
HOW MUCH GUT CONTENT DATA IS REQUIRED TO PREDICT TROPHIC INTERACTIONS?

A PREPRINT

Anubhav Gupta *

Department of Evolutionary Biology and Environmental Studies
University of Zurich
8057 Zurich, Switzerland
anubhav.gupta@ieu.uzh.ch

Eoin O' Gorman

School of Life Sciences
University of Essex
CO4 3SQ Colchester, UK
e.ogorman@essex.ac.uk

Other authors

XXX XXX
XXX XXX
XXX XXX
XXX XXX

Owen L. Petchey

Department of Evolutionary Biology and Environmental Studies
University of Zurich
8057 Zurich, Switzerland
owen.petchey@ieu.uzh.ch

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Abstract

- 1) Presence absence data of species interactions such as gut content data is used to parameterise food web models such as the allometric diet breadth model (ADBM), thereby predicting interactions. Collecting and analysing these data from the field is, however, an expensive and time consuming task. Therefore, it is crucial to know how much gut content data is required to parameterise food web models with high accuracy and high precision.
- 2) ~~We apply to this problem a recently developed approach, namely~~ Bayesian computation to parameterise the ADBM, and true skill statistics to measure the goodness of fit, and do so while varying the amount of gut content data ~~is~~ used in the parameterisation.
- 3) We estimated the minimum ~~number~~ of gut content data required for seven different food webs that resulted in 95% of the maximum true skill statistics achieved by the ADBM when all available gut content data was used. We found that incomplete gut content

*Corresponding author

data can be used to parameterise the ADBM with the lowest amount of gut content data being 28% of the available gut content data.

- 4) These results suggest that one need not collect such a large quantity of gut content data to predict a food web structure using a food web model, thereby reducing sampling effort considerably, while having little effect on precision or accuracy of predictions.

Keywords gut content data · ADBM · food web accuracy · food web prediction

1 Introduction

Knowledge about the trophic interactions in a food web is crucial in ecology for purposes ranging from identifying keystone species (Jord'an 2009) to quantifying robustness of a food web to species extinctions (Dunne, Williams, and Martinez 2002). This has led to the development of numerous food web models (Allesina, Alonso, and Pascual 2008; Cohen, Newman, and Steele 1985; Gravel et al. 2013; Petchey et al. 2008; Tamaddoni-Nezhad et al. 2013). Along with inferring missing links in an observed food web, the food web models are also used for ecological forecasting (Hattab et al. 2016; Lindegren et al. 2010) and for understanding the underlying mechanism governing the interactions in a food web (Gorman et al. 2019).

Although food web models are constructed using prior theory about the factors that determine trophic interactions, empirical data about interactions is required to parameterise a model. For example, Petchey et al. (2008) used presence-absence information about trophic interactions to parameterise the allometric diet breadth model and thereby predict species interactions. These empirical information about interactions can come from diverse set of methods such as gut content analysis (Peralta-Maraver, Lopez-Rodriguez, and de Figueroa 2017), stable isotope ratio analysis of tissues (Layman et al. 2007), experimentation (Warren 1989), DNA metabarcoding of gut contents or faeces (Roslin and Majaneva 2016) and literature research (Gray et al. 2015; Cohen and Mulder 2014a; Goldwasser and Roughgarden 1993a).

Each of these sources of information about trophic interactions has shortcomings. Stable isotope ratio analysis of the organism's tissue does gives indirect information of the diet of that organism via revealing approximate trophic position of that species in the food web. Although mixing models can be used to determine what prey items are most likely fed upon by a predator, this results in uncertainty in the estimates (Kadoya, Osada, and Takimoto 2012; Crawford, McDonald, and Bearhop 2008). Experimentation (e.g. feeding trials) may create unrealistic conditions where a predator is confined in a small space with a potential "prey" and is effectively "forced" into eating it (reference). DNA metabarcoding could have many issues such as failure to relate OTUs to species, or inability to distinguish secondary predation, i.e. the DNA signature of the prey consumed by the ~~prey consumed by the~~ primary item found in the predator gut. Another approach to infer missing links is literature research which involves assuming that a link will occur because another author described it in some other system, or for related predator/prey species, e.g. from the same genus or

family (Gray et al. 2015; Cohen and Mulder 2014b; Goldwasser and Roughgarden 1993b). This typically results in a food web that has false positives—links included when in reality no link would occur (reference). Nielsen et al. (2018) have shown that gut content analysis method has a better match with real diet when compared to other methods

Acquiring food web data from gut content analysis is time consuming and expensive (AG: Do we need a reference? Next sentence explains the reason.). In part this is due to the perception that many gut contents must be collected and analysed in order to be confident that the majority of possible trophic links among species have been observed. Furthermore, considerable time, resource investment, and expertise is required to process the collected samples. Hence, there is of considerable importance to know the minimum number of gut contents and of which consumer species that are required to parameterise a food web model with high accuracy and high precision, so that one knows when is a good time to stop collecting any further empirical data on the food web.

Therefore, the key question we are interested in answering is how much presence-absence information, in the form of gut content data, is required to infer food web structure from a food web model with high accuracy and high precision. In other words, how many samples of gut content should one collect from the field to parameterise a food web model? To answer this question, we use the presence-absence information from gut content data to parameterise the allometric diet breadth model (ADBM) thereby predicting trophic interactions in seven different food webs using rejection approximate Bayesian computation, where the fit of the model was measured using true skill statistics. We computed the true skill statistics of the predicted food webs for different number of predator guts to calculate the minimum number of gut content data to infer food web structure. Our study provides a guideline on how many gut content data is required to predict food web structure using a food web model.

2 Materials and Methods

In the upcoming sections, we present the empirical food webs, the allometric diet breadth model (ADBM), and the gut content data used to infer the trophic interactions. We also give a detailed account of using partial gut content data to parameterise the ADBM using rejection approximate Bayesian computation (ABC). We assessed model predictions using the true skill statistic for comparison across food webs.

2.1 The Empirical Food Webs

In our study, we used food webs for which gut content data is available at an individual level and data that is or that we could make F (Wilkinson et al. 2016). Presence and absence interactions of food web data can be aggregated in different ways (Gilljam et al. 2011). A common way of aggregating food web data is the taxonomic approach, in which nodes in the food web are taxa (e.g. species), or life stages of taxa, and one

species is said to feed on another species if at least one individual of the latter is found in at least one gut of the former. Another approach is based on size, rather than taxonomy, and in this the nodes in the food web are size classes. Here, a feeding link occurs between two size classes if at least one prey item within a size class was found in the gut of another size class, irrespective of their taxonomy.

In our study, we aggregate the gut content data on the basis of size class because the food webs constructed using this approach were better predicted by the ADBM compared to the taxonomic approach (Woodward et al. 2010a), and this is because the ADBM is based on foraging rules defined using the body sizes of organisms (Petchey et al. 2008).

Our study is based on the assumption that the food web constructed using the complete gut content data is the true food web. However, this might not be the case because the links are still under-sampled for many nodes (Woodward et al. 2010b). This could result in a lower true skill statistic (TSS) of the predicted food web from the ADBM, which could result in a biased estimate of the minimum number of gut content data required to achieve 95% of the TSS achieved using complete gut content data.

In the following sections 2.1.1-2.1.5, we briefly explain seven empirical food webs used in our study. The text used in those sections are paraphrased from Gilljam et al. (2011).

2.1.1 Broadstone Stream

Broadstone Stream (51° 05' N 0° 03' E; 120 m above sea-level) is a second-order tributary of the River Medway in south-east England. At the time of sampling in 1996–1997, the stream was acidic (pH 4.7–6.6) and fishless. About 31 common species make up the macroinvertebrate food web, including six major predators and detritivores like stoneflies and chironomids (Woodward, Speirs, and Hildrew 2005).

Between June 1996 and April 1997, thirty randomly scattered benthic Surber sample-units (25cm × 25cm quadrat; mesh aperture 330mm) were taken every two months and kept in 5% formalin. All individuals retrieved from the benthos and identified in stomach contents had their linear body dimensions quantified and converted to dry mass using known regression formulae (listed in Woodward and Hildrew (2002)).

The predators' foreguts were dissected and analysed with 400 magnification in the Surber samples. The individual body masses of eaten prey were calculated using the same methods as for the benthic samples, using reference slides as a guide (Woodward, Speirs, and Hildrew 2005). Over the six sample instances, a single dataset was produced. Each predator and prey individual involved in a feeding relationship was measured and converted into their respective body masses, resulting in a total of 2893 individuals.

2.1.2 Celtic Sea

The Celtic Sea is a continental shelf area that is bounded by Ireland, the United Kingdom, and the Bay of Biscay. Because the Barnes et al. (2009) dataset, from which the data utilised in this chapter were taken, did

not provide precise sampling sites and dates, the data was pooled throughout the whole time period and locations to capture broad tendencies. Only places that were sampled consistently from 1987 to 2001 were used (Blanchard et al. 2005).

In a published global dataset of individual predator and prey body sizes and taxonomy (Barnes et al., 2008), the feeding linkages of fish in the Celtic Sea were described. The original stomach contents data were acquired during annual surveys conducted by the Centre for Environment, Fisheries, and Aquaculture Science (Cefas) on board research vessels during dissections (Pinnegar et al. 2003). Barnes et al. (2008) used known regression equations to measure predator and prey lengths and convert them to body mass.

2.1.3 Afon Hirnant

Three sites in the Afon Hirnant, in North Wales, UK ($52^{\circ} 52' N$ $03^{\circ} 34' W$), were used for the study. The average yearly discharge was 2.08 to 7.26 m^3/s , with a pH ranging from 5.5 to 7. (check Figueroa (2007) and Woodward et al. (2010c) for full details). Invertebrates were collected using a Hess sampler (sampling area: 0.028 m^2 ; mesh aperture 80 μm), with 15 sample-units obtained at random at each site and season, totaling 180 samples across the sampling period. The invertebrate fauna was promptly preserved in 100% ethanol and sorted in the lab. By removing predators' foreguts, which were mounted in Euparal media and viewed at 400 magnification, feeding interactions were determined.

Every predator's linear dimensions (for example, body length) and individual prey items inside each predator's foregut were measured and then translated to body mass values using published regression equations for each taxon (presented in Woodward et al. (2010c)). If the prey items were highly digested, the average body length of individuals in the same family (Ephemeroptera, Plecoptera, or Trichoptera) in the habitat was used. The body lengths of Chironomidae (Diptera) were calculated using previously established species-specific regressions between head capsule width and body length (Figueroa 2007).

2.1.4 Tadnoll Brook

The Tadnoll Brook is a tributary of the River Frome in Southern England, UK, with a mean annual discharge of 0.35 m^3/s and a pH of 6.9–7.7. (Edwards et al., 2009b).

A 240-m reach was sampled every two months between February and December 2005 to create the summery food web. A Surber sampler was used to collect invertebrates every two months (0.06 m^2 ; mesh aperture 300 μm). 20 random samples were taken on each occasion, stored in the field in 4% (w/v) formalin, and then sorted for invertebrates. Fish were captured with an electrofisher, anaesthetized with 2-phenoxyethanol, recognised to species, measured, and weighed on each occasion (Woodward et al., 2010). The guts of trout (*Salmo trutta* L.) with fork lengths more than 70 mm were then flushed with a tiny manual water pump and stored in 4% formalin. For smaller trout and other fish species (*Cottus gobio*, *Anguilla*

anguilla, *Phoxinus phoxinus*, *Barbatula barbatula*, *Gasterosteus aculeatus*), specimens were sacrificed and frozen for subsequent dissection.

Gut contents analysis was performed on each sample occasion for the fish assemblage, whereas invertebrates had far less varied diets and were only characterised in May and October. Individuals of the benthos' numerically dominant or trophically important invertebrate taxa were taken from the Surber samples, dissected, and the contents of the foregut investigated for animal prey, which were recognised at 400× magnification by comparison with reference specimens. The taxa used to examine stomach contents covered more than 95% of the individuals observed in the Benthos. Wherever possible, predators' gut contents were matched to species, and linear body dimensions were measured. Using established regression equations, the dry mass of prey items and invertebrate predators was calculated (Benke et al. 1999; Ganihar 1997; Burgherr and Meyer 1997; Gonzalez, Basaguren, and Pozo 2002; Smock 1980; Edwards et al. 2009; MEYER 1989).

2.1.5 Guampoe, Coilaco and Trancura Rivers, Chile

Three rivers (the Coilaco, Guampoe, and Trancura Rivers) in the catchment area of the Tolten River in south Chile, South America, were studied in a similar way. The Coilaco River (discharge 2.1–16.8 m^3/s), Guampoe River (output 1.8–7.5 m^3/s), and Trancura River (discharge 8.8–49.3 m^3/s) are all pH 6.7–7.6 circumneutral rivers (Figuerola 2007).

In each river, eight benthic samples were taken in each season between 1984 and 1985, totaling 96 sample-units for the whole sampling period (Campos et al., 1985). Invertebrates were gathered using a Surber sampler (sampling area: 0.09 m^2 ; mesh aperture 250 μm) and stored in 70% ethanol before being transported to the lab for species identification and food web analysis.

The feeding linkages were discovered by analysing the gut contents of all individuals observed in each sample. Large invertebrates had their guts removed and mounted in Euparal, whilst small specimens were mounted whole and studied with 400× magnification. Following Schmid (1993) and (Schmid-Araya et al. 2002), species prey items detected on each gut were identified using previously mounted reference slides. Using known regression equations (mentioned in Reiss and Schmid-Araya (2008); Baumgärtner and Rothhaupt (2003); Miserendino (2001); Woodward et al. (2010b)), all linear dimensions were translated to body mass estimates.

2.2 Allometric Diet Breadth Model (ADBM)

The allometric diet breadth model (ADBM) is based on optimal foraging theory, specifically the contingency foraging model (MacArthur and Pianka 1966). We chose this model for various reasons, including because it uses the body size of organisms as input to predict feeding interactions, and because of our familiarity with it. The ADBM predicts the set of prey types (e.g. species or sizes classes) a consumer should feed upon to

maximise its rate of energy intake (Petchey et al. 2008). The foraging variables in the model are: energy content of the resources, handling times of the prey, space clearance rate, and prey densities. These are allometrically scaled to the body sizes of the species. Further details on the foraging rules defined in the ADBM and ADBM’s predictive power across different food webs can be found in Petchey et al. (2008).

2.3 Assessment of prediction

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

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

where a is the number of observed links that are predicted by the model (true positives), d is the number of observed absences of links that are correctly predicted (true negatives), b is the number of false positives, and c is the number of false negatives. The TSS ranges from -1 to 1 , where $+1$ indicates a perfect prediction. A TSS value of zero or less indicates a performance no better than random (Allouche, Tsoar, and Kadmon 2006).

2.4 Inferring food web using partial gut content data

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From an empirical dataset of gut content data, we take a random sample of gut contents of specific size (see below) to create a partial gut content dataset. We then fit the ADBM to this partial dataset.

To fit the ADBM to a gut content dataset (be it complete or partial), we used the rejection ABC method we previously developed in Gupta, Furrer, and Petchey (2022) to accept a parameter value from a prior distribution which would have resulted in the minimum distance, where distance = $1 - TSS$ skill statistic. The true skill statistic was computed between the diets predicted from the ADBM, and those observed in the sampled gut content data. We repeated this process n (≥ 10) 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 the observed diet matrix containing ones and zeros.

- A model prediction $model(\theta) : ADBM(\theta) = \{d_{p_1}, d_{p_1}, \dots, d_{p_k}\}$, where d_{p_k} is the predicted diet matrix of predator k containing ones and zeros.
- A summary statistic $s(x) : s(x) \subseteq model(\theta)$, where $s(x)$ is the diet of some or all of the predators.
- A distance function $d(x_i, y) : d(x_i, y) = 1 - TSS(x_i, y)$, which quantifies how close the observed diet is to the predicted diet of some or all of the predators.
- An observed food web $Y : Y = \{d'_{p_1}, d'_{p_1}, \dots, d'_{p_k}\}$, where d'_{p_k} is the observed diet matrix of predator k containing ones and zeros.

Sampling:

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

- for $j = 1, \dots, nsample$ where $nsample$ is the number of independent samples to be drawn
 - Draw a set of gut content data $y = \{g_1, g_2, \dots, g_i\}$ from the pool of gut content data G
 - for $k = 1, \dots, npar$ where $npar$ is the number of parameter values to be sampled
 - * Draw a set of parameter values θ_k from the prior distribution $\pi(\theta)$
 - * Compute the model result $x_i = model(\theta_k)$
 - * Compute $s(x_i)$ and $d(s(x_i), y)$
 - Accept θ_j , which results in the $min_i\{d(s(x_i), y)\}$
- Compute $TSS_i(x, y) = \{TSS(x_i, y) : x_i = ADBM(\theta_j), \theta_j \text{ computed from previous step}\}$ using the accepted $\theta_1, \dots, \theta_{nsample}$

Output:

The TSS between observed and predicted food webs, and the posterior parameter distributions for every i number of gut content data drawn from the pool of gut content data.

2.5 Computing the minimum gut content data

Using TSS of the predicted food webs for different number of predator guts, we computed the number of gut content data that results in the mean TSS equal to the 95% of the mean TSS achieved by the model using all the predator guts for a food web. We call this number of gut content data as the minimum gut content data.

3 Results

We first present how the accuracy of the food web model in predicting trophic interactions varies with increasing amount of gut content data provided to the food web model. Then, we calculate the number of gut content data for each food webs that results in accuracy equal to 95% of the maximum true skill statistics predicted by the food web model.

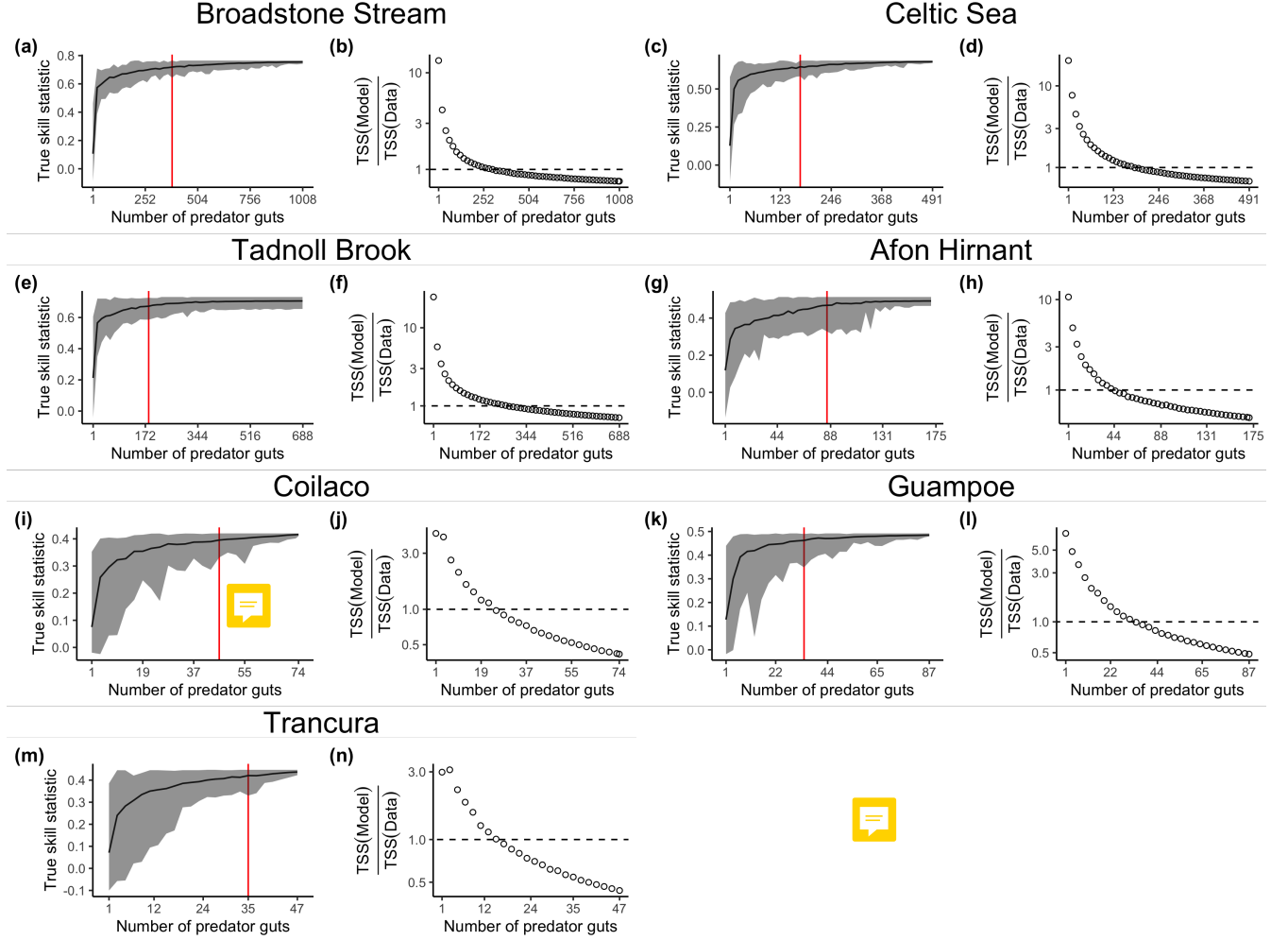


Figure 1: (a, c, e, g, i, k, m) Accuracy of the predicted food web measured using the true skill statistics, predicted by the ADBM parameterised using gut content data. Line and shaded grey region represents the mean and the prediction interval of 100 independent samples respectively. Red line represents the number of predator guts required to achieve a TSS of 95% of the maximum TSS. (b, d, f, h, j, l, n) Ratio of the true skill statistic of the predicted food web by the ADBM parameterised using gut content data to that of the predicted food web constructed using gut content data only. The dashed line shows where the ratio is one for reference.

3.1 Inferring trophic interactions using ADBM and incomplete gut content data

The true skill statistics of the food webs predicted by the ADBM using subsets of gut content data improved quickly for lower number of predator guts (Fig. 1) (a, c, e, g, i, k, m). Furthermore, the width of the prediction interval of the true skill statistics decreased with increasing number of predator guts with the mean TSS asymptoting to the maximum mean TSS achieved by the ADBM when all the gut content data was used. Although the maximum TSS varied among the food webs, the qualitative increase in the TSS was the same.

For Broadstone Stream food web, with only 381 gut contents which is 38% of the total gut content data, the ADBM predicted the food web with the mean TSS of 0.74 which was 95% of the mean TSS (0.78)

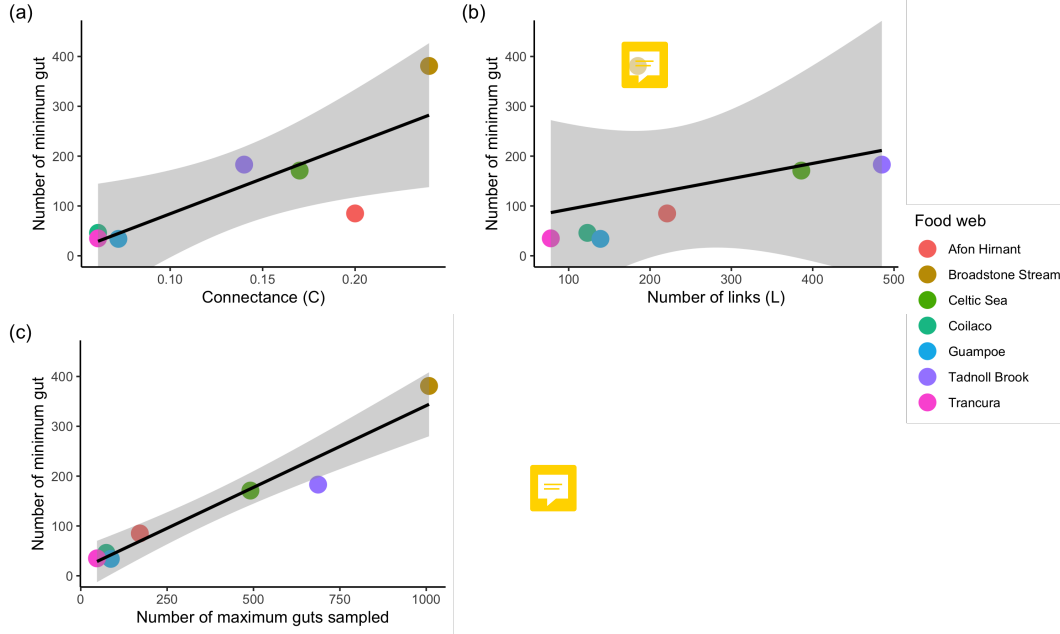


Figure 2: (a, b, c) Number of minimum gut content data (i.e the amount of gut content data used in order to ensure 95% of the maximum TSS) plotted against number of links (L), connectance (C) and number of maximum guts sampled respectively. Solid lines are linear regression ((a) $t = 3.138$, $df = 5$, $P = 0.0257$; (b) $t = 0.876$, $df = 5$, $P = 0.421$; (c) $t = 9.571$, $df = 5$, $P = 0.0002$) and grey region represents 95% confidence intervals.

achieved using complete gut content data (Fig. 1(a)). In case of the Celtic Sea food web, only 171 gut content data which is 35% of the total gut content data was required by the MLM to predict food web with TSS equal to 95% of the mean TSS (0.68) achieved using complete gut content data (Fig. 1(c)).

For a low number of predator guts, the TSS of the model predicted food web was higher than the TSS of the food web constructed from gut content data only (Fig. 1 (b, d, f, h, j, l, n)). An increase in the number of predator guts did reduce the ratio $TSS(Model)/TSS(data)$ reduced to less than one, and reduced further gradually. This shows that with less data available it is better to use the model, while if more data is available then it is better to use the data itself.

3.2 Dependence of the minimum gut content data on number of links and connectance

There was a significant positive relationship between the minimum number of gut content data (i.e the amount of gut content data used in order to ensure 95% of the maximum TSS) and the connectance of the food webs (Fig. 2 (a)). Similarly, we also observed a positive relationship between the minimum number of gut content data and the number of trophic links (L) in the food webs, however this relationship was not significant (Fig. 2 (b)). Furthermore, there was a significant positive relationship between the number of minimum gut content data and the the number of maximum gut content data sampled (Fig. 2 (c)) for food webs.

4 Discussion

We have demonstrated how a food web model can be used to predict food webs reasonably well even when incomplete data about trophic interactions is available. At lower amount of gut content data, predicting with the model is better than using the data itself, while at higher amounts of gut content data, it is better to only use the data. This can help inform how much gut content data to actually collect when we are using a food web model to infer trophic interactions. A future development could be to make the same assessment using other food web models, and to also use food web data other than gut content data to parameterise those models.

4.1 Why incomplete gut content data can be used to infer trophic interactions?

In all of the seven food webs, the ADBM was able to infer the trophic interactions using incomplete gut content data because the presence absence information from the gut content data was still sufficient to constrain the possible model parameter values of the ADBM that best explained the predators' diets. Although in theory the ADBM can predict trophic interactions using only body sizes of organisms as it is based on set of foraging rule, it still requires some presence absence data to constrain the posterior parameter space thereby making more accurate predictions.

4.2 Why does the minimum gut data differ among food webs?

We found the minimum amount of gut content data to vary across food webs and this could be due to the possibility that the food webs are sampled differently, i.e. some food webs are more extensively sampled than others (SI Fig. S2). Furthermore, it is possible that interactions in some of the food webs are more size-structured than others, and are therefore better predicted by the ADBM and consequently require a lower number of gut content data for model parameterisation.

4.3 Model fills up missing interactions and guides sampling direction

When little data about trophic interactions is available, the model can be used to add data about interactions for which data is missing. Furthermore, the model predictions can be used as a guide to sample those predator guts for which we do not have enough information on the presence of interactions from the empirical gut content samples but the model suggests there are interactions. Therefore, with enough number of predator guts sampled one might possibly observe those missed interactions.

4.4 Why is model's TSS less than one?

The food web model used (the ADBM) cannot explain all the interactions in any observed food web that it has been fit to. The foraging rules it encodes are based on the body size and have particular structure and

assumptions; not all of these are met by all observed interactions. For example, the ADBM can only predict diets that are contiguous with respect to the size of prey. I.e. it cannot predict that a predator will consume taxa of size 1 and 3, and not taxa of size 2. Hence, if the observed diets are not contiguous when prey are ordered by their size, the estimation process could lead to a lower value of the TSS.

Furthermore, the observed data may be missing links, e.g. links that rarely occur. Hence the ADBM's maximum predicted true skill statistic is less than one for all food webs it has so far been fit to.

4.5 TSS(Model)/TSS(Data) for different food webs

In all the food webs, the ratio TSS(Model)/TSS(Data) decreased with increasing number of predator guts (Fig. 1 (b, d, f, h, j, l, n)). This suggests when less data is available it is better to use the model and when more data is available it is better to only use the data to predict trophic interactions. At lower number of predator guts the model fills up the missing interactions that were not observed in the gut content data, therefore resulting in model performing better as compared to data alone. While at higher number of predator guts the model is probably predicting some presence or absence of links i.e. false positives and false negatives resulting in a lower TSS as compared to that of data alone.

4.6 Propagating uncertainty from gut content data to model's predictions

There is considerable uncertainty involved in gut content analysis (Baker, Buckland, and Sheaves 2014) such as in fish's guts, there are sometimes loose tissues that are not identifiable and cannot be assigned to a specific prey item with certainty. There are factors such as sample size of consumers, mechanical prey handling, differential digestion and evacuation rates of different prey types and volumes, and the ingestion order that in combination result in an unquantifiable error which is difficult to interpret in the predator diet (Hyslop 1980; Rindorf and Lewy 2004; Baker, Buckland, and Sheaves 2014). Therefore, a future development would be to consider how this uncertainty is propagated into food web prediction.

4.7 Comparing our study with other studies of predicting food webs using incomplete data

Some studies have presented how the accuracy of food web prediction change when we vary the amount of food web data (Gray et al. 2015). For example: Desjardins-Proulx et al. (2017) has used predictive machine learning models and Caron et al. (2022) has used predictive traits-based models on partial knowledge of interactions to reconstruct a food web accurately, in contrast to our study where we used a mechanistic food web model.

4.8 What is the generalisability of our results?

In our study, we have implemented the approach only with the ADBM. However, in principle, this approach could be extended to other food web models such as Williams and Martinez 2000; Gravel et al. 2013;

Allesina, Alonso, and Pascual 2008). A future prospect could be to study how well different food web models' prediction accuracy vary with different amount of gut content data. This can also help in making decision as to which food web model to chose from for a given a set of gut content data. We suspect the relationship (i.e shape of the curve) between the TSS of the predicted food web and the number of predator guts might vary within food web models

4.9 Assumption that the food web constructed with the total gut content data is the true food web and how can this be improved

Some of the food webs are not very well predicted using the ADBM. And this could possibly result in a lower value of minimum gut content data that was used to achieve 95% of the maximum TSS. This could be because our study is based on the assumption that the true food webs is the one which was constructed using the total gut content data. However, if the total gut content does not contain sufficient information to construct the complete food web, then the food web will miss some links. This would therefore result in a lower TSS of the predicted food web, which can eventually lead to a lower estimate of the minimum gut content data. A future prospect could be to incorporate other sources of presence-absence data such as stable isotope ratio, metabarcoding to complement any links that were missed by the gut content method.

4.10 How can we include other types of food web data?

A future prospect would be to include other types of food web data along with gut content simultaneously to parameterise the ADBM. For example, one could use the approximate trophic position inferred from stable isotope ratio data from a tissue of an individual and gut content data of a different predator simultaneously to parameterise a food web model such as the ADBM. In this case, trophic position would be an additional summary statistic required in the parameterisation method. This combination of different types of data about trophic interactions could be particularly useful when only a limited amount of diet information can be extracted by using a single method.

5 Acknowledgements

6 Author contributions

Reference

Allesina, Stefano, David Alonso, and Mercedes Pascual. 2008. "A General Model for Food Web Structure." *Science* 320 (5876): 658–61. <https://doi.org/10.1126/science.1156269>.

- Allouche, Omri, Asaf Tsoar, and Ronen Kadmon. 2006. “Assessing the Accuracy of Species Distribution Models: Prevalence, Kappa and the True Skill Statistic (TSS).” *Journal of Applied Ecology* 43 (6): 1223–32. <https://doi.org/10.1111/j.1365-2664.2006.01214.x>.
- Baker, Ronald, Amanda Buckland, and Marcus Sheaves. 2014. “Fish Gut Content Analysis: Robust Measures of Diet Composition.” *Fish and Fisheries* 15 (1): 170–77. <https://doi.org/10.1111/faf.12026>.
- Barnes, C., D. M. Bethea, R. D. Brodeur, J. Spitz, V. Ridoux, C. Pusineri, B. C. Chase, et al. 2008. “Predator and Prey Body Sizes in Marine Food Webs.” *Ecology* 89 (3): 881–81. <https://doi.org/10.1890/07-1551.1>.
- Baumgärtner, Daniel, and Karl-Otto Rothhaupt. 2003. “Predictive Length–Dry Mass Regressions for Freshwater Invertebrates in a Pre-Alpine Lake Littoral.” *International Review of Hydrobiology* 88 (5): 453–63. <https://doi.org/10.1002/iroh.200310632>.
- Benke, Arthur C., Alexander D. Huryn, Leonard A. Smock, and J. Bruce Wallace. 1999. “Length–Mass Relationships for Freshwater Macroinvertebrates in North America with Particular Reference to the Southeastern United States.” *Journal of the North American Benthological Society* 18 (3): 308–43. <https://doi.org/10.2307/1468447>.
- Blanchard, Julia L., Nicholas K. Dulvy, Simon Jennings, James R. Ellis, John K. Pinnegar, Alex Tidd, and Laurence T. Kell. 2005. “Do Climate and Fishing Influence Size-Based Indicators of Celtic Sea Fish Community Structure?” *ICES Journal of Marine Science* 62 (3): 405–11. <https://doi.org/10.1016/j.icesjms.2005.01.006>.
- Burgherr, Peter, and Elisabeth I. Meyer. 1997. “Regression Analysis of Linear Body Dimensions Vs. Dry Mass in Stream Macroinvertebrates.” *Archiv Für Hydrobiologie*, April, 101–12. <https://doi.org/10.1127/archiv-hydrobiol/139/1997/101>.
- Caron, Dominique, Luigi Maiorano, Wilfried Thuiller, and Laura J. Pollock. 2022. “Addressing the Eltonian Shortfall with Trait-Based Interaction Models.” *Ecology Letters* n/a (n/a). <https://doi.org/10.1111/ele.13966>.
- Cohen, Joel E., and Christian Mulder. 2014a. “Soil Invertebrates, Chemistry, Weather, Human Management, and Edaphic Food Webs at 135 Sites in The Netherlands: SIZEWEB.” *Ecology* 95 (2): 578–78. <https://doi.org/10.1890/13-1337.1>.
- . 2014b. “Soil Invertebrates, Chemistry, Weather, Human Management, and Edaphic Food Webs at 135 Sites in The Netherlands: SIZEWEB.” *Ecology* 95 (2): 578–78. <https://doi.org/10.1890/13-1337.1>.
- Cohen, Joel E., C. M. Newman, and John Hyslop Steele. 1985. “A Stochastic Theory of Community Food Webs I. Models and Aggregated Data.” *Proceedings of the Royal Society of London. Series B. Biological Sciences* 224 (1237): 421–48. <https://doi.org/10.1098/rspb.1985.0042>.
- Crawford, Kerry, Robbie A. McDonald, and Stuart Bearhop. 2008. “Applications of Stable Isotope Techniques to the Ecology of Mammals.” *Mammal Review* 38 (1): 87–107. <https://doi.org/10.1111/j.1365-2907.2008.00120.x>.

- Desjardins-Proulx, Philippe, Idaline Laigle, Timoth'ee Poisot, and Dominique Gravel. 2017. "Ecological Interactions and the Netflix Problem." *PeerJ* 5 (August): e3644. <https://doi.org/10.7717/peerj.3644>.
- Dunne, Jennifer A., Richard J. Williams, and Neo D. Martinez. 2002. "Network Structure and Biodiversity Loss in Food Webs: Robustness Increases with Connectance." *Ecology Letters* 5 (4): 558–67. <https://doi.org/10.1046/j.1461-0248.2002.00354.x>.
- Edwards, François K. Lauridsen, Lucie Armand, Helen M. Vincent, and Iwan J. Jones. 2009. "The Relationship Between Length, Mass and Preservation Time for Three Species of Freshwater Leeches (Hirudinea)." *Fundamental and Applied Limnology* 173 (4): 321–27. <https://doi.org/10.1127/1863-9135/2009/0173-0321>.
- Figueroa, David. 2007. "Food Web Dynamics : New Patterns from Southern South America and North Wales UK, and the Role of Basal Species Structuring Food Webs." PhD thesis, University of London. <https://ethos.bl.uk/OrderDetails.do?uin=uk.bl.ethos.582554>.
- Ganihar, S. R. 1997. "Biomass Estimates of Terrestrial Arthropods Based on Body Length." *Journal of Biosciences* 22 (2): 219–24. <https://doi.org/10.1007/BF02704734>.
- Gilljam, David, Aaron Thierry, Francois K. Edwards, David Figueroa, Anton T. Ibbotson, J. Iwan Jones, Rasmus B. Lauridsen, Owen L. Petchey, Guy Woodward, and Bo Ebenman. 2011. "Seeing Double:" In *Advances in Ecological Research*, 45:67–133. Elsevier. <https://doi.org/10.1016/B978-0-12-386475-8.00003-4>.
- Goldwasser, Lloyd, and Jonathan Roughgarden. 1993a. "Construction and Analysis of a Large Caribbean Food Web." *Ecology* 74 (4): 1216–33. <https://doi.org/10.2307/1940492>.
- . 1993b. "Construction and Analysis of a Large Caribbean Food Web." *Ecology* 74 (4): 1216–33. <https://doi.org/10.2307/1940492>.
- Gonzalez, Jose M, Ana Basaguren, and Jesus Pozo. 2002. "Size-Mass Relationships of Stream Invertebrates in a Northern Spain Stream," 7.
- Gorman, Eoin J. O', Owen L. Petchey, Katy J. Faulkner, Bruno Gallo, Timothy A. C. Gordon, Joana Neto-Cerejeira, J'on S. 'Olafsson, Doris E. Pichler, Murray S. A. Thompson, and Guy Woodwar. 2019. "A Simple Model Predicts How Warming Simplifies Wild Food Webs." *Nature Climate Change* 9 (8, 8): 611–16. <https://doi.org/10.1038/s41558-019-0513-x>.
- Gravel, Dominique, Timoth'ee Poisot, Camille Albouy, Laure Velez, and David Mouillot. 2013. "Inferring Food Web Structure from Predator-Prey Body Size Relationships." Edited by Robert Freckleton. *Methods in Ecology and Evolution* 4 (11): 1083–90. <https://doi.org/10.1111/2041-210X.12103>.
- Gray, Clare, David H. Figueroa, Lawrence N. Hudson, Athen Ma, Dan Perkins, and Guy Woodward. 2015. "Joining the Dots: An Automated Method for Constructing Food Webs from Compendia of Published Interactions." *Food Webs* 5 (December): 11–20. <https://doi.org/10.1016/j.fooweb.2015.09.001>.

- Gupta, Anubhav, Reinhard Furrer, and Owen L. Petchey. 2022. “Simultaneously Estimating Food Web Connectance and Structure with Uncertainty.” *Ecology and Evolution* 12 (3): e8643. <https://doi.org/10.1002/ece3.8643>.
- Hattab, Tarek, Fabien Leprieur, Frida Ben Rais Lasram, Dominique Gravel, François Le Loc’h, and Camille Albouy. 2016. “Forecasting Fine-Scale Changes in the Food-Web Structure of Coastal Marine Communities Under Climate Change.” *Ecography* 39 (12): 1227–37. <https://doi.org/10.1111/ecog.01937>.
- Hyslop, E. J. 1980. “Stomach Contents Analysis—a Review of Methods and Their Application.” *Journal of Fish Biology* 17 (4): 411–29. <https://doi.org/10.1111/j.1095-8649.1980.tb02775.x>.
- Jord’an, Ferenc. 2009. “Keystone Species and Food Webs.” *Philosophical Transactions of the Royal Society B: Biological Sciences* 364 (1524): 1733–41. <https://doi.org/10.1098/rstb.2008.0335>.
- Kadoya, Taku, Yutaka Osada, and Gaku Takimoto. 2012. “IsoWeb: A Bayesian Isotope Mixing Model for Diet Analysis of the Whole Food Web.” Edited by Simon Thrush. *PLoS ONE* 7 (7): e41057. <https://doi.org/10.1371/journal.pone.0041057>.
- Layman, Craig A., D. Albrey Arrington, Carmen G. Montaña, and David M. Post. 2007. “Can Stable Isotope Ratios Provide for Community-Wide Measures of Trophic Structure?” *Ecology* 88 (1): 42–48. [https://doi.org/10.1890/0012-9658\(2007\)88%5B42:CSIRPF%5D2.0.CO;2](https://doi.org/10.1890/0012-9658(2007)88%5B42:CSIRPF%5D2.0.CO;2).
- Lindgren, Martin, Christian Möllmann, Anders Nielsen, Keith Brander, Brian R. MacKenzie, and Nils Chr. Stenseth. 2010. “Ecological Forecasting Under Climate Change: The Case of Baltic Cod.” *Proceedings of the Royal Society B: Biological Sciences* 277 (1691): 2121–30. <https://doi.org/10.1098/rspb.2010.0353>.
- MacArthur, Robert H., and Eric R. Pianka. 1966. “On Optimal Use of a Patchy Environment.” *The American Naturalist* 100 (916): 603–9. <https://www.jstor.org/stable/2459298>.
- MEYER, E. 1989. “The Relationship Between Body Length Parameters and Dry Mass in Running Water Invertebrates.” *Arch Hydrobiol* 117: 191–203. <https://ci.nii.ac.jp/naid/10019557615/>.
- Miserendino, María L. 2001. “Relaciones Longitud-Peso Para Macroinvertebrados de Ambientes Dulceacuicolas de Patagonia (Argentina).” *Ecología Austral* 11 (1): 3–8. http://www.scielo.org.ar/scielo.php?script=sci_abstract&pid=S1667-782X2001000100002&lng=es&nrm=iso&tlng=es.
- Nielsen, Jens M., Elizabeth L. Clare, Brian Hayden, Michael T. Brett, and Pavel Kratina. 2018. “Diet Tracing in Ecology: Method Comparison and Selection.” Edited by M. Thomas P. Gilbert. *Methods in Ecology and Evolution* 9 (2): 278–91. <https://doi.org/10.1111/2041-210X.12869>.
- Peralta-Maraver, I., M. J. Lopez-Rodriguez, and J. M. Tierno de Figueroa. 2017. “Structure, Dynamics and Stability of a Mediterranean River Food Web.” *Marine and Freshwater Research* 68 (3): 484–95. <https://doi.org/10.1071/MF15154>.
- Petchey, Owen L., Andrew P. Beckerman, Jens O. Riede, and Philip H. Warren. 2008. “Size, Foraging, and Food Web Structure.” *Proceedings of the National Academy of Sciences* 105: 4191–96. <https://doi.org/10.1073/pnas.0710672105>.

- Pinnegar, J. K., V. M. Trenkel, A. N. Tidd, W. A. Dawson, and M. H. Du buit. 2003. “Does Diet in Celtic Sea Fishes Reflect Prey Availability?” *Journal of Fish Biology* 63 (s1): 197–212. <https://doi.org/10.1111/j.1095-8649.2003.00204.x>.
- Reiss, Julia, and Jenny M. Schmid-Araya. 2008. “Existing in Plenty: Abundance, Biomass and Diversity of Ciliates and Meiofauna in Small Streams.” *Freshwater Biology* 53 (4): 652–68. <https://doi.org/10.1111/j.1365-2427.2007.01907.x>.
- Rindorf, A, and P Lewy. 2004. “Bias in Estimating Food Consumption of Fish by Stomach-Content Analysis” 61: 12.
- Roslin, Tomas, and Sanna Majaneva. 2016. “The Use of DNA Barcodes in Food Web Construction—Terrestrial and Aquatic Ecologists Unite!” Edited by Elizabeth Clare. *Genome* 59 (9): 603–28. <https://doi.org/10.1139/gen-2015-0229>.
- Schmid-Araya, Jenny M., Peter E. Schmid, Anne Robertson, Julie Winterbottom, Charlotte Gjerløv, and Alan G. Hildrew. 2002. “Connectance in Stream Food Webs.” *Journal of Animal Ecology* 71 (6): 1056–62. <https://www.jstor.org/stable/1555780>.
- Smock, Leonard A. 1980. “Relationships Between Body Size and Biomass of Aquatic Insects.” *Freshwater Biology* 10 (4): 375–83. <https://doi.org/10.1111/j.1365-2427.1980.tb01211.x>.
- Tamaddoni-Nezhad, Alireza, Ghazal Afroozi Milani, Alan Raybould, Stephen Muggleton, and David A. Bohan. 2013. “Construction and Validation of Food Webs Using Logic-Based Machine Learning and Text Mining.” In *Advances in Ecological Research*, 49:225–89. Elsevier. <https://doi.org/10.1016/B978-0-12-420002-9.00004-4>.
- Warren, Philip H. 1989. “Spatial and Temporal Variation in the Structure of a Freshwater Food Web.” *Oikos* 55 (3): 299. <https://doi.org/10.2307/3565588>.
- Wilkinson, Mark D., Michel Dumontier, IJsbrand Jan Aalbersberg, Gabrielle Appleton, Myles Axton, Arie Baak, Niklas Blomberg, et al. 2016. “The FAIR Guiding Principles for Scientific Data Management and Stewardship.” *Scientific Data* 3 (1, 1): 160018. <https://doi.org/10.1038/sdata.2016.18>.
- Williams, Richard J., and Neo D. Martinez. 2000. “Simple Rules Yield Complex Food Webs.” *Nature* 404 (6774, 6774): 180–83. <https://doi.org/10.1038/35004572>.
- Woodward, Guy, Julia Blanchard, Rasmus B. Lauridsen, Francois K. Edwards, J. Iwan Jones, David Figueroa, Philip H. Warren, and Owen L. Petchey. 2010b. “Individual-Based Food Webs.” In *Advances in Ecological Research*, 43:211–66. Elsevier. <https://doi.org/10.1016/B978-0-12-385005-8.00006-X>.
- . 2010a. “Individual-Based Food Webs.” In, 43:211–66. Elsevier. <https://doi.org/10.1016/B978-0-12-385005-8.00006-X>.
- . 2010c. “Chapter 6 - Individual-Based Food Webs: Species Identity, Body Size and Sampling Effects.” In *Advances in Ecological Research*, edited by Guy Woodward, 43:211–66. Integrative Ecology: From Molecules to Ecosystems. Academic Press. <https://doi.org/10.1016/B978-0-12-385005-8.00006-X>.

- 487 Woodward, Guy, and Alan G. Hildrew. 2002. "Body-Size Determinants of Niche Overlap and Intraguild
488 Predation Within a Complex Food Web." *Journal of Animal Ecology* 71 (6): 1063–74. [https://doi.
489 org/10.1046/j.1365-2656.2002.00669.x](https://doi.org/10.1046/j.1365-2656.2002.00669.x).
- 490 Woodward, Guy, Dougie C. Speirs, and Alan G. Hildrew. 2005. "Quantification and Resolution of a
491 Complex, Size-Structured Food Web." In *Advances in Ecological Research*, 36:85–135. Elsevier. [https:
492 //doi.org/10.1016/S0065-2504\(05\)36002-8](https://doi.org/10.1016/S0065-2504(05)36002-8).