
EcoDiet : A hierarchical Bayesian model to combine stomach, biotracer, and literature data into diet matrix estimation

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Abstract :

While, quantifying trophic interactions is a critical path to understanding and forecasting ecosystem functioning, fitting trophic models to field data remains challenging. It requires flexible statistical tools to combine different sources of information from the literature and fieldwork samples. We present EcoDiet, a hierarchical Bayesian modeling framework to simultaneously estimate food-web topology and diet composition of all consumers in the food web, by combining (i) a priori knowledge from the literature on both food-web topology and diet proportions; (ii) stomach content analyses, with frequencies of prey occurrence used as the primary source of data to update the prior knowledge on the topological food-web structure; (iii) and biotracers data through a mixing model (MM). Inferences are derived in a Bayesian probabilistic rationale that provides a formal way to incorporate prior information and quantifies uncertainty around both the topological structure of the food web and the dietary proportions. EcoDiet was implemented as an open-source R package, providing a user-friendly interface to execute the model as well as examples and guidelines to familiarize with its use. We used simulated data to demonstrate the benefits of EcoDiet and how the framework can improve inferences on diet matrix by comparison with classical network MM. We applied EcoDiet to the Celtic Sea ecosystem, and showed how combining multiple data types within an integrated approach provides a more robust and holistic picture of the food-web topology and diet matrices than the literature or classical MM approach alone. EcoDiet has the potential to become a reference method for building diet matrices as a preliminary step of ecosystem modeling and to improve our understanding of prey-predator interactions.

Keywords : Bayesian integrated model, Biotracers, Diet matrix, Ecosystem modeling, Food-web topology, Mixing Model, Stable isotope analyzes, Stomach content analyzes, Trophic ecology

1. Introduction

Trophic interactions are at the core of ecosystem modeling approaches, which are recognized as powerful tools for moving toward ecosystem-based management (Muller 2000, Canham et al. 2003), especially in the marine realm with application to fisheries management (Brodziak and Link 2002, Garcia 2003) and climate change adaptation (Gilman et al. 2010). In species-based ecosystem models, such as Ecopath with Ecosim (Christensen and Walters 2004) or Altlantis (Fulton et al. 2004), accurate prior knowledge on trophic relationships is critical (i) to build functional trophic groups; (ii) to define the qualitative structure of the network, i.e. the food-web topology through the presence or absence of trophic linkage between groups; and (iii) to quantify flow exchanges between groups. These latter elements are summarized in the “diet matrix” formed with prey as rows and predators as columns, and cells that contain the proportion of each prey in predators’ diets.

Diet matrices are generally built from stomach or gut content analyses (SCA) (Polovina, 1984). SCA provide a qualitative description of a consumer’s feeding habits through the taxonomical identification of prey items, as well as metrics used to characterize its diet (Hyslop 1980).

However, SCA only record food consumed over recent days or hours, representing a “snapshot” of diets. Additionally, prey items are often altered to the point that precludes reconstruction of the biomass ingested, and differences in digestion or evacuation rates between prey make the estimation of their relative contributions hazardous (Cortés 1997, Hansson 1998, Baker et al. 2014). Thus, SCA data may be more appropriate for prey identification and to derive occurrence-based metrics than for quantitative estimates of diet contribution.

The rapid development of biotracer analyses (BA) over recent decades (Pethybridge et al. 2018, Nielsen et al. 2018) has introduced a range of new tools for trophic ecology. In particular, bulk or

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compound-specific stable isotope analysis (SIA; Boecklen et al. 2011), DNA metabarcoding (Valentini et al. 2009), and fatty acid signature analysis (Iverson et al. 2004) have been recently used in trophic ecology as they can overcome some weaknesses of SCA. Biotracers integrate information on feeding habits over periods from weeks to months (Hesslein et al. 1993), or even years for specific tissues (e.g. bone, Dalerum et Angerbjorn 2005). In line with the “you are what you eat” theory (De Niro and Epstein 1976), first described for bulk SIA, the biotracer signature of a consumer is a mixture of that of its prey, modified by the trophic discrimination factor. Mixing models (MMs) were developed to infer the contributions of different prey to the diet of their consumers. Recent developments have shown how to handle biotracers of different nature within the same analysis (Neubauer et Jensen 2015). Bayesian implementation of these models provides new tools to account for various sources of uncertainty in diet estimates such as uncertainty around trophic discrimination factor values, and to integrate *a priori* information on dietary preferences (Moore et al. 2008, Parnell et al. 2013, Stock et al. 2018). Nonetheless, estimating diets from MM remains challenging. All those approaches rely on fixed topologies, i.e., the probability that trophic links exist is strictly one or zero, without considering any uncertainty associated with these assumptions. Also, those models require a tradeoff between accounting for the whole complexity of the food-web topology and the necessity to simplify it to ensure diet proportions can be solved by the model. Indeed, to obtain accurate estimates of diet proportions, no essential component of the mixture should be omitted (Phillips et al. 2014), while the inclusion of unnecessary prey should be avoided (Phillips and Gregg 2003).

Moreover, whatever the method used (SCA or BA), information on diets is generally collected by considering each consumer (species or trophic group) independently (but see Ainsworth et al. 2010 or Pacella et al. 2013), without simultaneously integrating all consumers into a single

framework. The IsoWeb model (Kadoya et al. 2012), represents a step toward a more ecosystem-oriented approach to dietary analysis. Based on a Bayesian stable isotope mixing model, the framework allows for estimating diet matrices of all food-web components simultaneously rather than studying the diet of each consumer separately.

However, the food-web topology remains a key input that must be specified and fixed before applying the IsoWeb model. While numerous studies infer the topology from expert knowledge or the literature, some use complementary data. For instance, Giraldo et al. (2017) first deduced a fixed topology from SCA (i.e., presence/absence of a trophic link if the prey is observed/missing in the predator's diet) and then applied the IsoWeb model to SIA data depending on this fixed topology. However, those approaches suppose that all stomach analyses provide the same quantity of information, regardless of the sample size (number of stomachs analyzed), and do not provide a consistent methodology to integrate uncertainty in expert knowledge brought on the topology of the trophic network.

Though they have been shown to provide complementary pictures of diets, SCA and SIA data have never been integrated through the same framework (e.g., Cresson et al. 2014, Divine et al. 2017, Day et al. 2019). In this paper, we present EcoDiet, a hierarchical Bayesian integrated model that combines different sources of data and prior information to simultaneously estimate the food-web topology and diet matrix. By utilizing the strength and minimizing the weaknesses of different data types, integrated models have been shown to provide more consistent parameter estimates compared with separate analyses of different data types (Parent and Rivot 2013, Gimenez et al. 2014, Zipkin et al. 2019). Integrated models have been widely applied in different fields of statistical ecology (e.g., Besbeas et al. 2002, Rivot et al. 2004, Schaub and Abadi 2011), but applications in trophic ecology remain rare (but see Ferguson et al. 2018, Moriarty et al.

2017). Specifically, the EcoDiet framework integrates (i) a priori knowledge from the literature on both food-web topology and dietary proportions, while offering flexibility to weigh the influence of the prior knowledge on the final results; (ii) SCA and BA, used to simultaneously update prior knowledge on the topological food-web structure and dietary proportions.

We first develop the workflow of the EcoDiet model. Then, we used simulated data based on a simplified trophic network to demonstrate the benefits of EcoDiet and especially how the framework can improve inferences on diet matrix by comparison with classical network MM. Finally, the EcoDiet model was applied to the Celtic Sea case study, a North-West European ecosystem of key importance for European fisheries (Moulllec et al. 2017).

2. Material and Methods

Fig. 1 provides an overview of the EcoDiet data flow. To facilitate its diffusion and use, the EcoDiet model has been implemented as an R package released on the Comprehensive R Archive Network (Théro *et al.*, 2020; code available at github.com/pyhernvann/EcoDiet). The package comes together with documentation and examples that allow the users to familiarize themselves with the use of EcoDiet.

2.1. Hierarchical structure of EcoDiet

The EcoDiet model integrates three modules in a Bayesian framework: (i) the joint prior distribution for both the food-web topology and the diet proportions, which allows for mobilizing a priori information (e.g., from the literature) on both components; (ii) the “SCA module” that develops the likelihood function used to integrate prey occurrences from SCA to update the prior information on the food-web topology; (iii) the “BA module” that develops the likelihood function used to assimilate biotracer analyses to update the prior information on the diet proportions. To simplify notations, we will use the brackets notation for probability distributions (Parent and Rivot, 2013). Thus, $[u]$ denotes the probability distribution of the variable u , and $[u|v]$ denotes the conditional probability of u given v .

EcoDiet can consider any food web where I trophic groups (below, a “trophic group” refers to a species or a group of aggregated species with similar biological and trophic characteristics) potentially interact together. Let us denote $i=1, \dots, I$ the subscript for trophic groups. The trophic network is then defined by two $I \times I$ matrices here denoted Λ and Π . The first matrix Λ defines the food-web topology, with its element $\Lambda_{i,j}$ being a Boolean random variable indicating whether the group i feeds on the group j ($\Lambda_{i,j} = 1$) or not ($\Lambda_{i,j} = 0$). The second matrix Π is built of all

the proportions $\Pi_{i,j}$ of the prey j in the diet of group i (for all predator i , $\sum_{j=1}^I \Pi_{i,j} = 1$). It is defined conditionally upon the food-web topology, meaning that $\Pi_{i,j} = 0$ if $\Lambda_{i,j} = 0$.

The food-web topology Λ and diet matrix Π are both treated as unknown and are simultaneously estimated after combining the prior information, the SCA and BA data. In the Bayesian setting, a joint prior distribution, denoted $[\Lambda, \Pi]$, is set on Λ and Π . The prior distribution of the diet matrix is defined conditionally upon a given food-web topology, then:

$$(1) \quad [\Lambda, \Pi] = [\Lambda] \times [\Pi|\Lambda]$$

The joint prior $[\Lambda, \Pi]$ can include various degrees of information to encapsulate a priori knowledge on the topology and diets (see hereafter).

Let us now denote X and Y the whole set of data available for the study, for SCA and BA, respectively. EcoDiet updates the joint prior $[\Lambda, \Pi]$ into the joint posterior distributions $[\Lambda, \Pi|X, Y]$ by integrating the data through the likelihoods of SCA and BA data, respectively denoted here $[X|\Lambda]$ and $[Y|\Pi]$:

$$(2) \quad [\Lambda, \Pi|X, Y] = \frac{[\Lambda] \times [\Pi|\Lambda] \times [X|\Lambda] \times [Y|\Pi]}{[X, Y]}$$

The denominator of the right term of eq. (2) (i.e., the “constant of integration”, Gelman et al. 2014) being of lower interest here as the joint posterior distribution is estimated through MCMC simulations.

In the following, we first develop the structure of the joint prior distribution $[\Lambda, \Pi]$. Likelihoods $[X|\Lambda]$ and $[Y|\Pi]$ are then successively described. Last, we present a framework to build

informative prior for $[\Lambda, \Pi]$ from the literature. A directed acyclic diagram of the model can be found in Appendix S1: Fig. S1. All parameters of the model are listed in Table 1.

2.2. Joint prior structure for the food-web topology and the diet matrix

To capture uncertainty on the food-web topology, all components $\Lambda_{i,j}$ of the topology matrix Λ are modeled a priori as independent Bernoulli random variables with parameter $\eta_{i,j}$, which is the expected probability of the existence of a trophic link between i and j :

$$(3) \quad \Lambda_{i,j} \sim \text{Bernoulli}(\eta_{i,j})$$

In practice, note that the user can exclude some links from the topology at the outset (then fixing $\eta_{i,j}=0$ a priori), relying on traits, allometric relationships or common ecological sense (e.g., plankton does not feed on whales) (See section on data simulation).

The prior distribution on the diet matrix Π is defined conditionally upon the topology matrix Λ . For any trophic group i (here considered as a consumer), the diet proportions $\Pi_{i,1}, \dots, \Pi_{i,I}$ are drawn from a Dirichlet prior of dimension I with parameters $\alpha_{i,1}, \dots, \alpha_{i,I}$, thus ensuring that the sum of all the prey contributions is one.

$$(4) \quad (\Pi_{i,1}, \dots, \Pi_{i,I}) \sim \text{Dirichlet}(\alpha_{i,1}, \dots, \alpha_{i,I})$$

An approach similar to the “spike-slab” prior model used in Bayesian variable selection (George and McCulloch 1997) is employed to condition the diet matrix to the topology. When $\Lambda_{i,j} = 0$, the corresponding Dirichlet coefficient $\alpha_{i,j}$ is set at 0, ensuring that the marginal prior on $\Pi_{i,j}$ has all its density mass at 0 (in practice, the difference from 0 will be imperceptible a priori or a posteriori). When $\Lambda_{i,j} = 1$, the corresponding $\alpha_{i,j}$ is set at a positive value defined from prior

knowledge so that updating of the $\Pi_{i,j}$ diet proportion with BA data is allowed. A benefit of this approach is that the effective dimension of the food web is random and the diet matrix Π (and then the dimension of the BA mixing model) automatically adapts to this effective dimension.

In any Bayesian analysis, how much weight should be given to a prior relative to the data is in users' hands, and depends on the purpose of the analysis (Gelman et al. 2014). In EcoDiet, we provide a comprehensive rationale to build informative priors on both topological and diet matrices Λ and Π by using information from the literature, and guidelines to weight the information conveyed by the prior relative to the available data regarding a Pedigree score that qualifies the quality of the literature information. The EcoDiet package also provides a default solution for non-informative prior for Λ and Π . To keep the manuscript as tight as possible, the priors are detailed in Appendix S2.

2.3. Likelihood of SCA and BA data

SCA data

For any group i , occurrences of prey j in stomachs are used to update the prior probability of the existence of a trophic link between i and j . The key idea is that the probability of the existence of a trophic link is considered proportional to the frequency of prey occurrences in stomachs, but with a precision that depends upon the sample size. Let us denote n^{SCA_i} the number of stomachs analyzed for the trophic group i . Observed occurrences $o_{i,j}$ of the prey j in these stomachs are modeled as a binomial likelihood:

$$(4) \quad o_{i,j} \sim \text{Binomial}(\eta_{i,j}, n^{SCA_i})$$

where $\eta_{i,j}$ is the probability of the existence of a trophic link between i and j . The binomial likelihood implies that the information provided by SCA depends on the number of stomachs analyzed: smaller sample sizes induce weaker information than larger ones. Some standardization of the data can be applied before analyses in order to account for low overall occurrences resulting from consumers' ecological and feeding characteristics (more details in Appendix S3).

BA data

The structure of the likelihood for BA data is inspired by the Bayesian stable isotope mixing model (MM) "IsoWeb" proposed by Kadoya et al. (2012). The formulation of the mixing model is similar to that of various single-species models (e.g. IsotopeR, MixSIR, SIAR) but with the following specificity: (i) EcoDiet treats all consumers simultaneously as a trophic network as in IsoWeb; (ii) EcoDiet fully integrates the uncertainty about the network structure, a novelty for a mixing model.

The mixing model involves two main components: (i) the calculation of the mean expected biotracer signature for each consumer, based on the mixture of its prey signatures and the diet matrix Π ; (ii) the likelihood of measurements of biotracer signatures from the samples regarding the mean expected isotopic signature.

Let's denote $k=1,\dots,K$ the index used for the biotracer k considered in the mixture (in our application, k represents elements and $K=2$ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotopes). For any consumer trophic group i , the mean biotracer signature of elements k , denoted $\mu_{i,k}$, is a latent variable calculated as a linear combination of its prey's mean biotracer signatures ($\mu_{j,k}$ in the equation below), increased by a trophic discrimination factor $\delta_{i,k}$ (specific to each consumer i and element k), and weighted by the respective prey's contributions to the predator's diet $\Pi_{i,j}$:

$$(5) \quad \mu_{i,k} = \frac{\sum_j \Pi_{i,j} \times q_{j,k} \times (\mu_{j,k} + \delta_{i,k})}{\sum_j \Pi_{i,j} \times q_{j,k}}$$

$q_{j,k}$ is the concentration of element k in the prey j (see Phillips and Koch, 2002), and is supposed known. Note that the network structure of EcoDiet allows considering cannibalism.

Trophic discrimination factors $\delta_{i,k}$ are modeled as variable among element and consumers, following informative normal prior distributions (see Post 2002) centered on a fixed element-specific mean Δ_k with both element- and consumer group-specific variance $\tau_{i,k}^2$ (see Tab. 1):

$$(6) \quad \delta_{i,k} \sim N(\Delta_k, \tau_{i,k}^2)$$

For any trophic group i , whether it is a consumer or a prey (thus including species at the base of the food web), the expected mean biotracer signature μ involved in eq. 5 (left or right-hand side) is related to the BA data. Let's denote $y_{i,1:K,l}$ the isotopic samples of the K elements available for the trophic group i (with $l = 1, \dots, n^{BA}_i$ if n^{BA}_i samples are available). Then, the n^{BA}_i biotracer measures are modeled as independent realizations of a multivariate Normal distribution of dimension K :

$$(7) \quad y_{i,1:K,l} \sim MVN(\mu_{i,1:K}, \Sigma_i)$$

where $\mu_{i,1:K}$ is the vector of expected values for the K isotopic elements for the trophic group i , and Σ_i the group-specific covariance matrix between the K elements' biotracer signatures, a priori defined as Inverse-Wishart distribution (Hopkins and Ferguson, 2012; Parnell et al, 2013; not accounted for in IsoWeb). The observation equation in eq. (7) is then analogous to the "residual error only" as defined by Stock et al. (2018). All measurements for a group i are modeled

independent. The whole likelihood of BA then writes as the product of multivariate normal likelihoods terms over all individuals $l=1, \dots, n^{BA}_i$ and all trophic groups i .

2.4. Indicators of the food-web structure and functioning

Various indicators characterizing the food-web structure and trophic groups' ecology can be calculated from EcoDiet outputs. Those indicators are derived quantities from the Bayesian model and have therefore a posterior probability distribution. Two indicators were calculated in the case study.

At the ecosystem scale, the connectance C , measures the connectivity, hence the overall complexity of the food web (Martinez 1992):

$$C = \frac{L}{S^2}$$

where L is the number of links actually observed in the food web, i.e. the sum of all A terms (with associated posterior distributions), and S is the number of compartments in the ecosystem (fixed).

At the trophic group scale, the trophic level (TL) was calculated from Π 's estimates, using the “enaR” R-package (Lau et al. 2017).

2.5. Application to simulated data

We used simulated data based on a simplified (but still realistic) trophic network to demonstrate the benefits of the EcoDiet integrated approach and the potential of the framework to improve inferences on diet matrix by comparison with classical network mixing models. More precisely, we compared estimates from EcoDiet under different configurations of the SCA data and

confronted them with those obtained from IsoWeb. These simulations were designed to assess the benefit of integrating the likelihood associated with SCA data in the mixing model, and ultimately to assess the influence of the quality of SCA data (quantity and accuracy of information) on the diet matrix inferences.

Diet matrix and associated topology for a trophic network accounting for 10 functional groups were built (8 consumers and 2 sources, i.e. group that are not consumers). Conditionally on the true topology and diet matrix, SIA and SCA data were simulated for each group. 10 replicates of SIA were simulated and SCA data were simulated according to 4 different scenarios, for which 10 replicates were drawn. In the first scenario (A), SCA data are representative of the true topology and with a high stomach sampling size. For each consumer, the prey content of 100 stomachs was simulated by randomly drawing the presence or absence of prey in each stomach in a Bernoulli distribution with a probability of presence fixed at $p=0.7$ for all stomachs, all consumers, and all preys. Scenario B has representative SCA data but a low sample size. SCA data are representative of the topology (presence/absence of preys simulated with a probability = 0.7) but the contents of only 10 stomachs were simulated for each consumer. Scenario C has SCA data that poorly represent the true topology but a high sample size (100 stomachs). The SCA data were simulated using the probability of the presence of preys in stomachs arbitrarily fixed to high or low values among preys. Heterogeneity in probabilities of presence arbitrarily fixed creates inaccurate SCA data poorly representative of the true topological structure of the network. Scenario D combines SCA data that poorly represent the true topology (same as in scenario 3) and low sample size (10 stomachs). See Appendix S4 and the simulated data made available at <https://doi.org/10.17882/81075> (Hervann et al. 2021) for details on the simulation procedure and simulated data.

EcoDiet was applied to SIA and SCA replicates, while IsoWeb was only applied to SIA data (same SIA replicates among scenarios). Our focus is not to assess the influence of priors. The default uniform Dirichlet prior was then used for both EcoDiet and IsoWeb runs. Diet estimates from the two models (using the default noninformative priors) were then compared to true values. As in Kadoya et al. (2012), the estimation performance of IsoWeb and EcoDiet were evaluated for each scenario using two indicators: the Discrimination (Accuracy in Kadoya et al., here renamed for the purposes of our study) and the Precision indexes. The Discrimination index is the slope of the linear regression between simulated and predicted values over the 10 replicates. Because the regression slope is sensible to points near 0 and 1, this index fairly captures the ability to discriminate between prey with a small and large contribution to the diet. The Precision index is the R^2 of this relationship and provides more information on the accuracy of these estimates.

2.6. Application to the Celtic Sea ecosystem

The Celtic Sea ecosystem

The Celtic Sea is a shelf ecosystem of the NW Europe characterized by a high biological diversity intensely exploited over decades (Guénette and Gascuel 2012, Hervann and Gascuel 2020) and still supporting important multi-specific fisheries (Martinez et al. 2013, Mateo et al. 2017). The Celtic Sea trophic network was particularly investigated during the 1990s (Du Buit 1995, 1996), providing key insights on predator-prey dynamics (Pinnegar et al. 2003) and supporting the construction of trophic models (Moullec et al. 2017, Hervann et al., 2020). The most recent model represents the Celtic Sea food web through 50 trophic groups and is

structured by a diet matrix mainly derived from the literature, lacking contemporary information on species feeding ecology.

SIA and SCA data from samples recently collected in the Celtic Sea (Rault et al. 2017, Issac et al. 2017, Kopp et al. 2018, Day et al. 2019) as part of the EATME project (Robert et al., under review) were combined in the EcoDiet framework to provide an updated estimate of the diet matrix. Sampling and analyzes protocols, and data preparation steps are presented in Appendix S3. SCA refers to 729 digestive tracts of ten commercial species matching 12 monospecific trophic groups (whiting *Merlangius merlangus*, haddock *Melanogrammus aeglefinus*, megrim *Lepidorhombus whiffiagonis*, sole *Solea solea*, plaice *Pleuronectes platessa*, blue whiting *Micromesistius poutassou* and large and small cod *Gadus morhua*, hake *Merluccius merluccius*, and anglerfish *Lophius sp.*). The SIA dataset includes 1166 analyses of both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for 92 taxa matching with 42 trophic groups of the Celtic Sea trophic model. SCA and SIA datasets are presented in Appendix S5 (Appendix S5: Table S2, Appendix S5: Table S3, Appendix S5: Fig. S1). To feed the literature module (Appendix S6), we reviewed diet studies on Celtic Sea species. Information was aggregated by trophic groups, and a Pedigree was attributed to each based on a decision tree (text in Appendix S6 and Appendix S6: Fig. S1). Stomach, isotope and literature data for the Celtic Sea are provided at <https://doi.org/10.17882/81075> (Hernvann et al. 2021).

Assessing the influence of different information sources

To quantify the information coming from each module of the model, we assessed how inferences on the diet matrix change while successively integrating various sources of information. Three configurations were considered (Tab. 2): 1. Estimating dietary proportions using SIA data only,

based on a fixed food-web topology (fixed from the literature) and uninformative priors on dietary proportions; 2. Simultaneously estimating the topology and dietary proportions using both SCA and SIA data and with uninformative priors; and 3. Full EcoDiet model, simultaneously estimating the food-web topology and dietary proportions using both SCA and SIA data but with informative priors built from the literature.

For all consumer groups i , changes in estimates between each configuration were quantified relative to the diet values estimated from the literature. For the food-web topology, we computed the average deviation AD_i between estimates of $\Lambda_{i,j}$ obtained under each configuration and values from the literature ($\Lambda_{i,j}^{lit}$):

$$AD_i = \sum_{j=1}^I \frac{(\Lambda_{i,j} - \Lambda_{i,j}^{lit})}{I}$$

Designed in this way, the sign of AD_i , positive or negative, indicates an increase or a decrease in the total prey number.

For the diet estimates, we used the total absolute deviation TD_i of the estimates of diet proportions $\Pi_{i,j}$ obtained under each configuration from the values of the literature $\alpha_{i,j}^{lit}$ (a simple deviation would be null since diet proportions):

$$TD_i = \sum_{j=1}^I |\Pi_{i,j} - \alpha_{i,j}^{lit}|$$

For each configuration, we first describe results at the scale of the entire food web. Then, we examine in greater detail the model behavior for three key species: haddock, whiting and anglerfish adult. These species were chosen to cover in few examples a large range of values for

the number of stomachs (from 26 to 119 for haddock and anglerfish) analyzed and prior Pedigree scores (from 0.4 to 0.6 for haddock and whiting) and display interesting match/mismatch cases between the different sources of information.

Finally, we conducted a sensitivity analysis to the quality of prior information introduced in the model (Appendix S7).

2.7. Computational details

Bayesian estimations were performed using the EcoDiet package version 1.0.0 (Théro et al. 2020) downloaded from the CRAN. EcoDiet is an open-source R software package that automatically writes and runs a JAGS model for the trophic network defined by the user (Plummer 2003; *rjags* package), to approximate Bayesian posterior distributions via Monte Carlo Markov Chain methods. Note that version 1.0.0 of the EcoDiet package does not formally allow running a configuration with fixed topology and only SIA data. For those configurations, we use an *ad hoc* model directly derived from a simplification of the EcoDiet code.

For both the toy example on simulated data and the application to the Celtic Sea ecosystem, three MCMC-independent chains were used. The first 500,000 iterations of each chain were discarded. After this “burn-in” period, inferences were derived from a sample of 3*500,000 iterations. MCMC simulations required 4 and 24 hours for the simulated example and the Celtic Sea case study, respectively using on a laptop with 4 GB of RAM and an Intel® Core™ i7 processor (Dell, Round Rock, TX, USA). All the modeling results underwent the Gelman-Rubin test as implemented in the “Coda” package of R to assess the convergence of MCMC chains. In EcoDiet, MCMC chains pass the convergence test if all variables in the model have a $R_{hat} < 1.1$. If at least

one of the variables failed, a warning message is automatically sent to the user. For part 2.5, IsoWeb was applied using the function provided in Kadoya et al. (2012).

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3. Results

3.1 Assessing the estimation performance through simulated data

We present here metrics quantifying the estimation performance of EcoDiet; the comparison of diet proportion estimates for all prey-predator pairs is available in Appendix S4.

The comparison of the estimation performance of IsoWeb and EcoDiet based on different simulated datasets reveals that the discrimination power of EcoDiet is systematically higher than that of IsoWeb (Fig. 2; left panel, higher values for Scenarios Sc A to D). For all configurations, even if unrepresentative SCA data are used in EcoDiet, EcoDiet better discriminates prey with contrasted contributions to the diet. However, the results reveal that the representativeness of SCA data relative to the true topology is critical to accurately estimate diet proportions. Whatever the sampling size, EcoDiet performed better than IsoWeb when SCA data was representative of the true topology (higher precision, i.e. estimates closer to the true diet proportions; Fig. 2; Sc A and B), and underperformed IsoWeb when SCA data was unrepresentative of the true topology (Fig. 2; Sc C and D; left panel). When applied to representative SCA data, the posterior probabilities of trophic link existence are similar among prey (Appendix S4) and EcoDiet provides more accurate estimates than IsoWeb, regardless of the sampling size (Fig. 2; estimates for Sc A and B closer to the true diet). By contrast, the Precision of EcoDiet estimates is systematically lower when SCA data are unrepresentative (Fig. 2; low values for Sc C and D, right-hand panel). In that case, the posterior probabilities of trophic link existence are unbalanced among prey (Appendix S4), and falsely constrain the components of the mixture. The higher the bias of the mixture towards the prioritization of prey with a very

specific signature (e.g., outside the true prey isospace), the higher the deviation from the true diet proportions (e.g., see crab's diet in Appendix S4).

The variability among replicates in Discrimination and Precision for IsoWeb predictions is negligible compared with EcoDiet as the latter integrates the uncertainty on the topology. For representative (Sc A & B) as unrepresentative SCA data (Sc C & D), the variability in Discrimination is much higher for small sampling sizes, indicating wide variation in the model estimates among replicates. Precision of estimates provided by EcoDiet is more variable among replicates in the case of non-representative SCA data (Scenarios C and D).

3.2 Inference on the Celtic Sea trophic network

Food-web topology

When relying on the literature only to define the Celtic Sea food-web topology (Config. 1), the food web displays a large number of trophic links, all considered certain, and is characterized by a large connectance ($C=0.31$, Fig. 3-A).

In EcoDiet, topology is not fixed but probabilistic. Trophic links are included ($A_{i,j}=1$) or excluded ($A_{i,j}=0$) from the topology according to their probability of existence η . Fewer prey types are observed in the SCA compared to the literature. The integration of SCA data (Config. 2) prioritizes particular trophic links in the Celtic Sea, and drastically decreases the overall complexity of the food web. Most of the changes in the topology by reference to Config. 1 are driven by trophic groups with available SCA (Fig. 4-A, top corners). Trophic links involving prey regularly observed in SCA are assigned a high probability of existence and are prioritized (e.g., benthic invertebrates prey for haddock, and shrimps for whiting on Fig. 5, left panels; as

opposed to pouts for whiting). Trophic links exclusively observed in the literature and not in the SCA have a posterior distribution of η stacked near zero (e.g., Norway lobster for anglerfish Fig. 5) and disappear (Fig. 3-B) from the network, while many others are dampened (Fig. 3-B).

Integrating informative priors (Config. 3; i.e., full EcoDiet) leads to a topology closer to that of the literature (Fig. 2-A), and of intermediate complexity (Fig. 3-C). Trophic links identified in the literature have a higher prior probability than in Config. 2 and balance the influence of SCA when available. The probability of the existence of trophic links are driven upward (distribution offset toward 1; e.g., horse mackerel for anglerfish, pouts for whiting; Fig. 5) or downward depending on whether the literature identified a group as prey or not (larger blue arrows in Fig. 3-C), and links only observed in the literature are estimated as more probable than in Config. 2.

The influence of priors on the topology depends on both the Pedigree (qualifying the literature accuracy) and the SCA sample size used in the binomial likelihood function. No changes are observed in η posterior means between Config. 2 and Config. 3 for haddock, a species with a high SCA sample size (Fig. 5). By contrast, η estimates are largely influenced by the prior for anglerfish, a less sampled species and with a medium Pedigree: η for its prey horse mackerel passes from 0.03 to 0.27 (Fig. 5).

A sensitivity analysis to the weight of the prior relative to SCA data is provided in Appendix S7. Along a gradient of this weight, the AD index gets closer to 0. The rate of changes in AD is inversely proportional to the number of stomachs analyzed and decreases along the gradient.

Estimate of the diet matrix

In Config. 1, all prey have similar contributions to their predator's diet, indicating that the model generally fails to discriminate between the food sources. Only a few consumers feeding on a limited range of resources (no more than 5) have contrasted estimates of dietary proportions (Fig. 3-D). Thus, the red polygon in Fig. 4-B can be interpreted as mostly representing the difference between a diet matrix composed of prey in equal proportions and the literature-derived diet matrix.

Assimilating SCA data to inform the topology (Config. 2) highly influences diet estimates. When no SCA information is available on a trophic link, no changes occur and prey discrimination generally remains poor (Fig. 3-E; Fig. 4-B). The divergence between a posteriori and a priori knowledge is larger for groups with available SCA (Fig. 3-E), but weaker when topologies are consistent between the literature and SCA data (e.g., smaller change for haddock than whiting). The larger the changes in the probability of the existence of a trophic link are, the larger changes in dietary proportions get (similar yellow polygons Fig. 4-A and B). Nonetheless, it does not mean that diet proportions are systematically driven toward the estimated probabilities of existence. SCA do not dominate SIA information, and even makes easier the discrimination between prey as highlighted by haddock (Fig. 5), for which hierarchy in diet proportions differs from that of frequencies of occurrences.

In Config. 3, informative priors on both the topology and diet matrices shrink estimates toward the prior knowledge (Fig. 4-B). Estimates of dietary proportions are pushed to a higher value (diet proportion of pouts for whiting, Fig. 5) or a lower value (shrimps for whiting). The influence of the prior is high for species without SCA, with diet estimates essentially driven by

informative prior (Fig. 3-F). Prior information may sometimes contradict SCA data. For instance, the main prey of whiting is shrimps according to SCA, and blue whiting according to the literature (Fig. 5). In a few specific cases, the identification of a prey in the literature, even with low contribution, drives EcoDiet to estimate a large diet proportion while the prey was not observed in SCA. For instance, Norway lobster is estimated to be a major feeding source of anglerfish (Fig. 5).

A sensitivity analysis to the weight of the prior relative to the biotracer data is provided in Appendix S7. Along a gradient of this weight, two behaviors are observed among predators. For those with the higher Pedigree scores, the TD index gets closer to 0 along the gradient. For those with lower Pedigree, the TD first gets closer to 0, then diverges from it.

Synthetic trophic indicators

Trophic indicators calculated from EcoDiet synthesize the modified perception of the whole food web when integrating different sources of information. The Celtic Sea trophic structure inferred from SCA data appears less complex than previously perceived (i.e., from the literature only). The integration of SCA for one-quarter of the trophic groups leads to a reduction of 40% in the connectance index (Fig. 6, right panel). Although the relative trophic levels of the main groups remain quite similar to prior knowledge, absolute values are significantly lower after the integration of multiple data sources, especially for whiting and anglerfish (Fig. 6, left panels). This is in line with the larger contribution of low TL benthic organisms to most trophic groups' diet estimated by EcoDiet. For instance, contrary to the literature, EcoDiet estimates that whiting feeds more on low TL shrimps than on medium TL pouts. The posterior uncertainty associated with TLs varies among consumers. Interquartile range of TL ranges from 0.28 (anglerfish) to

0.45 (whiting). The larger uncertainty observed for whiting directly results from is more uncertain diet estimates (Fig.4 B).

4. Discussion

4.1 Capacities and limitations of EcoDiet

Studies integrating SCA or BA at the food-web scale remain relatively rare and mostly rely on a single data type (Ainsworth et al. 2010, Kadoya et al. 2012, Pacella et al. 2013) or use BA to simply cross-validate trophic models built upon SCA (Milessi et al. 2010, Lassalle et al. 2014, Raoux et al. 2020). On the contrary; EcoDiet is an integrated modeling framework synthesizing a diversity of information, including fieldwork data and *a priori* knowledge, that all provide complementary insights on both food-web structure and flows to enhance the estimation of diet matrix. By explicitly integrating SCA data in a likelihood term, EcoDiet directly infers from stomach occurrences how relevant it is to consider a trophic group as a prey of the consumer's population. The conditional application of the BA mixing model to the topology enhances the ability of the EcoDiet to accurately infer the diet proportions. Moreover, it allows tracking the impact of topology uncertainty on final estimates. Last, EcoDiet uses the Bayesian rationale to incorporate priors on both topology and diet matrices, and proposes a comprehensive decision process for the elicitation of such priors and for weighting the prior information relative to the data.

Though the robust identification of prey is recognized as a key preliminary step before any BA application (Nielsen et al. 2018), few studies have explored the sensitivity of diet estimates to the mixture formulation so far (Ward et al. 2011). Our results on simulated data confirmed that a proper definition of food-web topology is a prerequisite to accurately estimate diet matrices.

When the topology is incorrectly informed, the components of the mixture are misspecified what in turn results in biased estimates of diet proportion. Simulations also highlighted that the

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integration of SCA is pertinent to inform the topology and leads to similar or even better estimates than simple Bayesian network MM. These results emphasize the pertinence of the EcoDiet framework to quantify trophic interactions.

To our knowledge, the only attempts of combining SCA and BA in the same modeling framework have consisted in using SCA to elicit priors on diet proportions within stable isotope MM (Ward et al. 2010, deVries et al. 2016). Contrary to these approaches that consider SCA is indicative of the diet (in fact ingested rather than assimilated), EcoDiet uses SCA for quantitative identification of the prey consumed (probabilistic topology), i.e. what SCA is acknowledged to more reliably inform (Buckland et al. 2017). EcoDiet provides an efficient rationale to prioritize the most relevant mixture components and maximize the chances that the MM produces correct diet proportion estimates. Most probable trophic links are emphasized in the topology, while the importance of minor ones is reduced. Both the prioritization of trophic links and the probabilistic nature of the topology in EcoDiet favor lower mixture dimension. Our simulations suggest that this lower complexity enhances the MM discrimination power and improves estimates with regards to other simpler Bayesian network MM like IsoWeb (Kadoya et al. 2012). Nonetheless, To prevent over-restriction of diet matrices when using EcoDiet, attention should be paid to low prey occurrence rates induced by particular fish feeding ecology (Vinson and Angradi 2011). Additionally, those advantages of the EcoDiet model do not solve all challenges of fitting MM. EcoDiet's ability to discriminate prey and estimate high contributions still declines when the dimension of the mixture increases (Phillips et al. 2014), hence accurately identifying the proportion of high dimensional mixture from BA data remains challenging.

One main advantage of the integrated model EcoDiet over sequential approaches (e.g., Giraldo et al. 2015) is that it explicitly considers the uncertainty around the food-web topology and makes

the inferences on the diet matrix directly marginalized over this uncertainty. In other words, the uncertainty on prey identification inherent in SCA, which largely depends on sampling size, is propagated to the final diet estimates. Note, however, that this paradigm shift from a fixed to a probabilistic ineluctably goes with larger uncertainty on diet estimates.

Like some other Bayesian MM, EcoDiet uses the Bayesian rationale to integrate informative priors. These priors may efficiently complement the lack of information in SCA or BA data. For a given functional group, they could even be used conjointly with the BA signatures of its prey and predators to handle missing BA data of the former; but we recommend the number of trophic groups with missing BA data to be kept as small as possible, especially for groups with numerous trophic interactions. Informative priors should be used with caution to avoid overweigh BA information (Ward et al. 2010, Stocks et al. 2016). Future development may even develop methods to weight priors according to the informative content of BA (Yeakel et al. 2011). Even when they are not informed by the literature, uniform Dirichlet priors on diet proportions can have a strong influence if the number of prey is important, which occurs when dealing with complex food webs and cannot be alleviated by only increasing the number of BA considered (Stocks et al. 2018). Sensitivity analyses to the precision of priors conducted in our study (Appendix S7) highlighted that constraints exerted on only a few diet proportions may affect posterior estimates of the mean isotopes signatures of key trophic groups, and propagate through the food web.

4.2 What we learned from EcoDiet application to the Celtic Sea

The application of EcoDiet to the Celtic Sea case study showed the pertinence of this tool for solving complex diet matrices and improve understanding of food webs *in natura*.

While almost all trophic groups had SIA data available, the greatest changes on the perception of the Celtic Sea came from those with SIA and SCA data available, stressing the utmost importance of the latter in food-web studies. Thus, extending the species sampled for SCA would further increase our comprehension of the Celtic Sea functioning. EcoDiet only requires prey occurrences (presence or absence) instead counts, volume and/or weight determination, which are often time-consuming and expensive. Thus, it would facilitate the acquisition of more SCA data (Vinson and Budy 2011).

One key result of our study is the lower connectance estimated from EcoDiet compared to that from the literature. This difference directly results from the probabilistic representation of the topology and the drastic reduction in its complexity. As in other systems, the extensive bibliographic search conducted to build the Celtic Sea ecosystem model may have led to the consideration of many false or fortuitous and nonsignificant trophic relationships that would not have been considered once updated by local SCA data. This highlights the need for more regular trophic sampling as part of ecosystem surveys (e.g. Doray et al. 2018). However, this divergence in prey identified between the literature and SCA could also result from the sampling design, conducted during one season only and not covering the whole mosaic of environmental conditions and all species assemblages of the Celtic Sea (Hervann et al. 2020). For instance, anglerfish's isotope signatures were consistent with substantial consumption of Norway lobster, while it was not identified as a putative prey in SCA data (Issac et al. 2017) but was observed in the predator's stomachs in a neighboring ecosystem at a different season (Crozier et al. 1985).

Compared with prior knowledge, EcoDiet revealed higher contributions of benthic and invertebrate compartments to the diet of most species, resulting in lower trophic levels for many predators and lower importance of the pelagic pathways in biomass flows. This suggests that the

overall functioning of the Celtic Sea may be closer to that of the neighboring English Channel than that of the pelagic-dominated Bay of Biscay (Cresson et al. 2020).

Because of the environmental diversity characterizing the Celtic Sea (Hervann et al. 2020, Walters et al. 2021), the generalist feeding behavior and ontogenetic diet shifts of some species (Rault et al. 2017, Issac et al. 2017, Day et al. 2019), the functional redundancy of several groups (Mérillet et al., under review) and benthic-pelagic coupling (Hervann et al., 2020), data exhibited high intra-group variability and among-group overlap in isotope signatures. Thus, posterior distributions of dietary proportions were often diffuse, pointing out the limits of bulk SIA for studying such complex ecosystems. Future research avenue to better quantify biomass flows in the Celtic Sea would consist in conducting other types of BA for which the version of EcoDiet presented in this study is already operational. More specifically, SIA could be performed and integrated into EcoDiet. SIA could be performed for other elements like sulfur ($\delta^{34}\text{S}$, McCutchan et al. 2003) or specific-compounds such as amino acids (McMahon et al. 2010), which would specifically improve baseline assignment. Like the FASTAR model (Galloway et al. 2015), EcoDiet could also be applied to fatty acids analyzes. The combination of such BA in Bayesian MM has already successfully proved to improve diet estimates (Brett et al. 2016, Neubauer and Jensen 2015).

4.3 A promising tool to enhance food-web studies

Benefitting from the associated R package, EcoDiet could be applied to other systems and has the capacity to make a substantial contribution to descriptive food-web studies and help to make trophic ecology and ecosystem modeling even more operational tools of integrated management of ecosystems.

EcoDiet may be a useful tool to valorize a large amount of SCA and BA data increasingly accessible through open-access databases of trophic data. For instance, the DAPSTOM database (Pinnegar and Stafford 2018) brings together more than 100,000 records of SCA over one century for the North-East Atlantic, while Jennings and Cogan (2015) record SIA of more than 5000 fish and squid individuals in a similar area. Mobilizing this wealth of information, EcoDiet provides an excellent opportunity to investigate changes in the feeding ecology of trophic guilds and the food-web structure of European ecosystems over several decades (Kortsch et al. 2021).

Diet matrices are key inputs of species-based ecosystem models (direct entry in Ecopath with Ecosim; used to calculate “availability” matrices in Atlantis, (Tarnecki et al. 2016)). EcoDiet may become a reference tool for estimating diet matrices in ecosystem models, improving the transparency of their construction and making easier inter-model comparisons. It could also be used to validate outputs of other types of ecosystem models, including the individual-based Osmose model (Shin and Cury 2001, Travers-Trolet et al. 2014). The uncertainty quantified by EcoDiet could be propagated to study the sensitivity of model outputs arising from the diet matrix (e.g., Essington 2007, Morzaria-Luna et al. 2018, Bentley et al. 2019).

Synthetic indicators estimated from EcoDiet outputs (eg., TL) in a probabilistic rationale could support integrated ecosystem assessments (Reed et al. 2016) or management policies (Rombouts et al. 2013). The use of the EcoDiet’s SCA module alone could also be a way to integrate data-related uncertainty into qualitative studies of trophic networks and propagate it to the calculation of topological indices such as connectance, mean shortest path length, generality, vulnerability, etc. (Dunne et al. 2002, Bersier et al. 2002). These approaches proved to be useful to quantify trophic network stability, robustness and reorganization under various pressures (Kortsch et al. 2018, Vinagre et al. 2019).

4.4 Perspectives for improving EcoDiet

Building on its ability to work at the trophic network scale, further improvements of the EcoDiet model could allow the exploration of key issues in multiple fields. For instance, this framework could improve the use of BA in trophic ecology. BA such as isotope analyses are largely influenced by local environmental conditions. Thus, they often need a baseline correction accounting for the spatio-temporal changes in the basal food-web source signatures (Post, 2002). Several baselines could be required to account for the fact that baselines of food-web sources can vary according to the pathways, e.g. benthic or pelagic (e.g., Kiljunen et al. 2020). The network structure of EcoDiet could allow correcting each group signature by different baselines, proportionally to the contribution of each pathway to their diet. EcoDiet could also be developed to bring light to changes in physiological characteristics through the food web. Our model estimates consumer-specific values of the trophic discrimination factors. By adapting the way that trophic discrimination factors are represented in the model, EcoDiet could be used to estimate *a posteriori* or integrate *a priori* relationships between trophic discrimination factors and functional group characteristics, e.g. the mean prey TL. Such analyses could provide fieldwork-based evidence of physiological patterns already identified through laboratory experiments (Caut et al. 2009, Hussey et al. 2014).

EcoDiet could also provide insights into the influence of factors such as seasons in the terrestrial realm, or depth in the marine realm (e.g., Parnell et al. 2013, Giraldo et al. 2017). Of particular interest would be the integration of environmental covariates in the topology and diet estimates within EcoDiet, especially through categorical or continuous effects as in Stock et al. (2018). Such new capacities would highlight global patterns in food-web structuration and functioning along time and environmental gradients.

Last, the present version of the EcoDiet model is not properly designed to integrate DNA data yet. Despite new approaches that have been recently developed, DNA metabarcoding of stomach contents remains more adapted to prey identification rather than diet quantification. In this context, future developments of EcoDiet could integrate DNA to infer the food-web topology. Though this would imply limited modifications of the model structure, potential adaptations may be required to, for instance, account for primers availability, likely lower sampling sizes than for SCA, higher detectability of irrelevant prey etc. The application of EcoDiet is limited so far to terrestrial and aquatic food webs dominated by macrofauna and megafauna for which stomach, gut or scat contents can be visually inspected. This integration of DNA data would enable the transfer of EcoDiet to other systems characterized by smaller organisms, like soil macro-mesofauna above ground food-webs, soil food-webs etc (e.g., Eitzinger et al. 2013, Roslinet and Majaneva 2016, Toju and Baba 2018), hence making available this tool for the whole community of food-web ecologists.

5. Acknowledgments

This work was part of a PhD funded by IFREMER and *Région Bretagne*. Data used in this study were issued from the EAMTE project, which was supported by *France Filière Pêche* and *Région Bretagne*. The authors thank Guillaume Allanic, Margaux Denamiel, and Dominique Huteau for their help onboard the R/V *Thalassa* and/or in the laboratory. We thank the Stable Isotopes in Nature Laboratory (SINLAB, New Brunswick, Canada) for having realized stable isotope analyses. The main author dedicates this work to Marie-Henriette Du Buit.

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7. Tables

Table 1 – Data, Parameters, variables and associated priors used in EcoDiet. Module: the module the variable belongs to; Origin: D for data, E for estimated, F for fixed values.

Module	Variables	Definition	Origin	Priors or fixed parameter values	
				Uninformative	Informative
LITERATURE	g_i	Pedigree score for the literature information on i's diet	F	–	Fixed according to the decision tree
	n^{lit}	number of "equivalent stomachs" for a literature information of Pedigree=1	F	–	30
	ζ_i	regulator on literature information on the topology	F	–	$n^{lit} * g_i$
SCA	$\eta_{i,k}$	probability of the existence of a link from i to k	E	$Beta(1,1)$	if observed in literature $Beta(\zeta_i - 1, 1)$ if not observed in literature $Beta(1, \zeta_i - 1)$
	$o_{i,k}$	occurrence of k in i	D	–	–
	n^{SCA}_i	number of i's stomachs analyzed	D	–	–
	s_i	number of feeding sources of i	E	$s_j = \sum A_{i,k}$	$s_j = \sum A_{i,k}$
	$A_{i,k}$	existence/absence of link from j to i	E	$Bernoulli(\eta_{i,k})$	$Bernoulli(\eta_{i,k})$
SIA	$\mu_{j,i}$	mean isotopic signature of trophic group i for element j	E	$Norm(0, 10^{-6})$	–
	$\Pi_{i,1}, \dots, \Pi_{i,I}$	proportions of 1 to I preys in j's diet	E	$Dirich(1, \dots, 1)$	$Dirich(\alpha_{i,1}, \dots, \alpha_{i,I})$
	$q_{j,k}$	concentration in element j of the trophic group i	D	–	–
	$\delta_{j,i}$	i's trophic discrimination factor for element j	E	–	$Norm(\Delta_j, \tau_{j,i})$
	$y_{j,i,l}$	observed isotopic signature in element j for species l th sample of group i	D	–	–
	Σ_i	covariance matrix between the E mean isotopic signatures of i	E	$Wish(Identity^E)$	–
	Δ_C	prior for mean trophic discrimination factor in element C	F	–	0.8‰
	Δ_N	prior for mean trophic discrimination factor in element N	F	–	3.4‰
	$\tau_{j,i}$	standard deviation of the trophic enrichment factor of element j for group i	E	$Half-Cauchy(0,25)$	–
LITERATURE	$\alpha_{i,1}, \dots, \alpha_{i,I}$	priors for $\Pi_{j,i}$ dietary proportions	F	$\alpha_{i,l} = \dots = \alpha_{i,I} = 1$	$\alpha_{i,k} = \frac{\Lambda_{i,k} * \alpha_{i,k}^{lit} * l_i * s_i}{\sum_{l=1}^I \Lambda_{i,l} * \alpha_{i,l}^{lit}}$

	$\alpha^{lit}_{i,1}, \dots, \alpha^{lit}_{i,I}$	dietary proportions from the literature	D	-	-
	CV_i^{ped}	coefficient of variation indicated by the Pedigree score of i	F	-	Fixed according to the decision tree
	t_i	sample size of informative priors on $\Pi_{i,1}, \dots, \Pi_{i,I}$	F	-	$t_i = \begin{cases} (s_i - 1)/CV_i^{ped} - 1 & \text{if } s_i > 1 \\ 1 & \text{if } s_i = 1 \end{cases}$

Table 2 – Sequential implementation and sensitivity analysis of the EcoDiet model applied to the Celtic Sea: data and informative priors required for configurations 1 to 3.

	SCA data	SIA data	Literature data	Hypothesis on the parameters	
				Topology	Dietary proportions
Configuration 1	none	X	none	Fixed topology based on the literature	Uninformative priors
Configuration 2	X	X	none	Uninformative priors	Uninformative priors
Configuration 3	X	X	X	Informative priors with $n^{\text{lit}} = 30$	Informative priors
Sensitivity 1	X	X		Informative prior with varying n^{lit} between 0 and 150	Informative priors same as Config. 2
Sensitivity 2	X	X		Informative priors with $n^{\text{lit}} = 30$	Informative prior with varying CV-Pedigree relationship

Figures

Legends

Figure 1 - Scheme of the workflow of EcoDiet. The informative prior module allows for defining informative priors on both the topological matrix and on the diet proportions. The SCA module integrates stomach contents data. The BA module integrates bio-tracers.

Figure 2 – Simulated data. Comparison of the estimation performance of IsoWeb and EcoDiet on simulated data. Boxplots represent Discrimination and Precision of diet estimates obtained under the different scenarios. EcoDiet model is applied to data simulated under 4 different scenarios, with varying quality and quantity of SCA data: Scenario A = SCA data representative and with large sampling size, B = representative with small sampling size, C = unrepresentative with large sampling size, and D = unrepresentative with small sampling size (details on the scenarios in the main text and Table S1, Appendix S4).

Figure 3 – Celtic Sea case study. Estimates of the food-web topology (A, B & C) and diet matrix (D, E & F) under the different configurations. Config. 1 (A & D): fixed topology from the literature, non-informative prior on diet and SIA data; Config. 2 (B & E): non-informative prior on topology and diet proportions combined with SCA and SIA data; Config. 3 (C & F) incorporation of literature-derived priors on food-web topology and dietary proportions, combined with SCA and SIA data. Appendix S5: Table S1 provides the trophic groups corresponding to all numbers represented in this figure.

A, B & C: only edges related to the trophic groups with SCA available were represented (circles); edge widths are proportional to the mean posterior probability that each link exists; blue, orange and purple edges respectively correspond to links whose existence is inferred from literature only, from SCA only or from both of them.

D, E& F: prey are rows and predators are columns; prey are ranked by decreasing trophic level (calculated based on the diet matrix from the literature); for each predator, dietary proportions are centered on 1 over the number of estimated proportions. A dominance of pale colors in a column indicates that similar proportions are estimated for all prey of the concerned predator; conversely, a column filled with bright colors indicates more diverse proportions of the prey in the diet of the predator. Predators' names are colored according to the available data: Literature only in blue, SIA and literature in orange, and SCA, SIA and literature in purple.

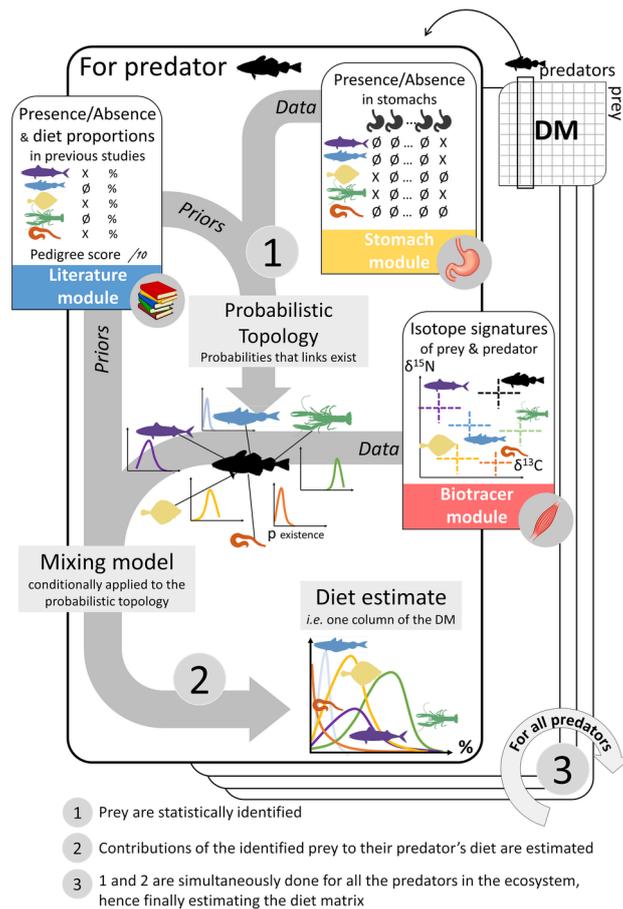
Figure 4 – Celtic sea case study. Deviation of EcoDiet estimates from the literature

knowledge according to the three configurations. (A): average deviation for the food-web topology; (B): total deviation for the diet estimates. Colors correspond to model configurations. Config. 1 (red): fixed topology from the literature, non-informative prior on diet and SIA data; Config. 2 (Yellow): non-informative prior on topology and diet proportions combined with SCA and SIA data; Config. 3 (Green) incorporation of literature-derived priors on food-web topology and dietary proportions, combined with SCA and SIA data. Changes in the estimates are explored for (i) the three focus species (Left: Whiting, Center: Anglerfish, Right: Haddock) (ii) all the trophic groups with SCA data available (mean over the species, top-right) and for (iii) all the trophic groups without SCA available (mean over the species, top-left). The full lines link to the mean values of the indicators over all the MCMC samples while the shaded ones link the indicators got for a given MCMC sample.

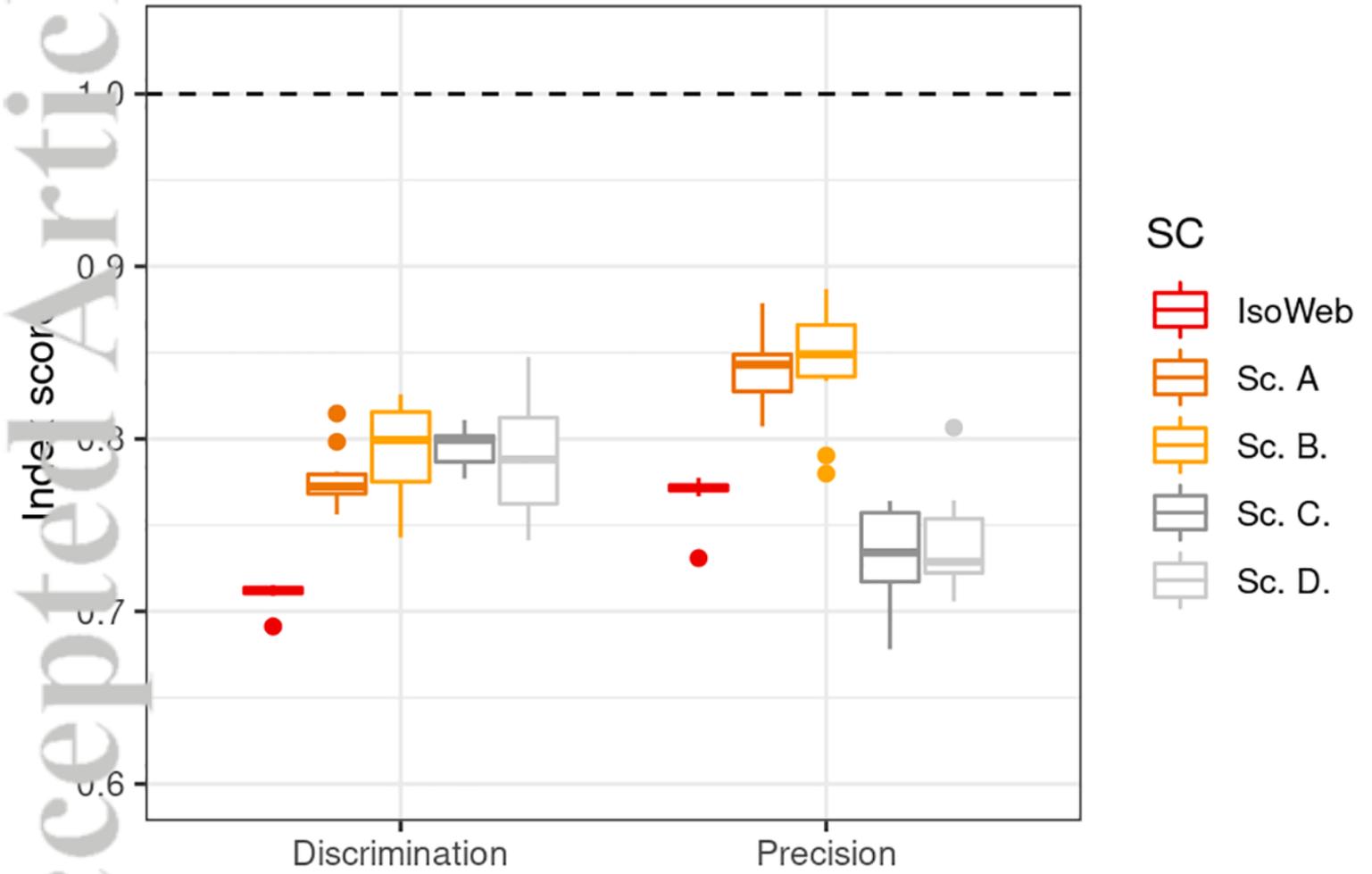
Figure 5 - Celtic sea case study. A selection of marginal prior and posterior distributions of the probabilities of the existence of a trophic link and the dietary proportions. Priors and posteriors are represented for prey-predator couples implying the three focus species and providing interesting illustrations on the functioning and behavior of EcoDiet. Left: Haddock,

Center: Anglerfish, Right: Whiting. The colors of the density function correspond to model configurations. Config. 1 (red): fixed topology from the literature, non-informative prior on diet and SIA data; Config. 2 (Yellow): non-informative prior on topology and diet proportions combined with SCA and SIA data; Config. 3 (Green) incorporation of literature-derived priors on food-web topology and dietary proportions, combined with SCA and SIA data. Blue curves correspond to priors derived from the literature.

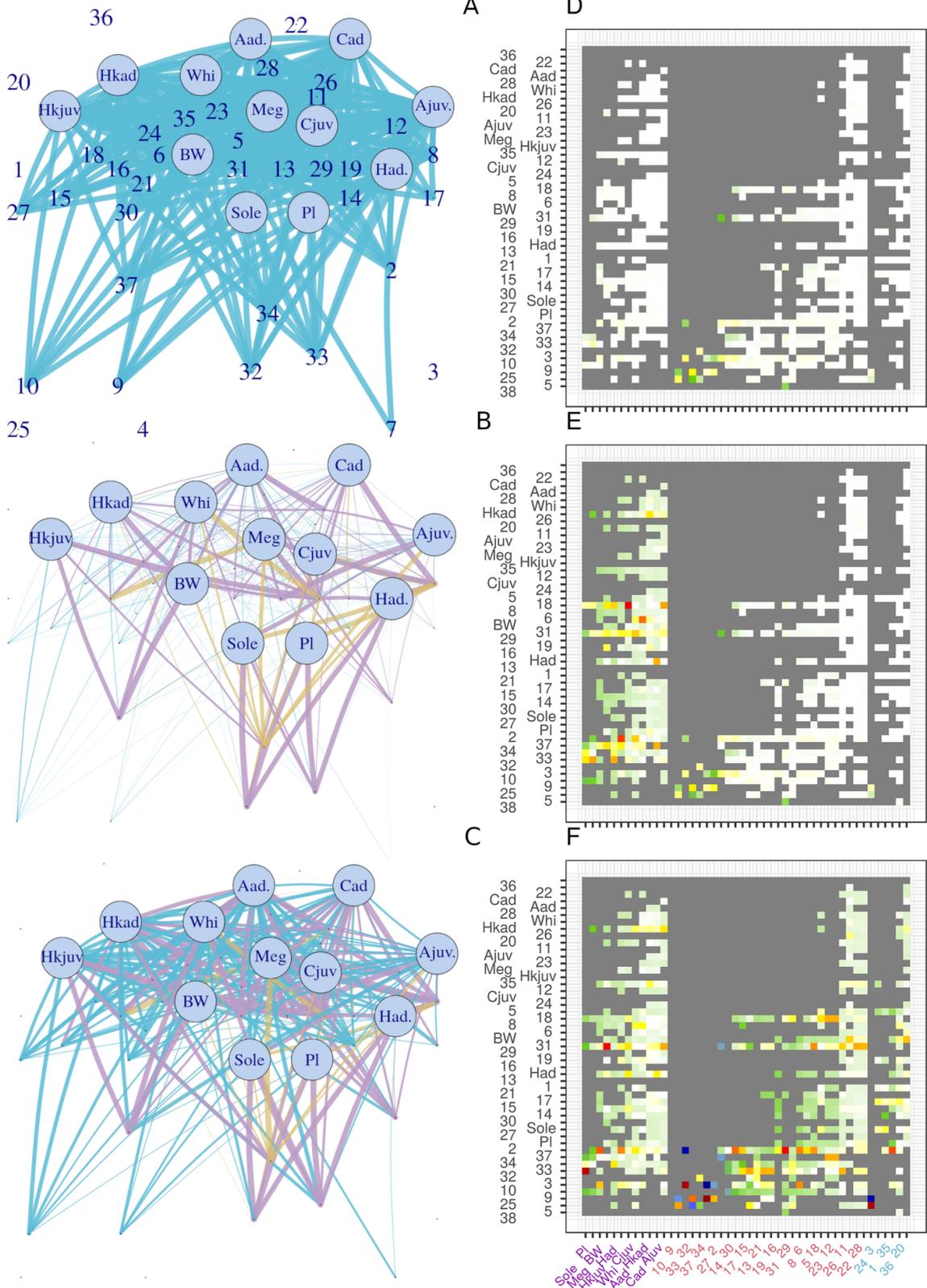
Figure 6 - Celtic Sea case study. Posterior distribution of trophic indicators calculated from EcoDiet outputs and comparison to the knowledge from the literature. Green boxplots represent estimates from the full EcoDiet model. Left panels: estimates of Trophic Levels for the three focus species; Right panel: the food-web connectance. Blue points correspond to the most credible values derived from the literature.



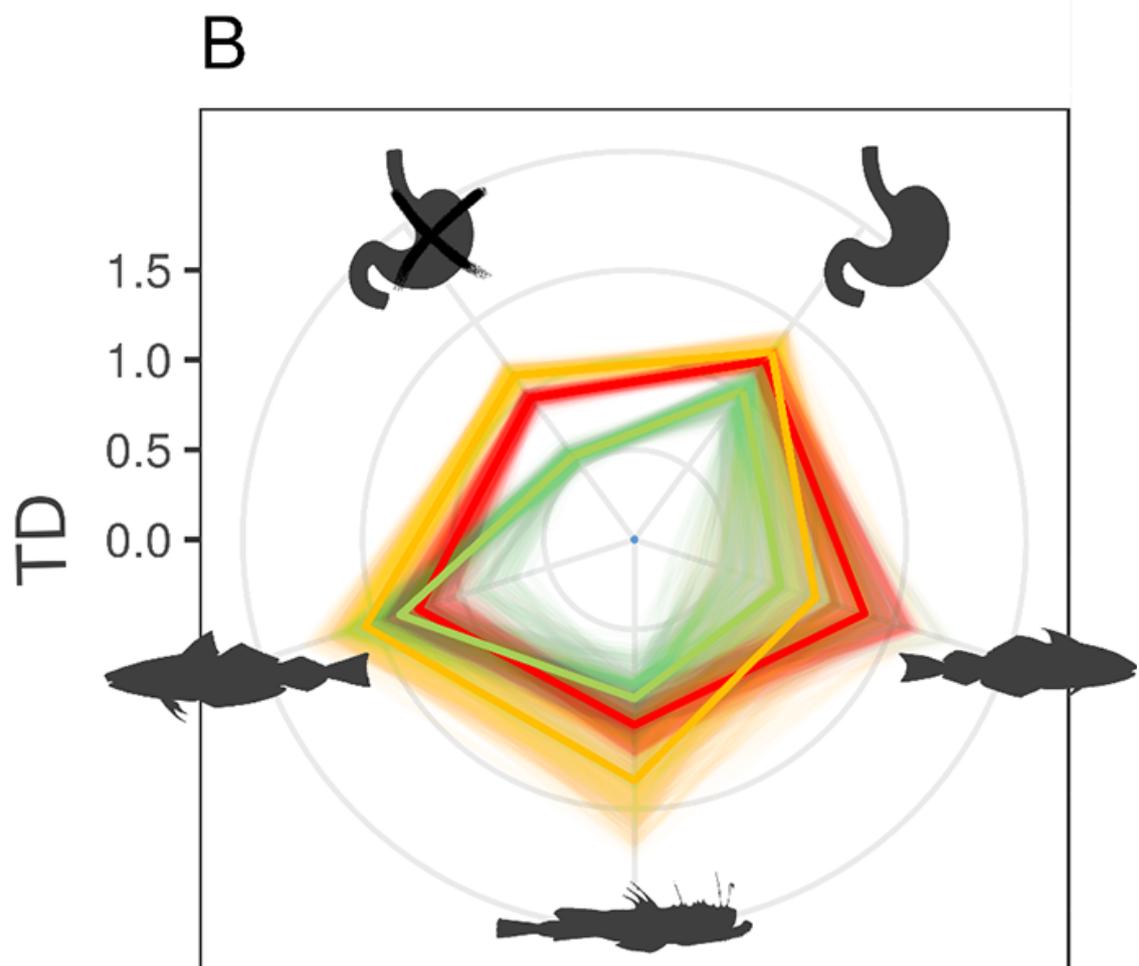
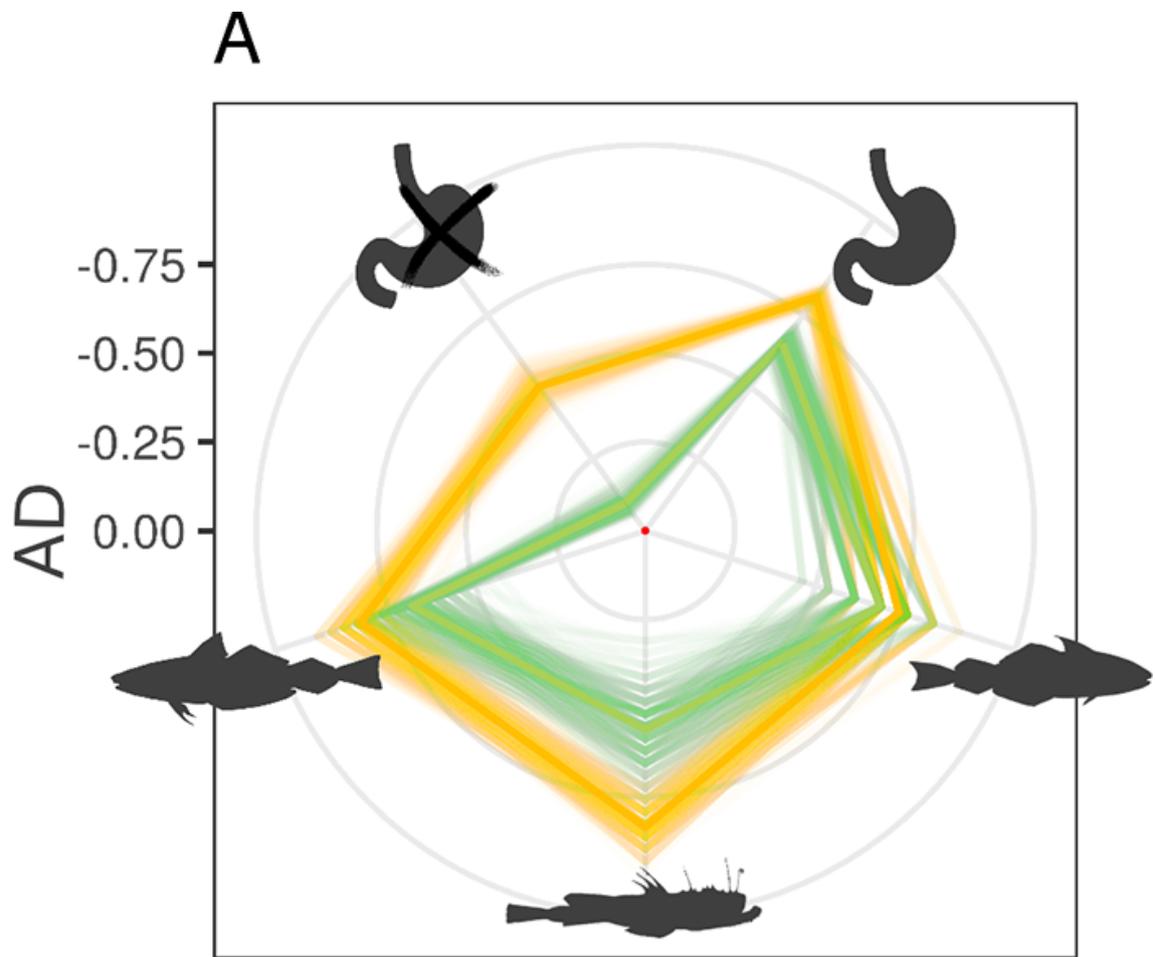
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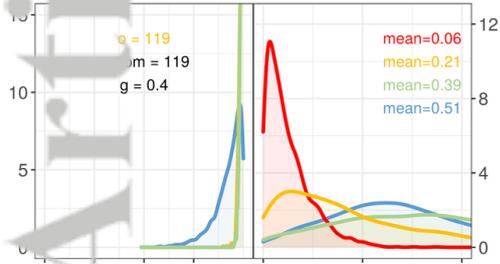


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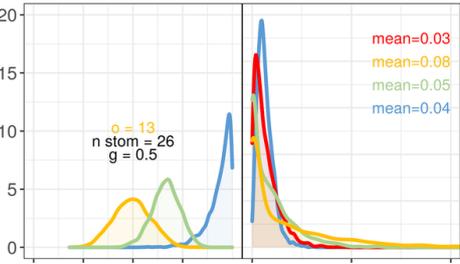




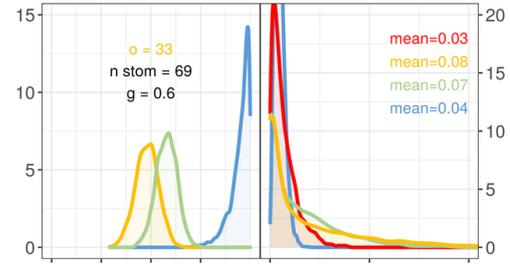
Carniv. & Necrophg.



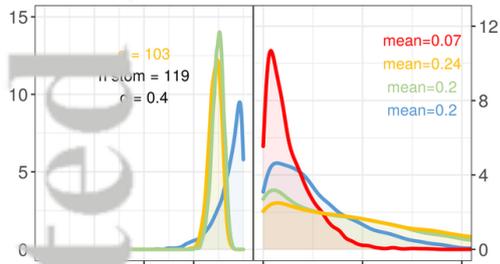
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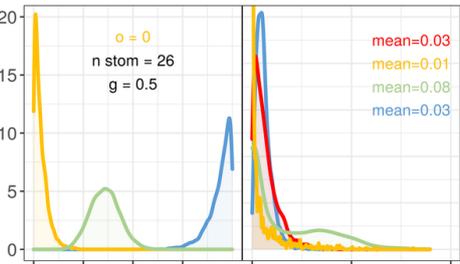
Blue whiting



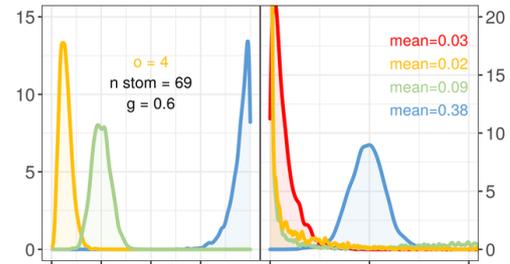
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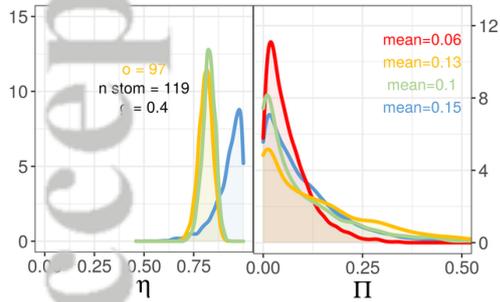
Norway lobster



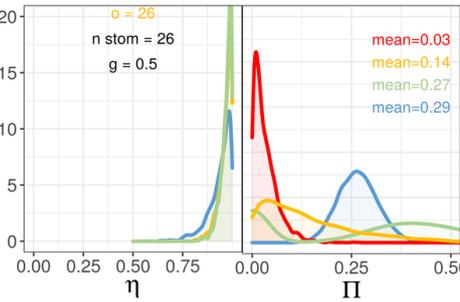
Pouts



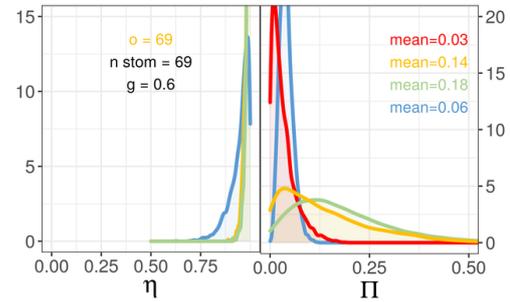
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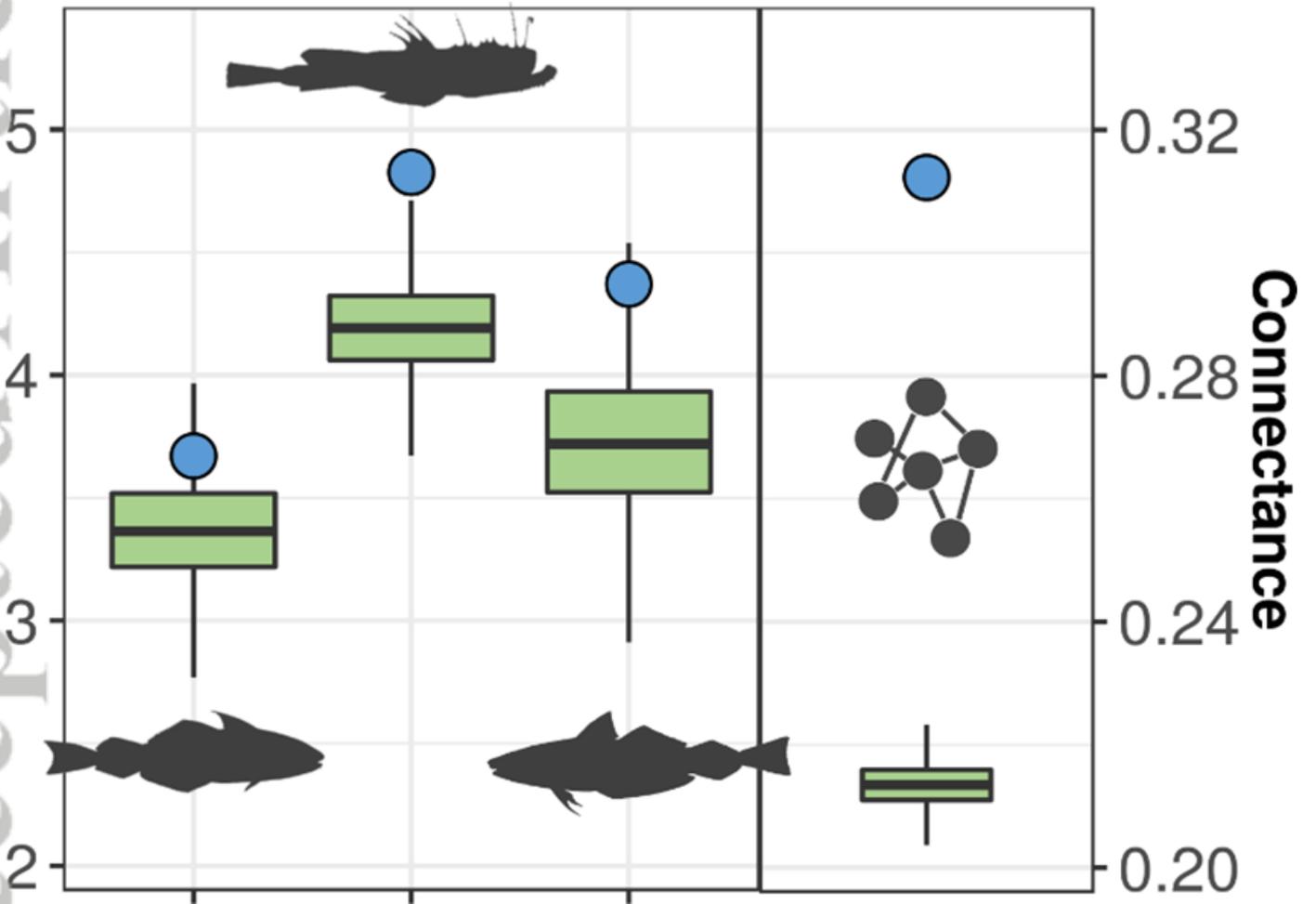
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Shrimps



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