

1 Effects of data composition and diversity on precision and accuracy
2 of network inference

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³⁴ **1 Abstract**

³⁵ **2 Introduction**

³⁶ **2.1 Why is knowing trophic interactions important?**

³⁷ Knowledge about the trophic interactions in a food web can be used to answer crucial ecological questions:
³⁸ Which species is a keystone species in a food web (Jordán 2009)? How would a food web respond if the
³⁹ top predators are removed (Knight et al. 2005)? Which species should be given priority when conservation
⁴⁰ efforts are implemented (McDonald-Madden et al. 2016)? How robust is a food web to extinctions (Dunne,
⁴¹ Williams, and Martinez 2002)?

⁴² **2.2 What are the methods for knowing interactions?**

⁴³ Species interactions can be inferred from different types of methods (Table 1) such as gut content analysis
⁴⁴ (Peralta-Maraver, Lopez-Rodriguez, and de Figueroa 2017), stable isotope ratio analysis of tissues (Layman
⁴⁵ et al. 2007), experimentation (Warren 1989) and DNA metabarcoding (Roslin and Majaneva 2016). The
⁴⁶ types of information extracted from these methods vary. E.g. Gut content analysis of a predator results in
⁴⁷ the identification of prey species fed upon by that predator, while the stable isotope ratio analysis of the
⁴⁸ organism's tissue can help us infer the approximate trophic position of that species in the food web.

⁴⁹ **2.3 Gut content analysis**

⁵⁰ Gut content analysis is performed to know what an individual has consumed recently. The diet of that
⁵¹ individual can be inferred from the items in the stomach. There is considerable uncertainty involved in this
⁵² method (Baker, Buckland, and Sheaves 2014). E.g. In fish, there is ambiguity while separating prey items in
⁵³ the gut. There are loose tissues that are not identifiable and cannot be assigned to a specific prey item with
⁵⁴ certainty. There are factors such as sample size of consumers, mechanical prey handling, differential digestion
⁵⁵ and evacuation rates of different types of different prey types and volumes, and the ingestion order that in
⁵⁶ combination result in an unquantifiable error which is difficult to interpret in the predator diet (Hyslop 1980;
⁵⁷ Rindorf and Lewy 2004; Baker, Buckland, and Sheaves 2014).

⁵⁸ **2.4 Stable isotope analysis**

⁵⁹ Stable isotope composition of a specific element in a consumer's tissue is given by the ratio of a rarer, heavier
⁶⁰ isotope to a more common lighter isotope (McCormack et al. 2019). Stable isotope analysis (SIA) of tissues
⁶¹ from a single individual can be used to quantify its diet over varying temporal and spatial scales from one
⁶² sample (Crawford, Mcdonald, and Bearhop 2008). Using SIA, several different sources of information can be
⁶³ extracted from a single sampling event as different tissues integrate diet over different temporal scales as well
⁶⁴ as spatial scales. However, there is uncertainty involved in this method which is due to variability in the
⁶⁵ isotopic fractionation values across multiple combinations of diets and tissues/species, unquantified temporal
⁶⁶ or spatial variation in prey isotopic values and variation caused by routing of particular dietary nutrients into
⁶⁷ particular tissues (Crawford, Mcdonald, and Bearhop 2008).

⁶⁸ Trophic level of a species i (TL_i) is calculated as:

$$TL_i = \frac{\delta^{15}N_i - \delta^{15}N_{base}}{\Delta^{15}N} + TL_{base}$$

⁶⁹ where $\delta^{15}N_i$ is the $\delta^{15}N$ value of species i , and TL_{base} and $\delta^{15}N_{base}$ are known TL and $\delta^{15}N$ values
⁷⁰ corresponding to a reference baseline species from a given food web. $\Delta^{15}N$ is the trophic fractionation value
⁷¹ (usually 3.4%)

⁷³ **2.5 Why inferring interactions is not easy?**

⁷⁴ As a food web can be quite complex with many species and trophic interactions (Williams and Martinez
⁷⁵ 2000; Berlow et al. 2009), inferring these trophic interactions with high accuracy and low uncertainty would
⁷⁶ require large amount of food web data (citreqd). E.g. One would need to sample many individuals for gut

Table 1: Studies showing the type of data used to infer trophic interactions in a food web

Data type	Study	Type of information inferred
Gut contents	O’Malley et al. (2017)	Predator diet
	Dixon et al. (2017)	Predator diet
	McClain-Counts et al. (2017)	Predator diet
	Peralta-Maraver et al. (2016)	Predator diet
Stable isotope composition		

77 content data, and processing these guts require a large amount of effort and time as well. Hence, there needs
 78 to be prioritisation of sampling based on an individual trait which is easily identifiable in the field, which
 79 would lead to high accuracy in predicting food web with minimal effort.

80 Even though when one had finally made a decision to use a single type of food web data to infer the
 81 species interactions, it might not be practically feasible to infer the complete food web structure from only a
 82 single type of food web data. E.g. Stable isotope analysis from tissues can only provide the approximate
 83 trophic position of the species which might not be sufficient to predict the complete food web structure. Also,
 84 gut content data might only be used to infer partial diet of a predator individual because gut content data
 85 only provides the information of the prey individuals that have been foraged by the predator recently. There
 86 is also a possibility that some of the information provided by these types of food web data are redundant
 87 i.e. taking into account any further food web data does not necessarily increase the food web prediction
 88 significantly. E.g. This can happen if the guts of two predator individuals give same information about the
 89 prey the predator has consumed.

90 Gut content data and stable isotope data provide different types of information about a food web on
 91 different taxonomic, spatial and temporal scales which results in different amount of uncertainties in inferring
 92 the species interactions. E.g. Gut content data provides information about the diet of an individual on a
 93 local scale whereas stable isotope provides the information about the diet on a bigger spatial scale which is
 94 dependent upon the amount of space dispersed by that species. Therefore, it is crucial to integrate these
 95 diverse information simultaneously from these methods so that information from different taxonomic, spatial
 96 and temporal scale can be integrated, requiring less sampling effort and resulting in a high accuracy of the
 97 food webs.

98 2.6 What we do in our study and how?

99 These questions are addressed *in silico* by simulating food web networks whose true parameters are known.
 100 We used the allometric diet breadth model (ADBM) to simulate the food webs and approximate Bayesian
 101 computation (ABC) to parameterise the ADBM. We simulated the food web data which were used to
 102 parameterise the ADBM using ABC. We also used real gut content data from Broadstone Stream food web
 103 to address those questions.

104 3 Materials and Methods

105 Firstly, we present an *in silico* approach (Fig. 1) to address the research questions where we simulated food
 106 web structure using the allometric diet breadth model (ADBM) whose true parameters were known. In the
 107 upcoming sections, we present methods to simulate gut content data and stable isotope ratio data with
 108 uncertainty. We vary the amount of **simulated data** and use **partial data** to predict food web using the ADBM
 109 parameterised via the rejection approximate Bayesian computation (ABC). Secondly, we used a gut content
 110 data from an observed Broadstone Stream food web to infer the trophic interactions.

111 3.1 Gut content data simulation

112 We simulated a food web using the ADBM for a given set of parameters. For a given set of predators, we
 113 subset the diet from the simulated food web. Then using a probability mass function (distribution), we

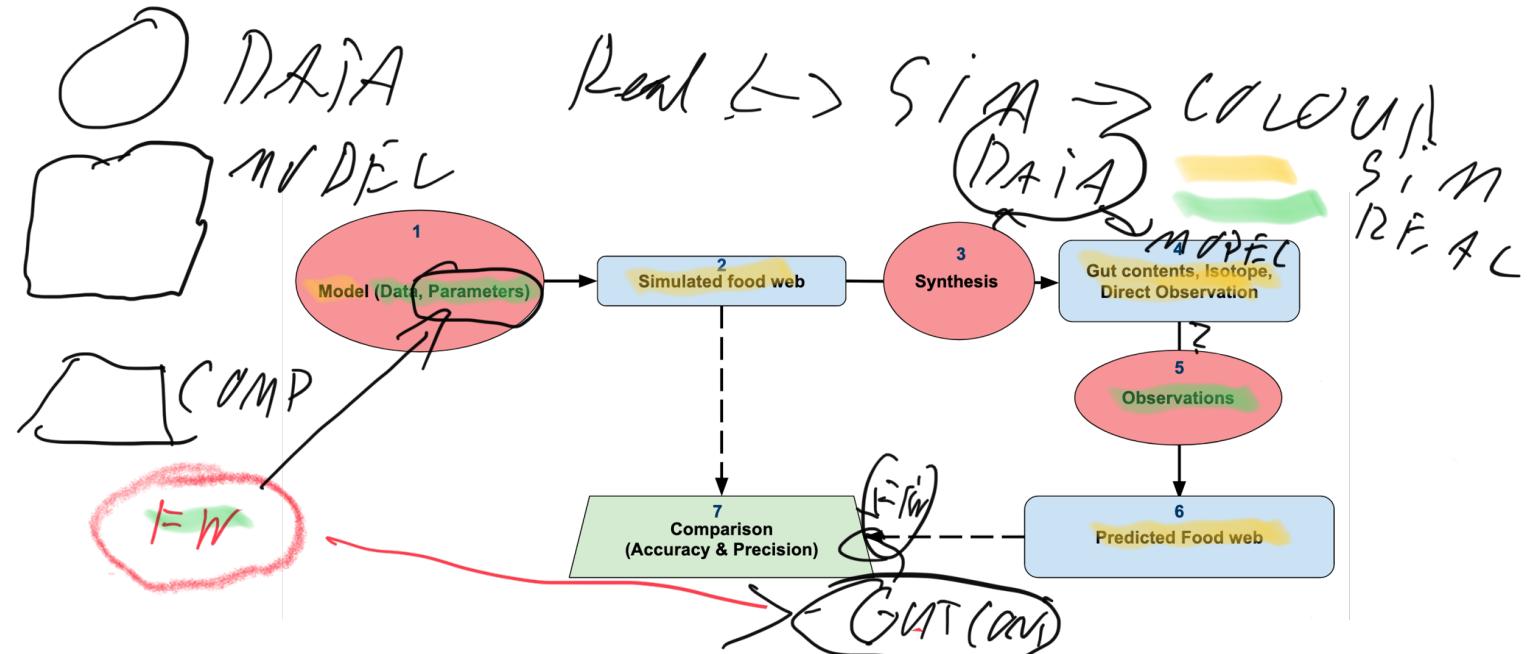


Figure 1: *In silico* approach for investigating the effect of quantity and composition of food web data in predicting food web structure using the ADBM.

sampled the gut content data from predators' diet thereby incorporating the uncertainty in the gut content data. We repeated this process multiple number of times for every predator in the food web.

Input: in what?

- Predators whose diet are to be simulated $P = \{p_1, \dots, p_n\}$
 - A simulated food web $ADBM(\theta_i) = \{d_{p_1}, d_{p_1}, \dots, d_{p_k}\}$, where d_{p_k} is a one-dimensional diet matrix of predator k containing ones and zeros.
 - A function which describes uncertainty in the diet $U(d)$
 - Number of independent guts to be simulated for a predator p_i : $ngut$
- Sampling: of what*
- for $p_i \in P$
 - for $j = 1, \dots, ngut$, where $ngut$ is the number of guts to be simulated
 - * Simulate a single gut of a predator p_i : $g(p_i) = d_{p_i} * U(d_{p_i})$
 - Set of gut of a predator p_i : $G(p_i) = \{g(p_i) : g(p_i) = d_{p_i} * U(d_{p_i})\}$

Output:

- We simulated a pool of gut content data which contains simulated gut content data $G(p_i)$ for every predator p_i

3.2 Inferring food web using gut content data

From a pool of gut content data, we draw a set of gut content data randomly. Then we used the rejection ABC to accept a parameter value which would have resulted in the minimum distance, where distance = 1 - True skill statistic and the true skill statistic was computed between the predators' diet predicted from the ADBM and the sampled gut content data. We repeated this process for n (= 100) number of times for every i number of guts, where i lies between 1 and total number of gut content data in the pool.

Input:

- Predators P : $P = \{p_1, p_2, \dots, p_k\}$
- A pool of gut content data G : $G = \{g_1, g_2, \dots, g_n\}$, where g_n is a one-dimensional matrix containing ones and zeros.

140 • A model prediction $model(\theta) : ADBM(\theta) = \{d_{p_1}, d_{p_1}, \dots, d_{p_k}\}$, where d_{p_k} is a one-dimensional diet
141 matrix of predator k containing ones and zeros.

142 • A summary statistic $s(x) : s(x) \subseteq model(\theta)$

143 • A distance function $d(x_i, y) : d(x_i, y) = 1 - TSS(x_i, y)$

144 • An observed food web $Y : Y = \{d'_{p_1}, d'_{p_1}, \dots, d'_{p_k}\}$

145 *Sampling:*

146 for $i = 1, \dots, tgut$ where $tgut$ is the total number of gut content data in the pool G

147 • for $j = 1, \dots, nsample$ where $nsample$ is the number of independent samples to be drawn

148 – Draw a set of gut content data $y = \{g_1, g_2, \dots, g_i\}$ from the pool of gut content data G

149 – for $k = 1, \dots, npar$ where $npar$ is the number of parameter values to be sampled

150 * Draw a set of parameter values θ_k from the prior distribution $\pi(\theta)$

151 * Compute the model result $x_i = model(\theta_k)$

152 * Compute $s(x_i)$ and $d(s(x_i), y)$

153 – Accept θ_j , which results in the $\min_i\{d(s(x_i), y)\}$

154 • Compute $TSS_i(x, y) = \{TSS(x_i, y) : x_i = ADBM(\theta_j), \theta_j \text{ computed from previous step}\}$ using the
155 accepted $\theta_1, \dots, \theta_{nsample}$

156 *Output:*

157 A prediction interval containing TSS between observed and predicted food webs for every i number of
158 gut content data drawn from the pool of gut content data.

3.1

159 3.3' Broadstone Stream food web

160 Broadstone Stream ($51^\circ 05' N 0^\circ 03' E$; 120 m above sea-level) is a second-order tributary of the River
161 Medway in south-east England. It is dominated by invertebrates as the acidity of the stream (pH 4.7-6.6)
162 excludes fish. The stream consists of 25 common invertebrate species (Woodward, Speirs, and Hildrew
163 2005a). Among the predators, the three large species are *Cordulegaster boltonii* Donovan, *Sialis fuliginosa*
164 Pict. and *Plectrocnemia conspersa* [Curtis] and the three small species are the larvae of the tanypod midges
165 *Macropelopia nebulosa* [Meigen], *Trissopelopia longimana* [Staeger], and *Zavrelimyia barbatipes* [Kieffer].
166 Broadstone Stream food web is one of the most completely described food webs for any system (Schmid-Araya
167 et al. 2002; Hildrew 2009; Layer et al. 2010; and Woodward, Speirs, and Hildrew 2005b).

168 The Broadstone Stream food web in our study was constructed by aggregating by size (Woodward et al.
169 2010a) i.e a node is defined as collection of individuals within a specified size range. There were a total of
170 1008 gut content data. The number of prey items in predator's gut varied within a predator size class (Fig.
171 2). A single gut cannot give information about the complete diet of a predator as can be observed from the
172 right skewed distribution (Fig. 2).

3.2

173 3.4 Allometric Diet Breadth Model (ADBM)

174 The allometric diet breadth model (ADBM) is based on optimal foraging theory, specifically the contingency
175 foraging model (MacArthur and Pianka 1966). The ADBM predicts the set of prey species a consumer
176 should feed upon to maximise its rate of energy intake (Petchey et al. 2008). The foraging variables in the
177 model: energy content of the resources, handling times of the prey, space clearance rate and prey densities
178 are allometrically scaled to the body sizes of the species.

179 The model correctly predicted a greater proportion of links when the trophic interactions were more
180 strongly dependent on size (Petchey et al. 2008). Indeed, constructing a food web based only on body size
181 (i.e. ignoring taxonomy) resulted in almost twice the number of correctly predicted links, i.e. 83%, in contrast
182 to taxonomy (Woodward et al. 2010b). The goodness of fit of the ADBM's predictions depends on the
183 types of interactions in the food webs (Petchey et al. 2008), because some of the interactions are more size
184 structured than other interactions. For instance, predacious and aquatic herbivore interations were predicted
185 better than parasitoid and herbivory ones (Petchey et al. 2008).

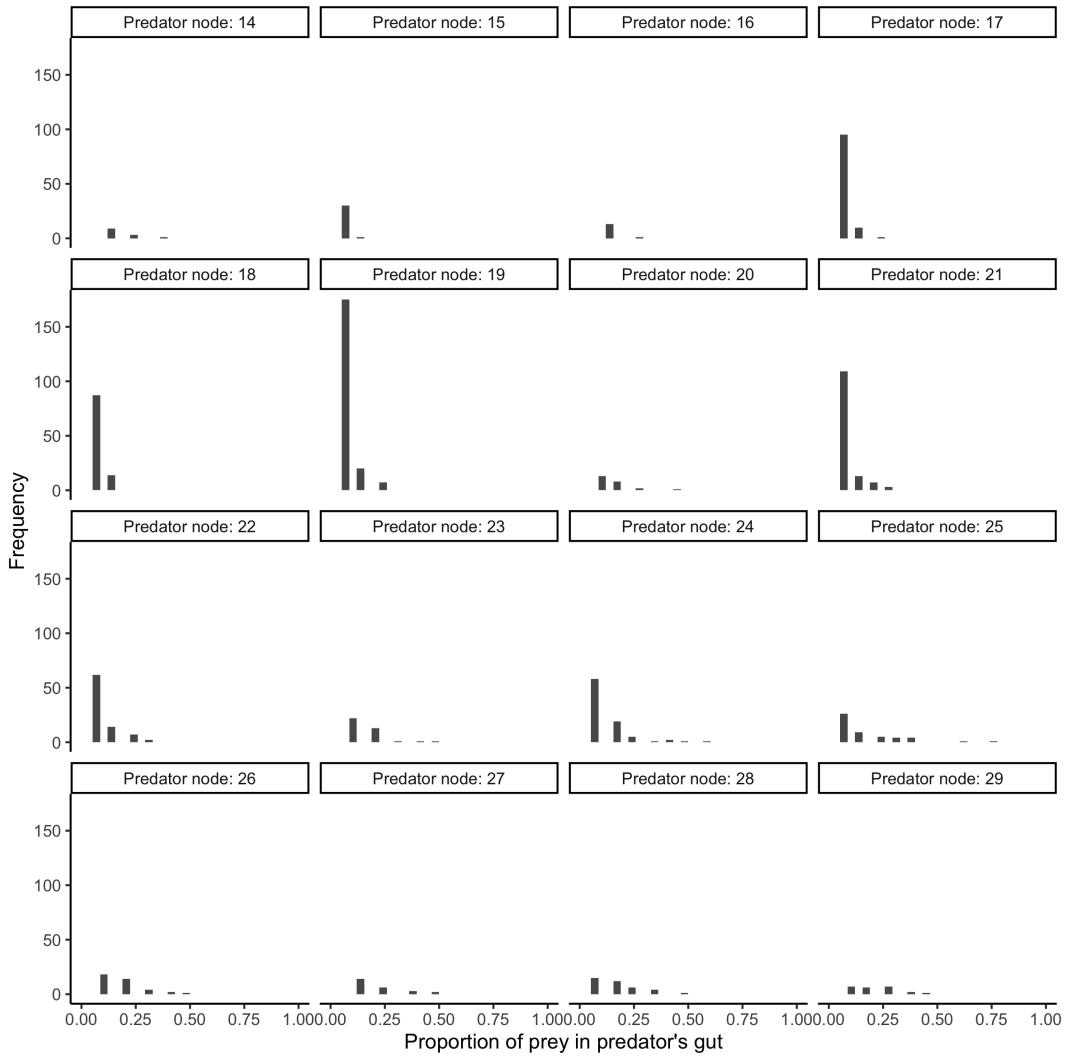


Figure 2: Distribution of proportion of prey in the gut of a predator belonging to a specific size class for Broadstone Stream food web. The proportion of prey in a predator's gut is calculated as number of unique prey items observed in the predator gut divided by the total number of unique prey items in all the gut of that predator.

186 **3.5 Assessment of prediction**

187 The accuracy of the predicted diet of the predators was defined using true skill statistic (TSS) which takes
188 into account the true and false predictions of both the presence and absence of links defined as:

$$\text{TSS} = \frac{ad - bc}{(a + c)(b + d)}$$

189 where a is the number of observed links that are predicted by the model (true positives), d is the number of
190 observed absences of links that are correctly predicted (true negatives), b is the number of false positives, and
191 c is the number of false negatives.

192 The TSS ranges from -1 to 1 , where $+1$ indicates a perfect prediction. A TSS value of zero or less
193 indicates a performance no better than random.

194 **4 Results**

195 We first present the ...

196 **4.1 Prediction using simulated gut content data from a simulated food web**

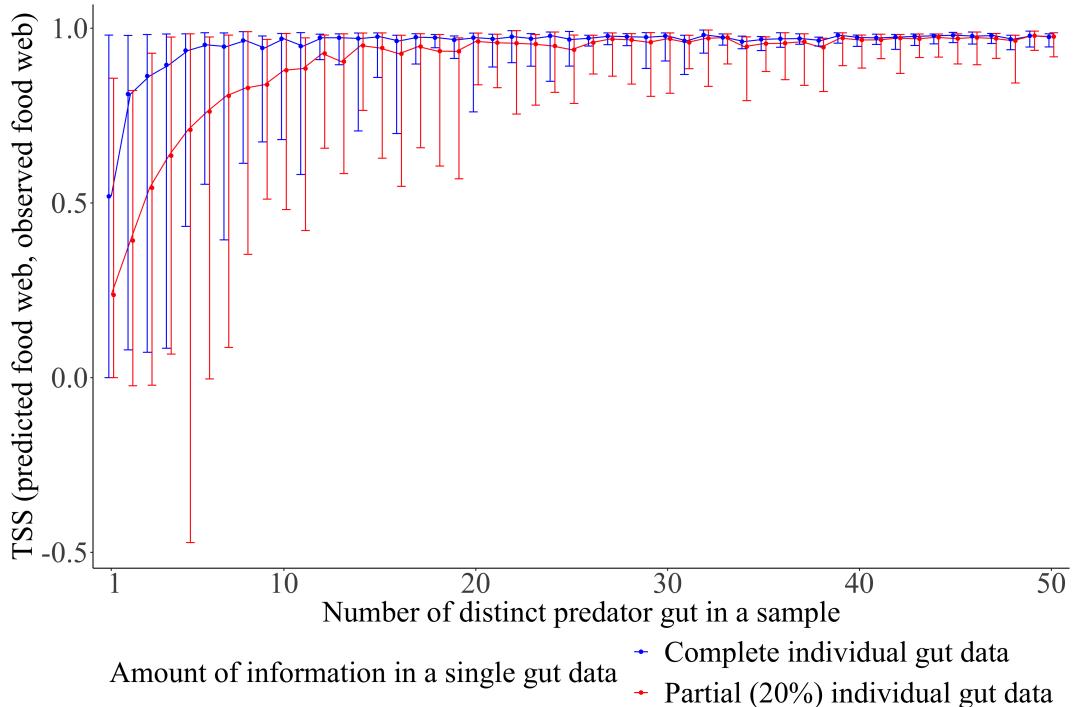


Figure 3: True skill statistics between predicted food web and observed food web for a simulated small reef food web estimated for distinct predator guts in a sample. The observed simulated food web consists of 50 species and ... links. The vertical bars correspond to the prediction intervals of the true skill statistics with filled circles representing the corresponding mean. A prediction interval of the TSS is formed using a set of 100 accepted TSS values using the ABC method.

197 The true skill statistics (TSS) between the predicted food web and observed food web saturated with
198 an increasing number of distinct predator guts in a sample (Fig. 3). The TSS of the predicted food webs
199 estimated using the complete individual gut data had shorter prediction intervals resulting in less uncertainty,
200 and higher mean TSS than that using the partial individual gut data. The maximum limit of the prediction
201 interval of TSS estimated using the complete gut data and the partial gut data were almost equal, with

202 the minimum limit of the prediction interval of TSS using partial gut data being lower than that from the
 203 complete gut data. Eventually, the gap between the mean TSS using the partial gut data and the complete
 204 gut data reduced with an increasing number of distinct predator guts suggesting when we have enough
 205 predator species' gut data, the achieved TSS was almost constant and hence independent of the amount of
 206 gut data.

207 The maximum TSS estimated using the complete gut data was very close to one and almost remained
 208 constant with an increasing number of different predator species sampled. With the gut data sample of
 209 only five distinct predator species, 95% of the maximum mean TSS was achieved when complete individual
 210 gut data was used, while the same was achieved with 15 predator species for partial gut data. This shows
 211 that one does not need to know the gut data of all the species to predict the food web and the accuracy is
 212 dependent on the completeness of an individual gut data.

213 **4.2 Prediction using real gut content data from the Broadstone Stream food
 214 web**

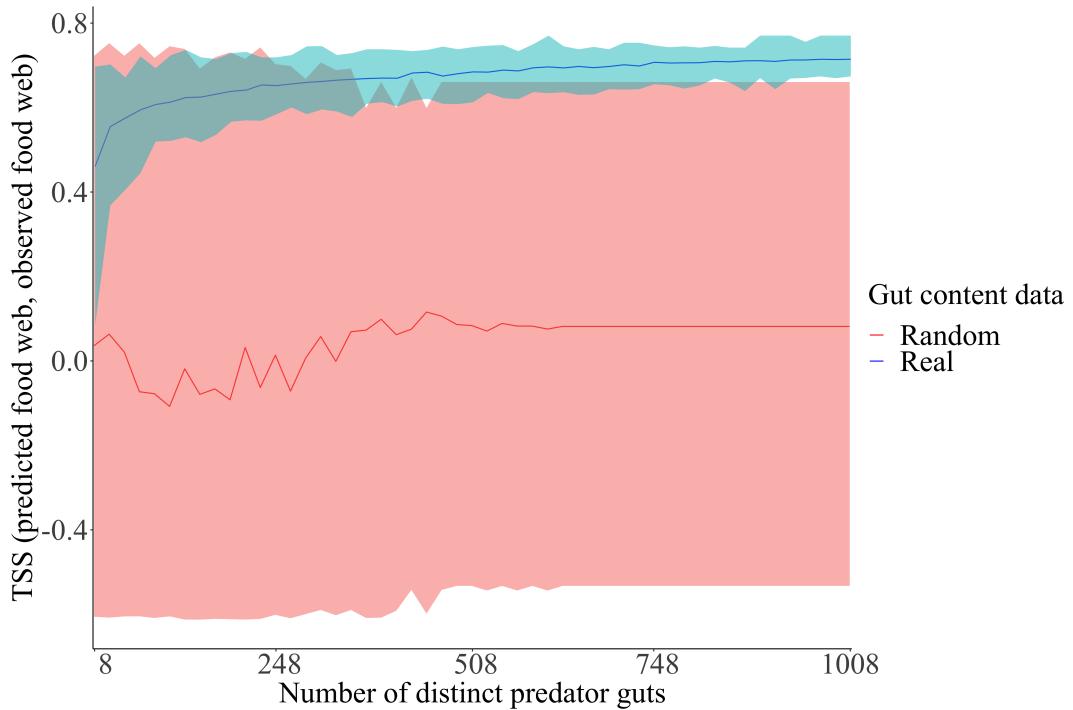


Figure 4: True skill statistics between the predicted and observed Broadstone Stream food web computed for number of different predator guts sampled. There were a total of 1008 guts from 29 species. Line represents the mean and shaded region represents the range/uncertainty. Blue and red curve/region correspond to real and randomly generated gut content data respectively.

215 The value of true skill statistics between the predicted food web and observed food web saturated quickly
 216 with the increasing number of distinct real predator guts (Fig. 4). With only 228 real predator guts, the
 217 ADBM parameterised with ABC predicted the food web with an accuracy of 90% of the maximum mean
 218 TSS (0.71). The uncertainty (red shaded region) in the TSS reduced with the increasing number of predators'
 219 guts. Although at a low number of predators' guts the maximum TSS was quite high the uncertainty was
 220 high as well. This was quite possibly just by chance which was suggested by the overlap of the TSS region
 221 with that of randomly generated gut content data.

222 True skill statistics between the predicted food web and the observed food web had a saturating curve
 223 with the increasing number of distinct predator guts (Fig. 5) for both sets of gut predator guts: First set of
 224 gut data consisted of predator body sizes which were smaller than the mean body size and second set of gut

225 data consisted of predator body sizes which were larger than the mean body size. However, the mean TSS
226 corresponding to the guts of predators smaller than the mean body size was higher when compared to that
227 from the guts of predators larger than the mean body size.

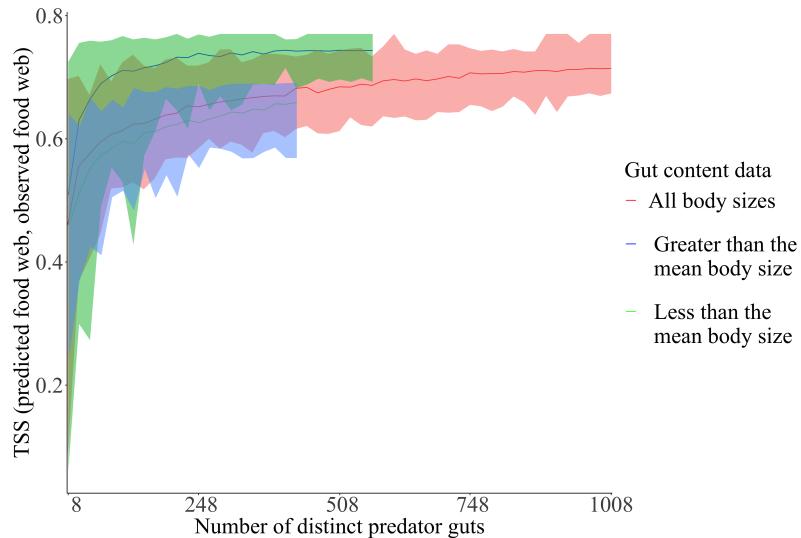


Figure 5: True skill statistics between predicted food web and observed food web estimated for different number of distinct predator guts. The estimation is done for three sets of gut data: gut content data of predators whose body sizes are smaller than the mean body size, larger than the mean body size, and all the gut content data.

228 **4.3 Prediction using simulated stable isotope ratio data from a simulated food
229 web**

230 **4.4 Prediction using both simulated stable isotope ratio and simulated gut
231 content data from a simulated food web**

232 **5 Discussion**

233 **5.1 Include digestion in the gut content simulation**

234 **5.2 On generalising ADBM's predictions over all food webs**

235 **5.3 Include other food web data type**

236 **5.4 Extension to other food web models**

237 **6 Conclusion**

238 **7 Appendix**

239 **8 References**

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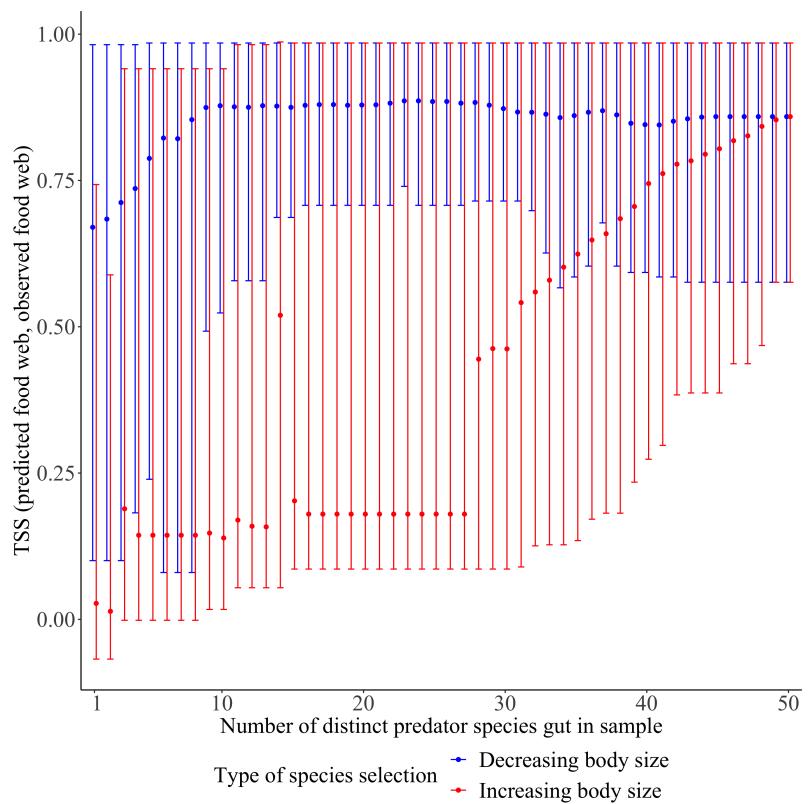


Figure 6: True skill statistics between predicted food web and observed food web for simulated small reef food web estimated for different number of predator species. For every value in the horizontal axis, there are 100 samples of randomly chosen species from a set of 50 species whose gut content data are simulated.

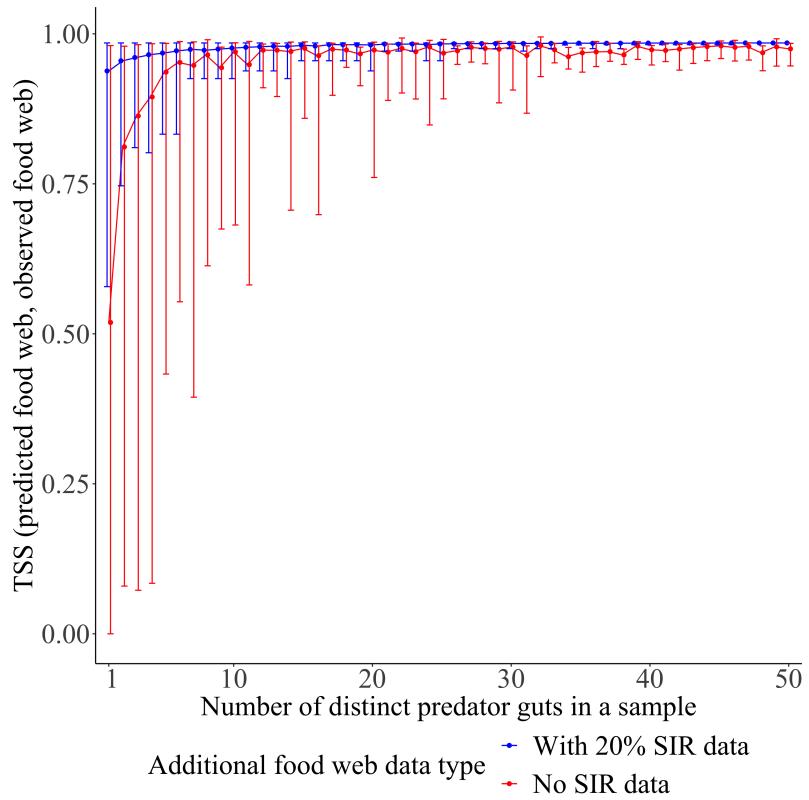


Figure 7: True skill statistics between predicted food web and observed food web for simulated small reef food web estimated for different number of predator species. For every value in the horizontal axis, there are 100 samples of randomly chosen species from a set of 50 species whose gut content data are simulated.

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