters with 4550 simulations. From the results of SA1, we first investigated the crashing

286 simulations (9 trajectories), then analyzed the Morris metrics (μ, μ^*, σ) for the non-crashing

287 (i.e., complete) trajectories (41 trajectories). Based on the results of that analysis, we

288 determined that the parameters implicated in the crashing simulations and those with the most

289 important effects were the parameters of the fixed-recruitment top-predator groups and the

290 plankton groups (see Table A.4 for a complete list of parameters in each analysis and values

291 for each level). Thus the complete SA is described in three steps: 1) analysis of parameter

292 values and combinations with extreme effect, i.e. those that crash the model in SA1 2)

293 analysis of parameter effects for the trajectories without crashing simulations for SA1, and 3)

294 analysis of parameter effects in SA2 for the core food web excluding top predator and

295 plankton groups.

296   For all the analyses, we ran the simulations for 100 years, enough time for the calibrated

297 model to reach a steady-state, and then took as outputs the average biomass for the last 10

298 years of the simulation (years 91-100) for the 40 groups in the model. Note that not all

299 parameter combinations in the SA allow the system to reach a steady-state, and we also

300 analyzed the system stability as discussed below. For the 21 vertebrate groups, we also

301 examined the average number of individuals for the last 10 years of the simulation. These

302 outputs are used during calibration and offer good insight into the system state. In order to

303 summarize the effects of a parameter for the system in addition to its effect on each group

304 individually, we examined total biomass (excluding detrital and bacteria groups) and total

305 numbers for vertebrates. Note that this does weight more massive or abundant groups higher,

306 but total biomass/numbers is a commonly used metric and we also report results for individual

307 groups. Finally, we also looked at the stability of the system by examining how many groups

308 achieved equilibrium in the last ten years of the simulation, an important criterion for model

309 calibration. Any group that had a biomass < 0.1 t (functionally extinct) in the last ten years

310 was defined to be non-stable, as well as all groups in crashing simulations. For the rest, we fit

311 a linear model to the last ten years of biomass values for each group, and defined stability as

312 the regression line staying within ±5% of the mean biomass of the last ten years. This criteria

313 is more flexible than simply examining the significance of the slope coefficient (possibly

314 significant even for very small changes in biomass) or a strict window approach (frequently

315 not met by plankton and recycling groups which exhibit cyclic behavior even at equilibrium),

316 but still detects groups that continue to increase or decrease at the end of the simulation. Note

317 that we are simply looking for any steady-state, not that the groups reach equilibrium at a

318 specific value as in model calibration. We examined the influence of parameters on system

319 stability by calculating the Morris metrics on the output of the percent of groups stable in the

320 simulations. All analysis was performed using R 3.6.0 (R Core Team 2019). We used Atlantis

321 version trunk rev 6290.

3 Results

3.1 Step 1: Crashing simulations and stability in SA1

324 *Crashing simulations*. Of the 4550 simulations in SA1, 244 simulations crashed, affecting

325 9 of the trajectories. In Atlantis, simulations crash when any flux reaches a fixed threshold. In

326 our simulations, the cause of the crash was the same in all cases, an accumulation of too much

327 detrital matter to be processed in the epibenthic layer, which was due to a population

328 explosion in some groups and extinction in others. We determined that the crashes were due

329 to a combination of low juvenile linear mortality rate and high reproduction rate for toothed

330 cetaceans (CET) (Appendix B). With no density dependence or trophic control for this top

331 predator, which uses fixed recruitment, this leads to a population explosion.

332 *Stability*. An average of 69% (range 0-95%) of groups were stable across all simulations

333 (including those that crashed which were considered unstable) , and in 6% of simulations

334 there were no groups stable (Fig. 2). Like with the results for the crashing simulations,

335 cetacean juvenile mortality and recruitment rates were extremely influential for determining

336 system stability (Fig. 3c). The juvenile mortality and recruitments rates for seabirds (SB) and

337 seals (SXX) were also influential for system stability, as were phytoplankton (PP) and

338 zooplankton (ZOO) growth rates.

3.2 Step 2: Trajectories without crashes in SA1

340 Parameters that had strong main effects (high μ^* values) also tended to have strong

341 interaction and/or nonlinear effects (high σ values), both for total biomass and numbers (Fig.

342 3) and for individual groups (Fig. B.2). Generally seabirds, seals, and especially toothed

343 cetacean parameters as well as those of phytoplankton and zooplankton had the strongest

344 effects (Fig. 3), including important effects across many groups (Figs. 4, B.2). While all

345 parameters influenced at least one group's biomass, most groups' biomass was strongly

346 affected by a small subset of parameters (Figs. 4, B.2). Recruitment parameters, generally that

347 of the same group, were also important to explain individual vertebrate groups' numbers (Fig.

348 B.3, B.4, Appendix B).

349   We next discuss the effects of the most influential parameters, those of plankton and fixed-

350 recruitment top predators, on biomass. For all other groups, the parameter effects can be

351 broadly divided into three categories 1) those with moderate to strong effects across many

352 groups' biomass, primarily consisting of the growth and mortality rates for benthic

353 invertebrates; 2) those with strong effects on their own group but no other groups, which was

354 true for many parameters, generally growth and mortality rates for invertebrates and growth

355 and recruitment rates for vertebrates; and finally, 3) those with weak or little effect, mostly

356 vertebrate mortality rates (other than top predators with fixed recruitment), top predator

357 growth and adult mortality rates, and some primary production parameters (Fig. 4). These

358 other groups are examined in more detail in SA2.

359   *3.2.1   Plankton production parameters.*

360   The growth rate parameters of phytoplankton and zooplankton had strong effects on nearly

361 all groups' biomass, demonstrating bottom up effects (Fig. 4, Fig. B.2). The direction of the

362 effect was consistent: increasing the phytoplankton growth rate had a strong positive effect,

363 and that of zooplankton a strong negative effect (Fig. 4, center panel). In fact, the only

364 groups' biomass not strongly influenced were the bird and mammal top predators using fixed

365 recruitment that were driven solely by their own parameters, as well as cephalopods (CEP)

366 and refractory detritus (DR) biomass, which were mostly affected by seabird and cetacean

367   parameters. The effects of zooplankton mortality rates on biomass were also broad, though

368   less consistent in direction of effect within some groups (i.e. μ small compared to μ^*,

369   indicating the sign of the effect varied across simulations for that group). Carnivorous (ZOC)

370   and gelatinous (ZOG) zooplankton parameters, as well as phytoplankton's mortality

371   parameter, generally had little effect across groups' biomass. The effects of lower trophic

372   level parameters on was stronger on biomass than vertebrate numbers (Appendix B).

373   *3.2.2   Top predator parameters.*

374   The recruitment and mortality parameters of top predators with fixed recruitment (seabirds,

375   seals, and particularly toothed cetaceans) strongly influenced the biomass of nearly all groups

376   (Fig. 4, B.2). The only groups relatively unaffected by these parameters were each other's

377   biomass, and that of planktons and scallops (SCE). Furthermore, these effects are likely

378   understated due to the removal of trajectories with crashing simulations, which were found to

379   be due to specific toothed cetacean parameter combinations. This interplay between

380   parameters could play a role in the strong interaction/nonlinear effects (large σ) observed. The

381   direction of the effect (μ) varied by group. While model crashes were only observed from

382   toothed cetacean parameters with low mortality and high recruitment, some combinations of

383   sea bird and seal parameters also caused their biomass to increase exponentially in some

384   simulations and correspondingly many of their prey species went extinct. The juvenile

385   mortality parameter appears to be the most sensitive. In the case of juvenile toothed cetacean

386   mortality parameters, any increase above the baseline value always resulted in their own

387   extinction, while decreases from the baseline value resulted in a range of outcomes from

388   extinction to exponential growth. The situation was similar but less extreme for sea bird and

389   seal parameters, and the direction of the effect was less consistent. The effects of these

390   population explosions and resulting extinctions can also be seen through the importance of top

391   predator recruitment and mortality parameters on vertebrate numbers (Appendix B).

392

3.3   Step 3: Core food web in SA2

394   Removing the most influential parameters from SA1 (those of top predators with fixed

395 recruitment and plankton, Table 1) focused the SA on the parameters for the core of the food

396 web with the system generally in a stable state, i.e. without the extinctions and exponential

397 growth that characterized many simulations in SA1. For total biomass of the system, the

398 growth rates and, to a lesser extent, mortality rates of benthic invertebrates had the strongest

399 influence, while total vertebrate numbers were primarily driven by the parameters of the most

400 numerous groups (Fig. 5). We next discuss the influential parameters for system stability and

401 groups' biomass in more detail. There were fewer influential parameters for vertebrate

402 numbers than for biomass, and a group's own recruitment rate was the most important

403 (Appendix B).

404   *3.3.1   Stability.*

405   Stability was considerably higher in SA2 than SA1 with an average of 95% (range 80-

406 100%) groups stable, and all 40 groups were stable in12% of simulations (Fig. 2). With the

407 narrower range of stability in SA2, there was a gradient of effect of the various parameters on

408 the system stability, though deposit feeder mortality was the most influential while Clupeidae

409 (CLU) quadratic mortality the least (Fig. 5). Thus, all the parameters had some influence on

410 the stability of the system in non-linear and/or interacting ways.

411   *3.3.2   Biomass.*

412   The most influential parameters on total biomass were the growth rates of benthic

413 invertebrates such as echinoderms (ECH), bivalves (BIV), deposit feeders (DEP), scallops,

414 and suspension feeders (SUS) (and to a lesser extent some of these groups' mortality rates)

415 (Fig. 5), and these same parameters are also important across numerous individual groups'

416 biomass (Figs. 6, B.5). The biomasses of plankton and recycling groups, which did not have

417 their parameters modified in SA2, were strongly influenced by nearly every parameter, while

418 the direction of effect for these parameters was generally inconsistent (Fig. 6) and with strong

419 non-linear/interaction effects (Fig. B.5). Groups differed in how linear or non-linear the

420 impact of influential parameters was on their biomass, likely due to different positions in the

421 food web (Fig. B.5). For example, the impact of most parameters was clearly non-monotonic

422 or with interactions/non-linearities for the biomass of cephalopods, echinoderms, lobsters

423 (LBE), Pollack (POL), suspension feeders, and whelk (WHE). On the contrary, the biomass

424 of pelagics and their predators, that is, Clupeids, mackerels, sparidae, cetaceans, sea birds and

425 seals, responded to parameters in a more linear way, probably because of the weaker

426 influence of benthic compartments.

427 Most groups' biomass was primarily influenced by between two and ten parameters, their

428 own and those of several other groups (Figs. 6 and B.5). The other group's parameters were

429 generally those of the more abundant vertebrate and invertebrate groups, and were frequently,

430 but not always, prey of the affected group. Groups' biomass being influenced by their

431 predators' parameters, on the other hand, was more rare, and only tended to occur with the

432 biomass of groups at the lowest tropic level. Finally, there were a handful of groups affected

433 almost solely by their own parameters (Clupeidae, mackerels (MAC), scallops, and sharks

434 (SHK)). These groups (except for sharks) have a plankton/detritus diet in common, the

435 parameters of which were not changed in SA2. However, suspension feeders share a similar

436 diet but their biomass was also influenced by their predators' parameters.

437 The food web interactions can be seen through the direction of the effect (Fig. 6, μ

438 columns). For example, bivalve's growth rate had a generally positive impact on other

439 groups' biomass, except for phytoplankton (prey) and suspension feeders (competition).

440 Similarly, deposit feeder's growth rate had a generally positive effect on other groups'

441 biomass except for their prey and competitors, while the growth rate of echinoderms almost

442 universally negatively affected other groups' biomass (except phytoplankton). For nearly all

443 vertebrate groups' biomass, as well as larger invertebrates like shrimp (SHP), lobsters, and

444 cephalopods, the groups' parameters strongly influenced that same group's biomass, but had

445 little effect on the biomass of other groups (excepting plankton and recycling groups

446 influenced by all or most parameters as noted above). The parameters for Clupeidae, and to a

447 lesser extent whiting (WHG), both of which are numerous in the system, had a strong

448 influence on the biomass of top bird and mammal predators, for which they are an important

449 food source, but little influence on their benthic prey. Interestingly, only seal biomass was

450 also influenced by a number of other fish groups' parameters, reflecting diet differences.

451 Mortality parameters were generally less influential than growth rate.

3.4   SA 1 and SA2 summary

453   To summarize the most important results of the SA, strong main effects of parameters

454 tended to go hand in hand with strong interaction and/or nonlinear effects, and all parameters

455 influenced system stability. The strongest effects were due to fixed recruitment top predators

456 (particularly the juvenile mortality and reproduction rates) and plankton (particularly

457 phytoplankton and zooplankton growth rates). There was also high sensitivity to benthos

458 parameters, particularly growth rate, across nearly all groups. Each group's biomass tended

459 to be highly sensitive to 2-10 parameters, their own and more commonly their prey than their

460 predators. Vertebrate numbers were most often linearly influenced by a group's own

461 recruitment rate.

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3.5 Number of trajectories

3.5.1 SA1.

In general, μ*and σ estimates for the most influential parameters for most groups in SA1 were robust with respect to the number of trajectories (Figs. B.8, B.9). Exceptions were parameters affecting fixed-recruitment top predators, phytoplankton, bacteria, and detrital groups, where smaller estimations of effect size were likely with fewer trajectories. Furthermore, interaction/nonlinear effects of the recruitment and mortality parameters of fixed-recruitment top predators were smaller for numerous groups. Perhaps more important is the relative ordering of the most important parameters, which was in agreement on average of 82% for μ* and 72% for σ even for only 10 trajectories. Across all groups and numbers of trajectories, the agreement in ordering the most influential parameters was higher for μ*than σ, demonstrating the increased difficulty in estimating the non-linear/interaction effects (Fig. B.10).

3.5.2 SA2.

The error with estimating SA metrics with fewer trajectories was greatly reduced in SA2 with greater system stability (Figs. B.11, B.12). The agreement for ordering the most influential parameters was generally quite good, except for some bacteria, detrital, and plankton groups whose parameters were not included in SA2 (Fig. B.15). Across all groups, the agreement averaged 87% for μ and 80% for σ for 10 trajectories, increasing to 95% and 93% respectively for 40 trajectories.

4 Discussion

While SA has long been recognized as an important part of ecological model development (Scott 1996, Shaeffer, D.L. 1980, Thornton et al. 1979), it has generally been neglected for

489 Atlantis models (but see Hansen et al. 2019, Kaplan et al. 2012, Ortega-Cisnerosa et al. 2017,

490 Sturludottir et al. 2018) due to computational challenges with long run times and technical

491 challenges with the large number of parameters. We demonstrate the feasibility of a large-

492 scale SA on a complex ecosystem model and illustrate a number of ways to accommodate a

493 large number of parameters. First, even if computationally feasible, the sheer number of

494 parameters in Atlantis means a complete SA on all parameters would be uninterpretable, and

495 thus some pre-selection of parameters must take place. In this paper we focused on the

496 growth, recruitment, and mortality parameters most frequently adjusted during calibration, but

497 other approaches are possible, such as examining the diet matrix (Morzaria-Luna et al. 2018),

498 choosing parameters to determine where the most improvement could be found through

499 improved data collection (LeBauer et al. 2013), or with an eye to uncertainty analysis to

500 quantify the impact of parameter uncertainty on output variability (Cariboni et al. 2007).

501 Another important technique we utilized was collapsing many-valued age-structured

502 parameters with a function utilizing a hyperparameter that was manipulated in the SA.

503 Additionally, we moved correlated parameters together, which both reduced the number of

504 parameters to consider in the SA and maintained ecological coherence among the set of

505 parameters. Using a Morris screening SA allowed us to perform a global analysis with

506 relatively few simulations and thus differentiate effects as approximately linear, monotonic, or

507 nonlinear/interactions. Finally, like Morzaria-Luna et al. (2018), our analysis would not have

508 been possible without access to supercomputer resources, and we suggest these resources are

509 generally essential to carrying out SAs of complex ecosystem models. Furthermore, we

510 suggest that these advances imply that new Atlantis model implementations should

511 incorporate SA in the model development, as suggested by modeling guidelines (Cariboni et

512 al. 2007) and which have already started being carried out (Hansen et al. 2019).

4.1   Interesting insights about the Atlantis-EEC model.

Our results highlight a difficulty, raised by Patus (2007), that finding parameters that are less sensitive and thus can be ignored in models that contain cyclic feedbacks like Atlantis is perhaps unrealistic. Our results generally confirm this, bearing in mind that we selected the parameters most frequently tuned during calibration and thus already known to be sensitive. There could certainly be insensitive parameters among the many remaining parameters in Atlantis. While there are perhaps only a handful of more influential parameters for any given group, the effects were almost never strictly linear and frequently show evidence of nonlinear/interaction effects. In addition, every parameter was influential for at least one group, illustrating why all parameters were important for system stability. Although in SA1 there were some growth and mortality parameters that had little effect on biomass across all groups (Fig. 4) and a subset of those that had little effect on numbers (Fig. B.3), these parameters did still affect system stability. Furthermore, for those parameters that were also included in SA2, all appear to influence biomass, at least interact with numbers, and especially contribute to system stability (Fig. 5). With that caveat, the least influential parameters were adult mortality and growth rates for vertebrates with fixed recruitment, juvenile mortality rate for some vertebrates with BH recruitment, cephalopod growth rate, growth and mortality rates for gelatinous zooplankton, and phytoplankton mortality rate. The lack of influence of the phytoplankton mortality rate was particularly striking given the strong effects of phytoplankton growth rates and of both growth and mortality rates for zooplankton.

The importance of both top-down and bottom-up effects is evident with the most influential parameters. These include those of top predators with fixed recruitment (i.e. toothed cetaceans, sea birds, seals) and illustrate a structural issue with the Atlantis-EEC model. These top predators are not density-dependent either through their recruitment or mortality, allowing them to increase exponentially. That is, they reproduce through pups

538 rather than a self-limiting BH recruitment function, and, like other vertebrates in the model

539 with the exception of Clupeidae, they have no quadratic mortality. Furthermore, they are not

540 impacted by the fishery and experience little predation themselves. These groups are thus very

541 sensitive to their parameterization, particularly the reproduction rate and the juvenile

542 mortality rate, which can quickly shift the population from extinction to unrealistic

543 exponential growth. To dampen these effects, different values of starvation mortality,

544 currently underutilized in Atlantis models (Pethybridge et al. 2019), should be explored in the

545 Atlantis-EEC model to better represent competition among top predators and the effects of

546 limited food. In addition, unfished top predators modeled with Atlantis could be controlled by

547 a quadratic mortality term and/or a modified fecundity using the ratio of reserve to structural

548 nitrogen. Additionally, the lack of starvation mortality likely explains the decoupling

549 observed between biomass and numbers in vertebrates: biomass and number do not react the

550 same way. Numbers are primarily determined by a group's own reproduction parameter (and

551 top predator parameters in SA1 which drove extinctions), while biomass is determined by

552 individual weights that depend on growth rates and prey abundance. Thus, it is possible to

553 have large numbers of individuals at below normal weights who do not die at increased rates.

554 This makes numbers less sensitive to trophic network effects than biomass.

555   Bottom-up control was emphasized by the other extremely sensitive parameters, the

556 growth rates of phytoplankton and zooplankton. Hansen et al. (2019) also found the strongest

557 effects in response to changing the growth rates for zooplankton groups. While the SA

558 performed by Ortega-Cisneros et al. (2015) only included the growth rate of phytoplankton

559 and zooplankton, they also observed large effects throughout the food web, particularly on

560 phytoplankton and zooplankton themselves and small pelagic fish, though large pelagic fish

561 were less sensitive. Sturludottir et al. (2018) found a strong response to phytoplankton growth

562 rate but not macrozooplankton growth rate, though other zooplankton groups were not

563 included. This sensitivity to plankton dynamics has also been found in other ecosystem

564 models (Steele & Ruzicka 2011), reflecting the importance of both primary producers to

565 bottom-up forcing, as well as the role of zooplankton in linking trophic levels (Carlotti &

566 Poggiale 2010, Rose et al. 2010). However, this importance of plankton dynamics also

567 highlights a challenge of parameterizing end-to-end ecosystem models given data limitations

568 for plankton communities. This is further complicated by the fact that, for reasons of the

569 relatively coarse spatiotemporal scale, the plankton dynamics are represented with less detail

570 in comparison with existing NPZ models (Baretta et al. 1995, Butenschön et al. 2016, Kishi et

571 al. 2007, Schrum et al. 2006).

572   The universal positive effect of a higher phytoplankton growth rate on all groups is

573 unsurprising, but the opposite universally negative effect of a higher zooplankton growth rate,

574 even for zooplankton itself, is striking and counterintuitive. There are several possible

575 reasons. First, Atlantis does not explicitly model the larval stage for fish (the option for

576 phytoplankton and/or zooplankton abundance to affect recruitment is not utilized in the

577 Atlantis-EEC model), which depend heavily on zooplankton (Last 1978a, 1978b). However,

578 zooplankton makes up the majority of the diet (80-99%) for mackerels, Clupeidae (which

579 both migrate outside the system), carnivorous zooplankton, and gelatinous zooplankton, as

580 well as a significant portion of the diet (5-20%) for Mulgilidae, shrimps, and zooplankton

581 itself. More likely, a higher zooplankton growth rate causes the zooplankton to increase and

582 consume all the phytoplankton which then cannot regrow (i.e., the extreme case of Lotka

583 Voltera dynamics: no oscillation). This would cut off the pelagic pathway, and could cut off

584 the benthic pathway in the ecosystem, as many benthic invertebrates are planktivores, and

585 phytoplankton is particularly important in the diet of suspension feeders and scallops. Finally,

586 an increase in the zooplankton growth rate might divert energy from the detrital-benthic

587 pathway by consuming plankton that would otherwise die and so could contribute the

588 negative response seen across groups. Even in relatively simple NPZ models, where multiple

589 functional forms are used for zooplankton grazing (e.g. Eq. 1), this relationship is known to be

590 problematic and a strong determinant of system dynamics (Franks 2002).

591   Examining the direction of the effects (μ) of different parameters elucidates the complex

592 food web dynamics captured in the Atlantis-EEC model. The inconsistent direction of effects

593 of top predator parameters demonstrates indirect effects, that is, negative effects on their

594 prey's biomass, but positive effects on the biomass of their prey's prey. While fixed-

595 recruitment top predators do appear to structure the entire ecosystem in the sense of a trophic

596 cascade (Paine 1980, Ripple et al. 2016) in SA1, this is not the case under more stable

597 conditions in SA2 where we saw weaker effects of upper trophic-level predators' parameters

598 on other groups' biomass in the system. For example, the parameters of the more abundant

599 predators, such as whiting and other Gadidae (GAD), had little effect on their benthic prey's

600 biomass. Rather, the most influential parameters were those of the invertebrate benthic

601 groups, particularly the growth rates, thus confirming the bottom-up dynamics of the system.

602 The SA thus supported our hypothesis of important effect from benthic parameters based on

603 the strong bentho-pelagic coupling in the system and this would be interesting to confirm with

604 a more thorough validation analysis of the model. The EEC ecosystem is a shallow

605 continental shelf sea driven by benthic productivity (Dauvin & Desroy 2005, Desroy et al.

606 2003, Garcia et al. 2011). The food web structure is comprised of benthic and pelagic

607 pathways, and the benthic-pelagic coupling increases in shallow coastal areas where both

608 benthic and pelagic sources are easily available (Kopp et al. 2015). Benthic sources make up

609 the majority of the diet for all trophic groups, ranging from just over 50% for even pelagic

610 piscivorous fish to 100% for groups such as benthic predators and demersal piscivorous fish

611 (Giraldo et al. 2017). Furthermore, this importance of benthos to EEC ecosystem functioning

612 has also been found with a variety of modeling approaches (Daskalov et al. 2011, Girardin et

613 al. 2018, Travers-Trolet et al. 2019).

4.2   Implications for other Atlantis models.

615   Although some insights are specific to the precise formulation of the Atlantis-EEC model

616 (Girardin et al. 2018), such as its trophic and physical structure, there is also learning that

617 could apply to other Atlantis implementations. New Atlantis implementations continue to be

618 developed (Weijerman et al. 2016), and calibration of these models is a challenging

619 undertaking. The results of this SA can provide additional information to complement existing

620 advice for how to approach calibration (Audzijonyte et al. 2019, Pethybridge et al. 2019).

621 While we were unable to find a simple list of parameters with minimal effects across all

622 groups, this is unsurprising given that we focused on a subset of the most frequently

623 calibrated parameters (Pethybridge et al. 2019) and the known feedback interactions present

624 in Atlantis through the trophic structure (Pantus 2007). However, there were still differences

625 in the strength of effect among parameters. One important distinction, particularly when

626 calibrating models, is that between parameters that have a strong main effect on the outcomes

627 of many or nearly all groups versus those parameters whose main effect is primarily on the

628 group itself. While the ubiquity of nonlinear/interaction effects means there are no parameters

629 that are strictly limited to only influencing their own groups, there are clear differences in the

630 degree of interactions.

631   The strong contribution of the plankton parameters to system stability and the

632 determination of most groups' biomass suggests a useful approach is to first calibrate a

633 simplified NPZ model (Pethybridge et al. 2019), which was successfully applied for the

634 calibration of the Atlantis-EEC model (Girardin et al. 2018). While the representation of

635 lower trophic levels in Atlantis is necessarily coarse given its spatial and temporal resolution

636 (Pethybridge et al. 2019), it is still likely that a subset of these groups will be highly

637 influential for the entire system, though which subset appears to be model-dependent (Ortega-

638 Cisneros et al. 2017, Hansen et al. 2019, Sturludottir et al. 2018). Further, the large influence

639 of fixed-recruitment top predator parameters on system stability despite those groups'

640 comparatively small biomass suggests that it is essential to set parameters for these groups

641 approximately correctly early in the calibration process. There was hardly any interaction

642 between fixed-recruitment top predator and plankton parameters, suggesting the lowest and

643 highest trophic levels could be calibrated sequentially.

644   Once the highest and lowest trophic levels are stabilized (i.e. SA2), many parameter

645 interactions fall into the monotonic or almost monotonic zone for individual outputs (though

646 not total system biomass or stability). One surprising discovery was the relatively localized

647 and monotonic effect of manipulating BH recruitment (*BHalpha*), with only the group itself

648 affected and no other parameters contributing in most cases. In these groups, generally fish,

649 nonlinear/interaction effects were more prevalent with growth and mortality parameters. In

650 general, growth rates were more important than mortality rates for determining biomass,

651 though mortality rates appeared important for controlling system stability. For vertebrate

652 groups, this may be because most mortality is captured through predation and fishing

653 mortality. While mortality rates were more important for invertebrate groups, they were still

654 less important than growth rates, and this may be due to natural mortality rates being low for

655 invertebrates in the baseline model. For context, nearly all vertebrate mortality rates (that

656 were not zero) were above the 1e-5 day^{-1} threshold Pethybridge et al. (2019) consider high

657 additional mortality, while nearly all invertebrate mortality rates, other than plankton, were

658 below the threshold. Groups whose parameters were important to other groups tended to be

659 the most abundant benthic invertebrates and planktivorous fish. While it is unclear how much

660 these results depend on the specific trophic network and environment of the Atlantis-EEC

661 model, we can make some preliminary suggestions on the order in which to tackle groups

662 within the context of other advice on calibrating Atlantis models (Audzijonyte et al. 2019,

663 Pethybridge et al. 2019). That is, 1) calibrate the plankton and recycling groups, perhaps as a

664 simplified NPZ model, 2) ensure reasonable (avoiding extinction or exponential growth)

665 mortality and recruitment rates of fixed- or constant-recruitment groups, generally top

666 predators, 3) adjust growth rates of non-age-structured groups, 4) adjust growth rates of age-

667 structured groups, focusing on high-abundance groups, 5) adjust mortality rates as needed for

668 stability, 6) adjust BH recruitment to match numbers, 7) continue to iteratively fine tune

669 groups. Furthermore, if resources are available, we suggest that once reasonable starting

670 points for parameters are identified, a SA, even with few trajectories, can be very useful for

671 calibration efforts.

672   An important consideration for performing a SA on an Atlantis model is what resources are

673 available given the long simulation running times. Our results indicate that useful information

674 can still be obtained even from many fewer trajectories than the 50 we used here. While some

675 form of parallelization would still be essential, this may not necessarily require access to a

676 supercomputer. There are several considerations with using relatively few trajectories in a

677 highly parameterized and complex model suggested by our analysis. Most importantly,

678 interaction/nonlinear effects are likely to be underestimated, particularly with very small

679 trajectory samples. In general, while the effect sizes may vary with smaller numbers of

680 trajectories, the approximate ordering of parameters was still fairly accurate. These issues

681 may be accentuated if the system frequently becomes unstable in the SA simulations (i.e.

682 groups exploding or going extinct, crashes), so that repeating the SA in that context may not

683 give consistent results.

684   While a SA generally provides information on how much each parameter influences the

685 output, an uncertainty analysis (UA) focuses rather on how much the results are influenced by

686 the uncertainty of the inputs. UA comprises a broader context than a SA; for example, Link et

687 al. (2012) list six major categories of uncertainty in ecosystem models: natural variability;

688 observation error; inadequate communication among scientists, decision-makers and

689 stakeholders; model structural complexity; outcome uncertainty; and unclear management

690 objectives. UAs of complex ecosystem models are also relatively rare. UAs can highlight how

691 uncertainty in parameter specification translates to uncertainty in model outputs (Morzaria-

692 Luna et al. 2018), and cross-model comparisons can give insight into the effects of

693 uncertainty in process specification (Fulton et al. 2003, Smith et al. 2015). Investigating

694 model uncertainty is a current focus of the Atlantis community (Weijerman et al. 2015). Our

695 results suggest that one possible starting point would be to include uncertainty in the plankton

696 dynamics, as these tend to be data poor (particularly zooplankton dynamics and

697 phytoplankton species composition) but also influential to system stability and dynamics.

698 Zooplankton are a key feature of end-to-end ecosystem models linking lower and upper

699 trophic levels, as compared to NPZ models which focus on biogeochemical cycling or

700 multispecies fish models with simplified representations (Rose et al. 2010). Other parameters

701 to consider in a UA scenario could be determined from uncertainty based on the data pedigree

702 (Pethybridge et al. 2019) combined with information from a SA like the one presented here.

703 This analysis could be limited to or weighted by the key groups depending on the scenario

704 investigated (e.g. commercially important or threatened species). This would allow comparing

705 the magnitude of impact on output of model uncertainties and management alternatives, as

706 well as propagating uncertainty in the analysis.

4.3 Future directions

708   While comprehensive, the current SA is still only a first step in understanding the

709 sensitivity of the Atlantis-EEC model to its input parameters. Here we covered the most

710 frequently calibrated growth, mortality, and recruitment parameters, which are not known

711 precisely but for which some insight is available. Other parameters which could be crucial but

712 which are rarely changed in Atlantis models, such as assimilation efficiency or environmental

713 response functions like temperature dependent growth, would be interesting to explore. Future

714 analyses could also take into account how the fishing fleets are parameterized and how the

715 predator-prey diet availability matrix is defined. Earlier work has already demonstrated how

716 species life history traits drive responses to fishing pressure (Kaplan et al.2012). Furthermore,

717 an uncertainty analysis of the diet availability matrix showed great variation in the biomass

718 and catch predicted as well as provided a possible framework for conducting a SA of the diet

719 availability matrix (Morzaria-Luna et al. 2018). Finally, the sensitivity to model structure,

720 such as which functional response or recruitment relationship is used, could be important.

721   We considered the direct outputs of biomass and vertebrate numbers as well as system

722 stability, but future analyses could also include additional outputs like size-at-age for

723 vertebrates, realized diet, or consider the outputs spatially rather than aggregated. Here our

724 aim was two-fold: to gain insight into model functioning and to provide guidance for

725 calibration. Therefore we used biomass and numbers as our outputs of interest. In order to

726 more precisely inform an automated calibration, the sensitivity of the objective function (OF)

727 could also be investigated. Indeed, 1) depending on the formulation of the OF, other

728 parameters than those affecting absolute biomass and numbers may be shown to be influential

729 and 2) it is worth exploring the sensitivity of alternative formulations of the OF beforehand to

730 ensure responsiveness. Automatic calibration has been successfully implemented for other

731 ecosystem models such as OSMOSE (Duboz et al. 2010) and NEMURO (Rose et al. 2007),

732 but has not yet been attempted for an Atlantis model. A successful automatic calibration

733 framework for Atlantis models would provide advantages such as reducing the time necessary

734 to calibrate the model and providing an objective common ground for calibrating different

735 implementations of the model. Given the complexity and highly-parameterized nature of

736 Atlantis, substantial uncertainty may remain in the parameters that should be characterized,

737 and a unique set of parameter values may not be obtained (Janssen & Heuberger 1995).

738 Furthermore, a sequential calibration approach, like that used with OSMOSE, may be helpful.

739 Conducting SAs across other Atlantis model implementations would allow better

740 understanding of whether parameter sensitivities are due to structural design of the Atlantis

741 model, locale-specific environmental or trophic network effects, or perhaps even common

742 trophic structures across models. SAs of Atlantis models, including this one, have consistently

743 found plankton growth parameters to be important drivers of biomass across groups (Hansen

744 et al. 2019, Ortega-Cisneros et al. 2017, Sturludottir et al. 2018). In particular, we recommend

745 the Morris screening method (Morris 1991) as well-suited to the complexity and long running

746 time of Atlantis models. It provides the ability to gain information on nonlinear/interaction

747 effects with no linearity assumptions of the model but with the number of simulations

748 required still on the order of a simple OAT analysis (Saltelli & Annoni 2010), and has been

749 successfully applied to other end-to-end marine ecosystem models (Morris et al. 2014). More

750 and more thorough SAs across a variety of Atlantis models may also allow the simplification

751 of some model processes (Fulton et al. 2003, Van Nes & Scheffer 2005).

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761 **Author contributions (CRediT)**

762   Chloe Bracis: Conceptualization, Methodology, Software, Formal analysis, Writing - Original

763 Draft; Sigrid Lehuta: Methodology, Writing - Review & Editing; Marie Savina Rolland: Methodology,

764 Writing - Review & Editing; Morgane Travers-Trolet: Methodology, Writing - Review & Editing;

765 Raphaël Girardin: Conceptualization, Methodology, Writing - Review & Editing, Supervision.

766

767 **Tables**

768 Table 1: Parameters included in the SA applied across 35 vertebrate and invertebrate/plankton groups (that is,
769 omitting detritus and bacteria groups), see Table A.4 for a complete list of parameters and their values used in the SA
770 and Table A.1 for a complete list of groups.

Parameter	Meaning	Min bound	Max bound	Notes
C	clearance rate, similar to a search volume	-50% baseline value	+100% baseline value	For vertebrate groups, a_i controls C across age classes
Mum	maximum consumption rate	-50% baseline value (invertebrates) 3*C (vertebrates)	+100% baseline value (invertebrates) 3*C (vertebrates)	Moved synchronously with C (note PP only has mum and no C)
BHalpha	controls the asymptote of the stock-recruit relationship (Beverton-Holt recruitment)	5th percentile of percent changes from mean recruitment biomass times baseline value	95th percentile of percent change from mean recruitment biomass times baseline value	For fish, sharks, rays
BHbeta	controls how quickly the asymptote of the stock-recruit	NA	NA	Not included in SA

	relationship is reached (Beverton-Holt recruitment)			
KDENR	number of new recruits arriving each year (fixed recruitment)	-50% baseline value	+100% baseline value	For seabirds and marine mammals (CET, SB, SXX)
mL	Linear mortality (mortality in addition to fishing and predation)	-50% baseline value	+100% baseline value	For top predators (SXX, CET, SB, SHK, RAY, LBT), other fish (CLU, POL) and primary production (PP, ZOO, ZOC, ZOG) Single value for invertebrates, juvenile and adult values for vertebrates and CEP.
mQ	Quadratic mortality, used to enforce density dependence	-50% baseline value	+100% baseline value	For invertebrate groups (CRA, WHE, ECH, SHP, LBE, SCE, SUS, BIV, DEP) and CLU

				(juvenile and adult values, but adult value is 0)

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Figures

Fig. 1 The main submodels making up the Atlantis-EEC model. On bottom, the hydrographic submodel comprising climate, oceanography, and biogeochemistry. In the middle, the ecology submodel, which was the target of the SA, comprising 40 different groups, each with its own population dynamics and trophic connections (see Table A.1), and shown here organized by guilds. On top, the human impacts submodel represented by the fishing fleet.

Fig. 2 Proportion of groups stable in each simulation in SA1 and SA2.

Fig. 3 Relationship between μ^* vs. σ for total biomass (left), total vertebrate numbers (center), and stability (right) in SA1. Lines demarcate zones $\sigma/\mu^*=0.1$ (almost linear, dashed), $\sigma/\mu^*=0.5$ (monotonic, dotted), $\sigma/\mu^*=1$ (almost monotonic, dashed-dotted), with the upper triangle being non-linear/interactions. For biomass and numbers, values are shown on a log-log scale.

Fig. 4 Heat map of the metrics μ^* (left), μ (center), and σ (right) for the effects of parameters on the biomass of each group in SA1.Values are normalized in [0,1] ([-1,1] for μ) for each group by dividing each parameter's metric value by the maximum for the group.

791 Guilds have been identified through colors (left hand side) valid both for input parameter

792 (rows) and output biomass (columns). Heat map were realized using BiocManager package

793 (Gu et al. 2016).Fig. 5 Relationship between μ^* vs. σ for total biomass (left), total vertebrate

794 numbers (center), and stability (right) in SA2. Lines demarcate zones $\sigma/\mu^*=0.1$ (almost linear,

795 dashed), $\sigma/\mu^*=0.5$ (monotonic, dotted), $\sigma/\mu^*=1$ (almost monotonic, dashed-dotted), with the

796 upper triangle being non-linear/interactions.

797 Fig. 6 Heat map of the metrics μ^* (left), μ (center), and σ (right) for the effects of parameters

798 on the biomass of each group in SA2.Values are normalized in [0,1] ([-1,1] for μ) for each

799 group by dividing each parameter's metric value by the maximum for the group. Guilds have

800 been identified through colors (left hand side) valid both for input parameter (rows) and

801 output biomass (columns). Heat map were realized using BiocManager package (Gu et al.

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803

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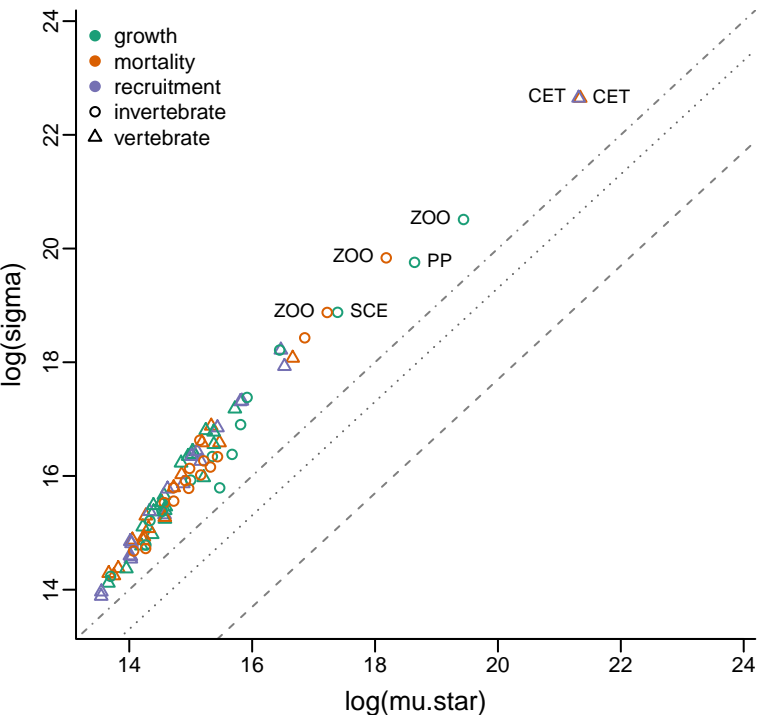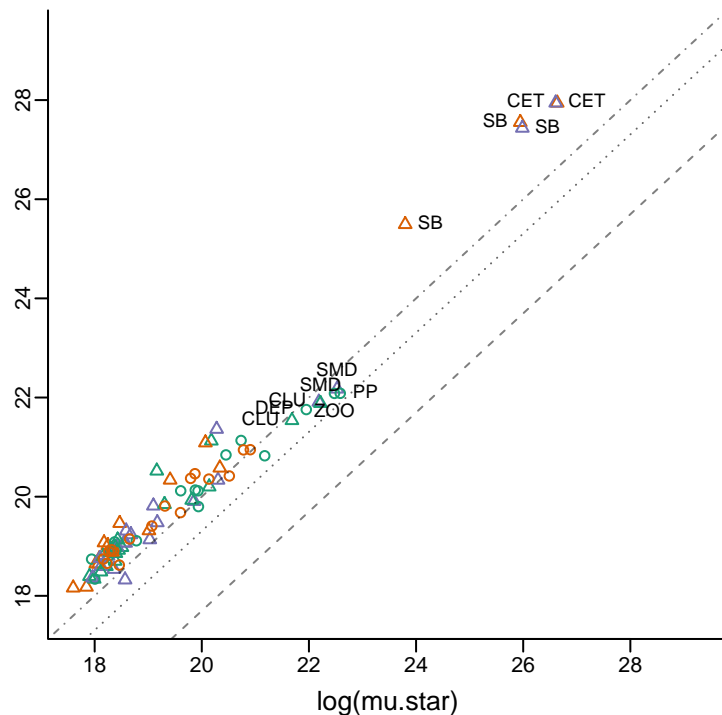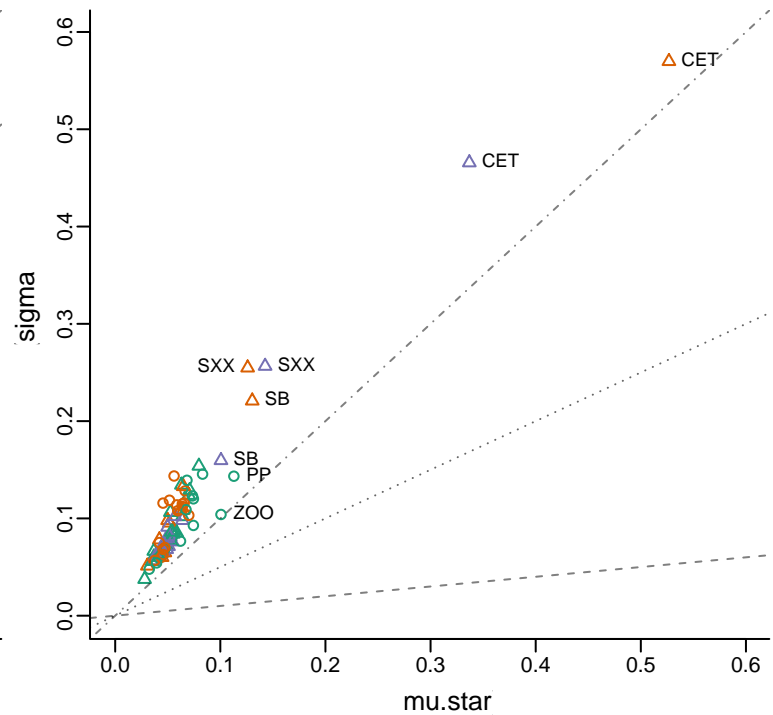
1004   11(3), e0152577.

1005

FISHING FLEET

FOOD WEB

Sharks/Rays

Birds/Mammals

Demersal Fish

Squid

Pelagic Fish

Epibenthos

Filter Feeder

Zooplankton

Recycle/Primary Prod

CLIMATE/OCEANOGRAPHY

BIOGEOCHEMISTRY

N
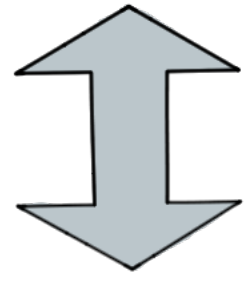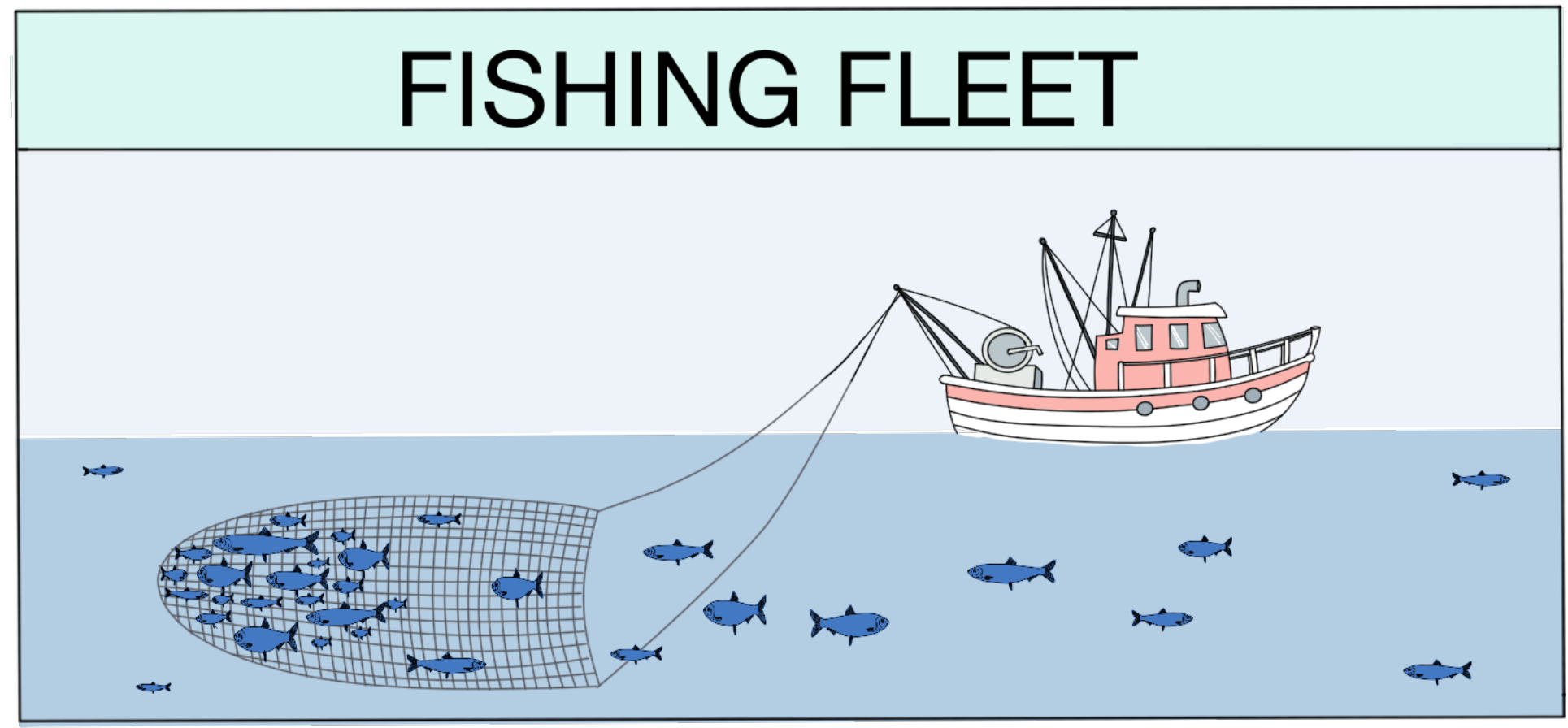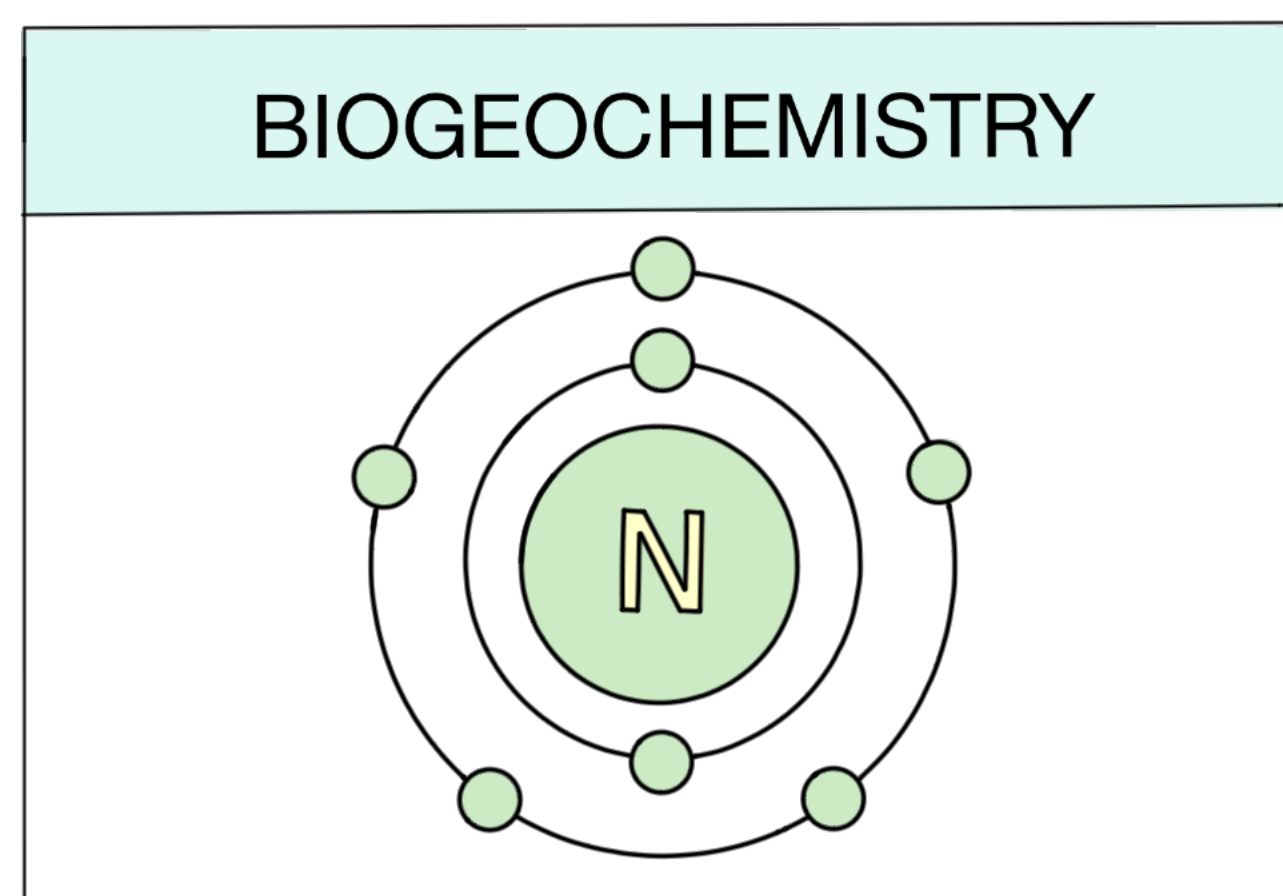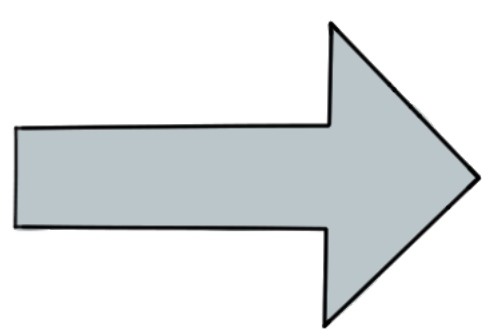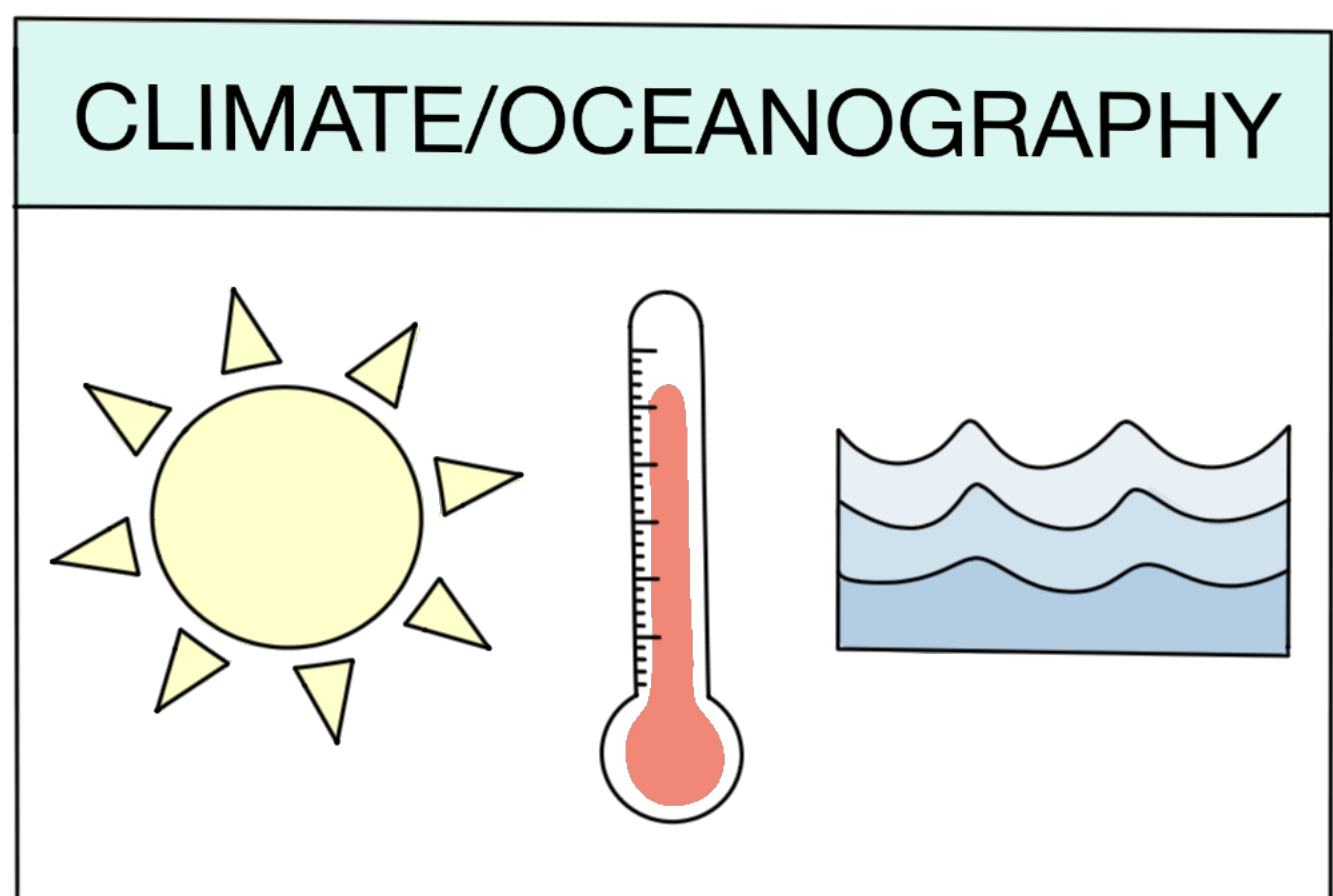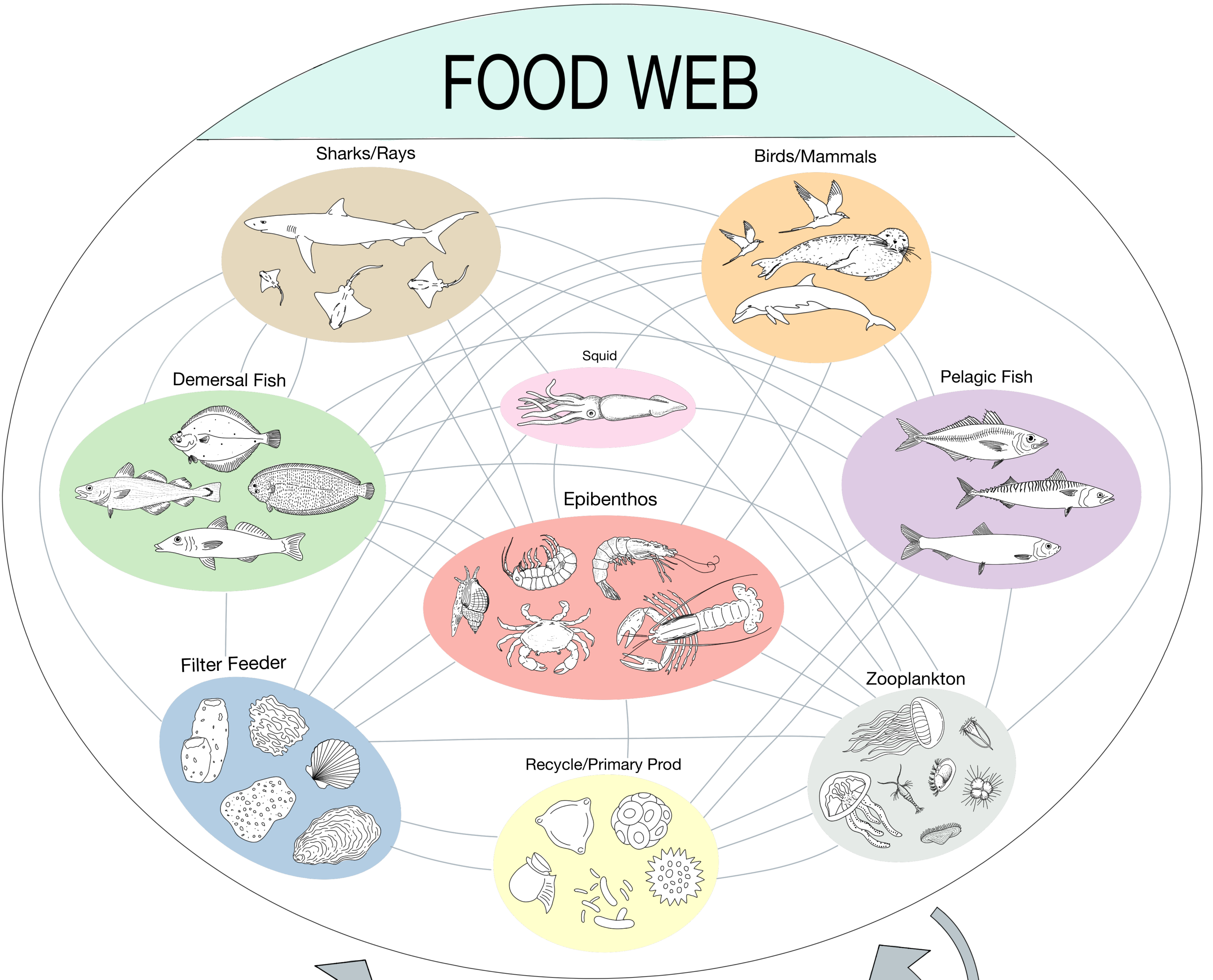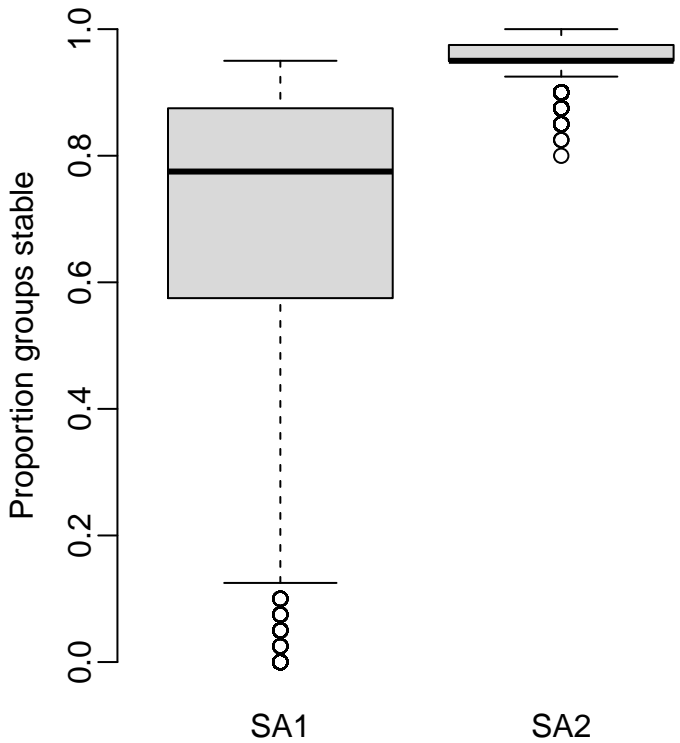
Total biomass — Total numbers — Proportion groups stable
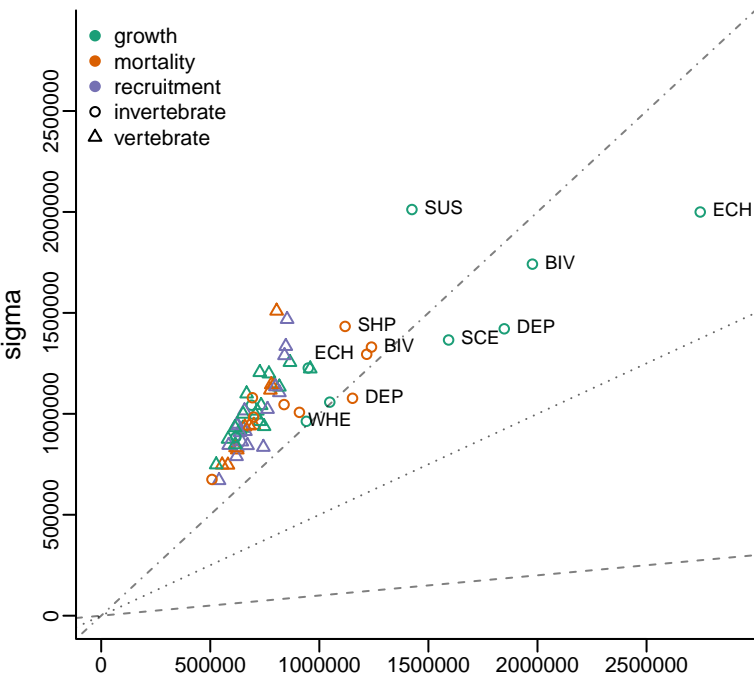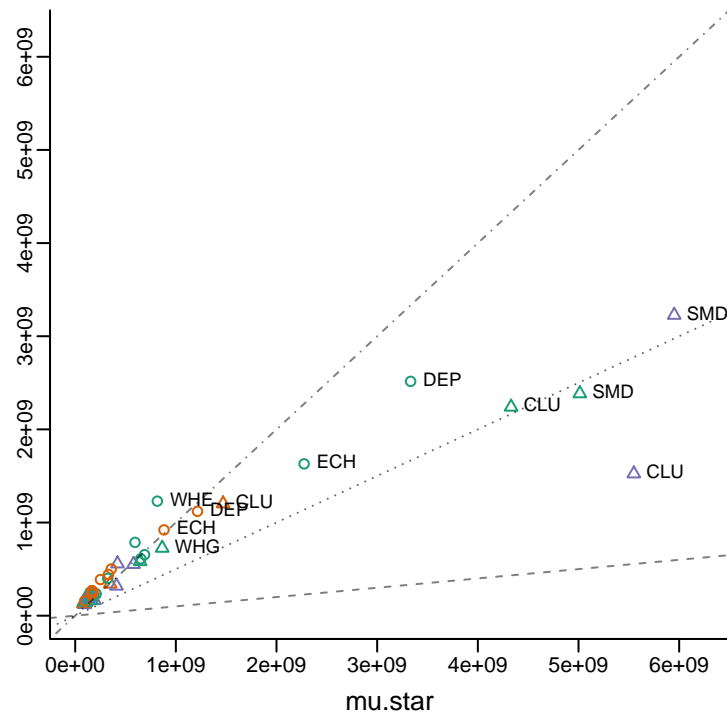
● growth	
● mortality	
● recruitment	
○ invertebrate	
△ vertebrate	

Total biomass — y-axis: sigma

Total numbers — x-axis: mu.star

Proportion groups stable