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RESEARCH ARTICLE

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Integrating abundance and diet data to improve inferences of food web dynamics

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Abstract

1. Both population abundances and chemical tracers are useful tools for studying consumer-resource interactions. Food web models parameterized with abundances are often used to understand how interactions structure communities and to inform management decisions of complex ecological systems. Unfortunately, collecting abundance data to parameterize these models is often expensive and time-consuming. Another approach is to use chemical tracers to estimate the proportional diets of consumers by relating the tracers in their tissues to those found in their food sources. Although tracer data are often inexpensive to collect, these diet proportions provide little information on the per-capita consumption rates of consumers. Here, we show how coupling these data sources leads to better estimates of consumption rates.
2. Our modelling approach integrates traditional multispecies population abundance models with proportional diet estimates. We used simulations to determine whether integrated food web datasets were more informative than the standard abundance datasets and demonstrated the use of our integrated approach by estimating consumption rates of hump-back whales *Megaptera novaeangliae* in the western Gulf of Alaska using abundances coupled with stable isotopes as tracers.
3. Our simulations demonstrated that integrated models improved the ability to resolve alternative hypotheses about the functional response and yielded more precise parameter estimates relative to standard food web models. The integrated data approach was especially informative under low sample sizes or high process variance. Our application of the integrated modelling approach to humpback whales indicated that fish averaged about 25% of whale diets, though this proportion declined over the course of the study. We also found that traditional abundance model estimates of humpback whale consumption were non-estimable and that the integrated food web model led to estimable consumption rates.
4. Our results show that integrating stable isotopes and abundance datasets provides an exciting way forward for parameterizing multispecies models in data-limited systems. We expect that future developments of these integrated approaches will extend current food web theory by allowing ecologists to study predation dynamics over seasonal time-scales and at the individual level.

KEYWORDS
ecological tracers, food web model, functional response, integrated modelling, multispecies modelling, nonlinear time series, stable isotopes

1 | BACKGROUND

Food web models allow ecologists to study how interspecific interactions drive the emergent complexity of communities (Thompson et al., 2012). These models have revealed important relationships between biodiversity and ecosystem stability (May, 1972) and have practical applications for understanding the sensitivity of populations to the indirect effects of management decisions (Yodzis, 1998). Unfortunately, the difficulties inherent in parameterizing food webs limit both our ability to study empirical patterns in these complex systems and the empirical applications of these models.

Collecting abundance data, which is commonly used to parameterize dynamic food web models (e.g., Ives, Dennis, Cottingham, & Carpenter, 2003), is time-intensive and costly, as multiple species must be surveyed. The sampled populations are also often a subset of all the relevant biotic and abiotic factors in the system. Standard abundance models rely on using correlations between abundances through time to infer consumption rates. This approach has the potential to misidentify the influence of factors such as unsampled populations and climate factors as direct interactions between the sampled populations. A classic example of this phenomenon is apparent competition, in which two negatively correlated populations appear to be competing but instead are regulated by an unobserved consumer (Holt, 1977).

Bioenergetics modelling is another approach sometimes used to obtain consumption rates for multispecies models. This method uses routinely collected data to partition the energy obtained from food to an individual's growth, metabolism and waste products (Ney, 1993). In the few cases where validation of this approach is possible, estimates have routinely overestimated consumption, sometimes by several orders of magnitude (Chipps & Wahl, 2008). One previous study has coupled stable isotopes with bioenergetics models to determine prey consumption (Caut, Roemer, Donlan, & Courchamp, 2006). This approach, while useful, suffered from similar issues as standard bioenergetics models. Thus it is not clear that the bioenergetics approach is currently capable of producing reliable consumption rates for multispecies models.

Direct measurements of individual diet through the use of ecological tracers has proven to be a breakthrough in nutritional ecology (Galloway et al., 2015; Kartzinel et al., 2015; Phillips & Gregg, 2001). Stable isotopes, in particular, have been used to estimate the trophic position of species (Vander Zanden, Casselman, & Rasmussen, 1999), the proportional diets of consumers (Phillips & Gregg, 2001) and parameterize ecological networks (Yeakel et al., 2012). Unfortunately, ecological tracers such as stable isotopes have been of limited use for understanding food web dynamics as they only measure diet proportions, which contain information on relative consumption, rather than the per-capita consumption values necessary to model the effect of predators on their prey.

In this study, we propose a new integrated modelling approach for parameterizing food webs. We show how to combine population abundance data collected at multiple trophic levels with proportional diets of consumers, derived from stable isotopes, to estimate the functional response of consumers. Combining multiple independent data sources mirrors integrated methods in population demography, which have successfully been used to parameterize complex models (Schaub, Gimenez, Sierro, & Arlettaz, 2007). Our approach constrains consumption estimates to be consistent with both the observed population dynamics and diets thus leading to predictions that are consistent with empirical dynamics.

2 | MATERIALS AND METHODS

We demonstrate our integrated modelling approach in two ways. First, we simulated the discrete-time dynamics of a consumer–resource interaction. We then fit two types of models to these simulated datasets, abundance and integrated data models (described in detail below). This comparison allowed us to investigate how well each of the data models performed in both model selection and parameter estimation. Second, we fit the abundance and integrated models to data collected on humpback whales *Megaptera novaeangliae* and their prey in the western Gulf of Alaska using continuous-time models. These continuous-time models illustrate how to account for isotopic turnover in tissues occurring due to tissue replacement.

2.1 | Models

2.1.1 | Dynamical models

In this section, we describe two sets of models that can be used to describe how the processes of population growth and regulation as well as interspecific interactions drive community dynamics. The following section then describes how to connect these models to the data we collect.

The first set of difference equations is used to simulate time series of population abundances and of proportional diets. Discrete-time models may not be biologically realistic for many predator–prey processes but they are often reasonable approximations, and for simulation studies they have the additional advantage that they are fast to simulate. The second set of models are continuous-time models of predation that we fit to a dataset of humpback whales and their prey. We use these continuous models to highlight how to the incorporate isotopic turnover of tissues.

Our system of difference equations contain a predator (P) and two prey (N_1, N_2):

$$\begin{aligned} P(t+1) &= \left[\varepsilon_1 N_1(t)\left(1-e^{-g_1(P(t),N_1(t),N_2(t))}\right)\right. \\ &\quad \left.+\epsilon_2 N_2(t)\left(1-e^{-g_2(P(t),N_1(t),N_2(t))}\right)+P(t)e^{-\mu}\right] e^{\sigma_P Z_P(t)} \\ N_1(t+1) &= \left[r_1 N_1(t) e^{-s_1 N_1(t)-g_1(P(t),N_1(t),N_2(t))}\right] e^{\sigma_1 Z_1(t)} \\ N_2(t+1) &= \left[r_2 N_2(t) e^{-s_2 N_2(t)-g_2(P(t),N_1(t),N_2(t))}\right] e^{\sigma_2 Z_2(t)}. \end{aligned} \quad (1)$$

The reproductive rate and strength of density dependence of each prey population is given by r and s respectively. The density-independent mortality rate of the consumer is given by μ. Populations are subjected to process error at each time step, $Z(t)$, drawn from a standard normal distribution scaled by σ, the standard deviation. This error can be interpreted as temporal variation in the reproductive rate (Ferguson & Ponciano, 2015). The term, $1-e^{-g(P(t),N_1(t),N_2(t))}$, is the probability that an individual in the prey population does not escape consumption, while the efficiency of converting prey to new enemies is given by ε. Here we examined discrete-time equivalents of the type I and type II functional response. For a discrete-time type I response, $g(P(t), N_1(t), N_2(t))$ is given by $cP(t)$, where c is the per-capita consumption rate of the predator on the prey. For the type II response of the predator on the first prey population it is $\frac{c_1 P(t)}{1+c_1 h_1 N_1(t)+c_2 h_2 N_2(t)}$ (Mills & Getz, 1996) and the functional response for the second prey population is given by $g_2(P(t),N_1(t),N_2(t))=\frac{c_2 P(t)}{1+c_2 h_2 N_2(t)+c_1 h_1 N_1(t)}$. Parameters used to simulate system 1 are given in Table 1.

A discrete-time system is appropriate for host–parasite interactions or predator–prey interactions when the sampling frequency is high relative to reproductive and consumption rates. However, continuous-time models may be more suitable for many other systems. We consider such a continuous-time process in our analysis of a dataset of humpback whales and their prey (data described in Section). This system is

$$\begin{aligned} \frac{N_{\text{fish}}}{dt} &= r_{\text{fish}} N_{\text{fish}} - c_{\text{fish}} P N_{\text{fish}} \\ \frac{N_{\text{zoo}}}{dt} &= r_{\text{zoo}} N_{\text{zoo}} - c_{\text{zoo}} P N_{\text{zoo}}. \end{aligned} \quad (2)$$

TABLE 1 Parameters used for simulations

Parameter	Symbol	Value
Conversion efficiency		
Type I and II response	$\varepsilon_1, \varepsilon_2$	0.6, 0.6
Consumption rate		
Type I response	c_1, c_2	0.0002, 0.00024
Type II response	c_1, c_2	0.001, 0.003
Half-saturation coefficient		
Type II response	h_1, h_2	5, 5
Predator mortality rate	μ	0.1
Prey growth rate	r_1, r_2	1.8, 1.8
Strength of prey density dependence process error	s_1, s_2	0.001, 0.001
Type I and II response	$\sigma_P, \sigma_1, \sigma_2$	Varied

The growth rates of fish and zooplankton are given by r_{fish} and r_{zoo}, whereas the per-capita consumption rates of fish and zooplankton by whales are given by c_{fish} and c_{zoo}. We denote abundances of fish as N_{fish}, zooplankton as N_{zoo}, and whales as P. We did not build an explanatory model of within-year changes in humpback whales (P) because we assumed that this slow-growing population did not change throughout the feeding season and that changes between years may reflect factors other than limitation by prey, such as the humpback whales relatively recent release from commercial harvest (Gabriele et al., 2017).

2.1.2 | Data models

In this section, we describe how to fit food web models using either abundance data or abundance data coupled with proportional diet data. Parameterizing these models with abundance data is a well-developed approach (see Ives et al., 2003; Koen-Alonzo & Yodzis, 2005), how-ever linking information about the proportional diets to these dynamics is novel. This link is achieved by understanding that the proportional diet is the total number of prey of a certain type consumed in a given time period relative to all other prey consumed during that same time period. The number of consumed prey is given by the integral of the functional response.

Our first data model was informed using only the time series of abundances. This abundance model assumed that the population abundance at each time step followed a log-normal probability distribution representing fluctuations in the environment that were not accounted by our model. At each time step we conditioned abundance predictions on the previous time step, except for the first observation, which was only used to predict the second observation (following, Ferguson & Ponciano, 2014). When fitting the humpback whale dataset, we also included the uncertainty in estimated abundances (P, N_{fish} and N_{zoo}) as observation error. The full specification of this state-space model is given in Appendix S1.

Our second approach is an integrated data model that utilizes both the abundance and proportional diet data to inform the models. The estimated dietary proportion data is linked to abundances by recognizing that this proportion can be written in terms of the consumed prey predicted by the functional response in the dynamical model. For the first prey population in a discrete-time system with type I functional response this proportion is, $p_1(t+1)=\frac{N_1(t)(1-e^{-c_1 P(t)})}{N_1(t)(1-e^{-c_1 P(t)})+N_2(t)(1-e^{-c_2 P(t)})}$ We are particularly interested in applying this model to proportional diet data derived from stable isotopes, where we may also need to account for isotopic turnover, the time required for the isotopic composition of an animal to reflect its diet (Vander Zanden, Clayton, Moody, Solomon, & Weidel, 2015). In this approach, the predicted diet at time $t+1$ is the integrated consumption of prey weighted by the isotopic turnover rate. This gives the diet proportion:

$$p_1(t+1)=\frac{\int_t^{t+1} e^{-\lambda(1-t)} f_1(P(t),N_1(t),N_2(t))\,dt}{\int_t^{t+1} e^{-\lambda(1-t)} f_1(P(t),N_1(t),N_2(t))\,dt+\int_t^{t+1} e^{-\lambda(1-t)} f_2(P(t),N_1(t),N_2(t))\,dt}, \quad (3)$$

where λ is the rate of isotopic turnover and the functions f_1 and f_2 are the functional responses of the predator for each of the two prey populations. When the turnover rate is very low, such that $\lambda \approx 0$, this integral is the average proportional diet over the survey period. As the turnover rate increases, this becomes a weighted average where more recently consumed items are more important.

We fit the predicted diet proportions to the observed diet proportions using a nonlinear logistic regression model with a mean given by the logit transform of the predicted proportion. The integrated log-likelihood is then the sum of the contributions from the logistic and the abundance time-series models.

2.2 | Simulation study

We used simulated data generated from dynamical system 1 to test how informative the addition of proportional diet data is for parameter estimation and on the ability to select the generating model from a set of alternative hypotheses. We simulated data under each of the type I and type II functional responses and fit both types of functional response as competing hypotheses to the generated data. In these simulations, we assumed that isotopic turnover could be ignored. This assumption is safe to make in scenarios when the turnover rate of the sampled tissue is approximately zero over the sampling period (e.g. inert tissues, such as hair, that records the diet since the previous molt). It could also be safe to make this assumption when changes in abundance between sampling periods are small. We made this assumption primarily to reduce the amount of computation needed for these simulations but note that incorporating turnover will not change the relative performance of these models.

Simulated time series were generated from system 1 for the type I and type II functional response using low ($\sigma = 0.1$), medium ($\sigma = 0.25$) and high ($\sigma = 0.5$) levels of process error, where we assumed the same value of σ for both prey and the predator populations. To generate datasets, we first simulated 500 time steps to ensure that the populations reach stationarity. We then selected sets of 10–100 observations from the end of the 500 samples, incrementing over this range by 10 to explore the effects of sample size on inference. For each combination of process variance/sample size/functional response, we simulated 10,000 realizations of the process and fit the abundance and integrated data models to each dataset. We fit both type I and type II models to each simulated dataset. Models were fit in R using the NLOPTR package (Ypma, 2015) using a two-stage optimization procedure. We first used the global dividing rectangles algorithm (Gablonsky & Kelley, 2001), following this up with the Nelder–Mead algorithm (Box, 1965) to achieve convergence.

For each fitted dataset, we calculated the Bayesian Information Criterion (BIC) for the two competing functional response models to determine the most parsimonious model in the set (Burnham & Anderson, 2002). We then calculated the proportion of times that the generating model was selected by BIC using each data model for each process variance/sample size/functional response combination. We also calculated the bias of parameter estimates on the log-scale for each process variance/sample size/functional response combination. We note that the number of time points sampled is not equal to the sample size. For the abundance model with ten-time points, the total sample size is the 9-time points predicted by the model for each of the three populations sampled for a total sample size of 27. The integrated model has the sample size of the abundance dataset plus the number of diet proportions used. For a sample of 10-time points, this corresponds to a total sample size of 36 (27 abundance samples and nine diet proportion samples). All data and code used for these analyses are provided on the Dryad Digital Repository (https://doi.org/10.5061/dryad.5q136q2).

2.3 | Empirical study: The functional response of humpback whales

We used the abundance and integrated models to understand the impact of humpback whales on their prey populations in the western Gulf of Alaska. These migratory baleen whales play a major role in structuring this ecosystem through predation (Witteveen, Foy, & Wynne, 2006; Witteveen, Worthy, Foy, & Wynne, 2012; Wright, Witteveen, Wynne, & Horstmann-Dehn, 2015). Our dataset consisted of annual humpback abundances and the relative abundances of their zooplankton and fish prey estimated from past surveys (Witteveen, De Robertis, Guo, & Wynne, 2015; Wynne & Witteveen, 2015). We also estimated the proportional contributions of these major food sources to the diets of whales each year using the IsotopeR stable isotope mixing model (Hopkins & Ferguson, 2012). In particular, we used carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$) stable isotope ratios (expressed as $\delta^{13}C$ and $\delta^{15}N$) from individual whales ($n = 114$), fish ($n = 211$) and zooplankton ($n = 36$) to estimate dietary parameters. We then estimated consumption rates of humpback whales using both the standard abundance model and the integrated model and compared the results.

Wynne and Witteveen (2015) estimated whale abundances from photographs of individual whales taken during annual vessel surveys in 2004, 2005, 2007 and 2012–2014. We used the estimated abundances from the eastern portion of the study area because the relative densities of zooplankton and fish were also collected in this region during vessel surveys using acoustic volume backscatter; the relative frequency response was used to estimate relative zooplankton and fish densities (Witteveen et al., 2015; Wynne & Witteveen, 2015). These densities, described here as population indices, are proportional to the total relative abundance of each prey population.

We estimated the proportional assimilated diets of humpback whales using $\delta^{13}C$ and $\delta^{15}N$ derived from 119 skin samples (114 individuals) collected from adults ($n = 80$), juveniles ($n = 4$) and whales of unknown age (but not calves that were dependent on their mothers; $n = 35$). Skin samples of whales were collected from June through September of 2004–2014 using a pneumatic-dart system (Wright et al., 2015). We also used stable isotope values (Figure 5) and digestible elemental concentrations (Table S1) for fish (capelin, *Mallotus villosus*: $n = 84$; Pacific herring, *Clupea pallasii*: $n = 85$; Alaska

pollock, *Theragra chalcogramma*: $n = 42$) collected during vessel surveys in 2012 in areas with the highest acoustic backscatter densities. Sampling was done using a mid-water trawl net with 22 mm mesh cod-end liner (following Witteveen et al., 2012). Zooplankton were also collected using a 75 cm diameter twin-ring net (500/1,000 μmesh) and separated into taxonomic groups though not identified to species (e.g. euphausiids and copepods) (euphausiids: $n = 14$; copepods: $n = 22$) as reported in Witteveen and Wynne (2016).

We added stable isotope discrimination factors (small offsets of stable isotope values between dietary sources and animal tissues) to the isotope values of each sampled food. In particular, we added the mean discrimination factors for skin of fin whales that fed on krill ($\Delta^{13}C = 1.3 \pm 0.4$; $\Delta^{15}N = 2.8 \pm 0.3$; (Borrell, Abad-Oliva, Gómez-Campos, Giménez, & Aguilar, 2012)) to the stable isotope values of sampled zooplankton, and discrimination factors for killer whale *Orcinus orca* and bottlenose dolphin *Tursiops truncates* that fed on fish diets ($\Delta^{13}C = 2.4$; $\Delta^{15}N = 3.2$, Caut, Laran, Garcia-Hartmann, & Das, 2011) to the stable isotope values of fish sampled in this study.

We used IsotopeR (Ferguson & Hopkins, 2013) to estimate and the proportional diets (fish and zooplankton) of whales each year. We ran 3 MCMC chains with a burn-in of 10^3 draws followed by 10^4 draws from the posterior. We checked graphical and other diagnostic output for evidence of convergence. We reported the mean, 1 SD, median and 95% credible interval for each marginal posterior density distribution (i.e. proportional dietary contribution) for each major food source (https://doi.org/10.5061/dryad.5q136q2).

Stable isotope mixing models are used to measure the proportional contributions of digestible biomass from each prey item to consumers (Phillips, 2012), whereas population dynamics are often defined in terms of abundances. To get the proportional diet on the same scale as the per-capita consumption, we converted the per-capita consumption rate from a measure of consumed prey individuals to a measure of consumed biomass. First, we calculated the consumed biomass of each prey item by multiplying the total number of consumed prey (C) between observations ($C = \int_t^{t+1} e^{-\lambda(1-x)} f(P(x), N_1(x), N_2(x))dx$) by the average prey biomass (b). We then corrected the number consumed by the digestibility (D) to get the consumed biomass of each prey item $D \cdot b \cdot C$. Prey digestion of zooplankton was assumed to be 93%, consistent with minke whales *Balaenoptera acutorostrata* (Martensson, Nordoy, & Blix, 1994), and 100% for fish, as measured in some species of dolphin (Sekiguchi & Best, 1997).

2.3.1 | Parameter estimation

We used both the abundance and integrated data models to estimate the consumption of prey by humpback whales. We used n-step predictions (where n is the number of years between observations) because annual data were not available for the whole study period. We used 1-step predictions in 2005, 2013 and 2014; a 2-step prediction for 2007; and a 5-step prediction for 2012. We fit the type I functional response defined in system 2 to the abundances and assumed that predicted populations followed a log-normal distribution. To incorporate the known uncertainty in estimated whale, fish and zooplankton densities, we used a Bayesian model. All estimation was done in JAGS (Plummer, 2012) and code and data to reproduce the analysis are available on the Dryad Digital Repository (https://doi.org/10.5061/dryad.5q136q2).

In the integrated model, we incorporated isotopic turnover of humpback whales using Equation 3. Past work has suggested that equilibration of stable isotopes from food into whale skin can take anywhere from 7 days (Todd, Ostrom, Lien, & Abrajano, 1997; Witteveen et al., 2011) to 2 months (Hicks, Aubin, Geraci, & Brown, 1985). We assumed that these turnover times were equal to the half-life ($\ln(2)/\lambda$) of the tissue and ran our models with both $\lambda = 7/365$ and $\lambda = 60/365$.

3 | RESULTS

3.1 | Simulation study

Under all simulation conditions, integrated models performed better than abundance models at selecting the generating model (Figure 1). The ability to choose the generating model was dependent on the sample size, process variance and generating model. As expected, we found that higher variation in the data tended to reduce the ability to detect the generating model, whereas larger sample sizes increased capacity to select the generating model. An interesting exception to this pattern was the poor performance of the abundance model with type II functional response under low sample size and low process variance. In this case, model selection performed worse than more variable scenarios because there was not enough variation in the data to observe fluctuations in the functional response. When the generating model was the type I functional response, there was little difference between the data models with the generating model selected over 96% of the time for all simulation conditions (Figure 1a). When the generating model was the type II functional response, there was a large difference between the data models' ability to select the generating model. For example, in a sample of 10-time points with variance the abundance data model selected the generating model 26% of the time, whereas the integrated data model selected the generating model 80% of the time (Figure 1b). As the sample size increased, the performance differential of the data models decreased.

We report results of estimator bias under the type II functional response and high process variance (Figure 2). We note that the other simulation conditions led to similar conclusions, though performance differences decreased with lower process variance. We found that estimator bias was less for the integrated data model than the abundance data model with the same number of time points sampled (Figure 2) except for a couple of cases discussed below. The estimates of the half-saturation coefficient for prey 1 (h_1) and both of the consumption rates (c_1, c_2) improved the most under the integrated model. Interesting h_2 did not improve with the integrated

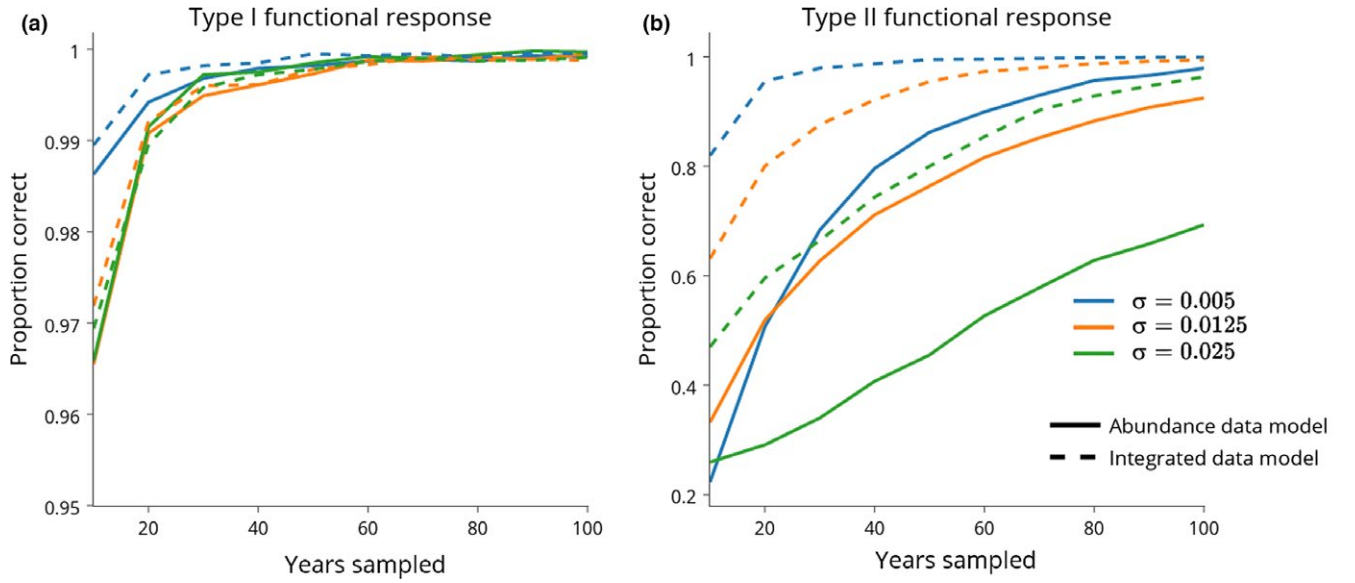

FIGURE 1 Proportion of correct functional response selections made using Bayesian Information Criterion (BIC) for each data model (solid lines for abundance data model, dashed lines for integrated data models). The *x*-axis is given in terms of the number of sample points used for the estimation, where samples occur yearly. In panel (a) the generating model is a type I functional response and panel (b) is for when the generating model is a type II functional response

model even though we saw improvements in h_1 and c_2. We also detected improvements in a number parameters that were not directly related to predator diet (e.g., r_1, s_1, Figure 2), even though the integrated model did not contain any direct information about these parameters. These improvements occur because well-estimated functional response parameters allow for the identification of other population parameters.

We did find some significant issues in the sampling distributions of the diet efficiencies and predator mortality terms (ε_1, ε_2, μ). The sampling distribution of these parameters was multimodal (Figure S1), though we found that the primary mode of the sampling distribution did appear to be a reasonable estimator. It is likely that multimodality occurs because these parameters are additive functions of the predator population in system 1; therefore, they can be difficult to identify statistically. Approaches to deal with this issue are to place biologically plausible constraints on the range of diet efficiencies or to determine reasonable starting points for parameter values from the literature then use local optimization instead of a global algorithm. We performed a small set of secondary simulations that indicate reasonable constraints on parameters removes the multimodal behaviour and lead to estimates that behave similarly to others in the study.

4 | EMPIRICAL STUDY: THE FUNCTIONAL RESPONSE OF HUMPBACK WHALES

4.1 | Abundance and proportional diets

Abundance estimates of the humpback whale population ranged from 1,665 whales in 2004 to 551 in 2012 (Figure 3), with a coefficient of variation of 0.41 over the course of the study. The population indices for fish and zooplankton were also highly variable with coefficients of variation of 0.69 and 1.08 respectively (Figure 3).

The stable isotope values measured from whale skin, fish and zooplankton data and sources are illustrated in Figure 4. Using Kruskal–Wallis tests, we found that unlike δ^{15}N (H = 7.792, df = 5, p = .1681), δ^{13}C values were different among years (H = 49.3747, df = 5, p < .005; Figure S1). Interestingly, δ^{13}C values seemed to decrease in a step-wise fashion (Figure S2). We also learned that both δ^{13}C and δ^{15}N values were lower for zooplankton (δ^{13}C:−18.2 ± 1.0; δ^{15}N: 11.9 ± 0.9) than fish (δ^{13}C: −15.4 ± 0.9; δ^{15}N: 15.7 ± 1.0) (Figure 4). We used these stable isotope data to estimate the diets of whales through time using IsotopeR and found that the annual mean contribution of fish varied substantially in the diets of whales from 45% in 2004 to 4% in 2014 (Figure 3 inset).

4.2 | Parameter estimation

The abundance data model had 15 observations for a system with six parameters. Incorporating diet data with the integrated data model increased the number of observations by 40% to 20 observations. Here, we report estimates assuming that the tissue half-life is 7 days, though we note increasing upper limit on the estimate of turnover 60 days does not alter the point estimates. We estimated the consumption rate of fish (c_{fish}) in our abundance model as $\hat{c}_{\text{fish}} = 5.06 \times 10^{-10}$ vs. the estimate from the integrated model of $\hat{c}_{\text{fish}} = 3.85 \times 10^{-13}$. Both estimates have credible intervals that extend to 0 (Figure 5a) and are thus weakly estimable (sensu Ponciano, Burleigh, Braun, & Taper, 2012), with a flat posterior distribution. The estimates of the consumption rate on zooplankton for the abundance data model estimated $\hat{c}_{\text{zoo}} = 1.34\times10^{-10}$ vs. 1.10×10^{-6} for the

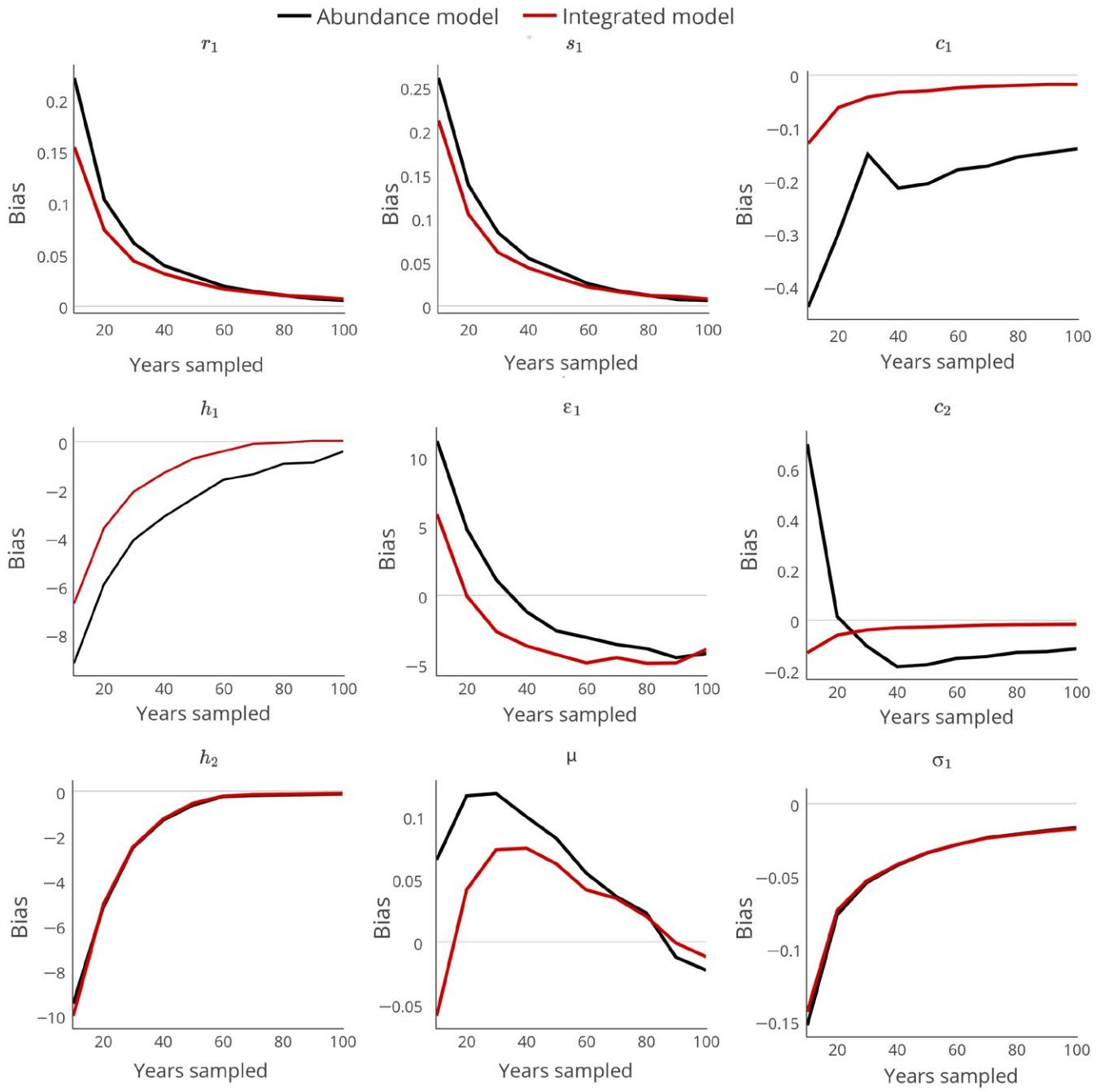

FIGURE 2 Estimator bias under a type II functional response with high process variance. Parameters ε_2, σ_2 and σ_p are not reported as their behaviour is similar to ε_1 and σ_1. Bias is given in terms of the difference between the log parameter values, the *x*-axis is given in terms of the number of sample points used for the estimation, where samples occur yearly

integrated data model. Incorporating the diet estimates in the integrated model led to this parameter becoming estimable (Figure 5b).

5 | DISCUSSION

We developed a framework to parameterize food web models by integrating proportional diet and population abundance data. The primary advantage of using proportional diet information is that it provides an independent measure of consumption, a quantity that dynamical models have estimated by relying on correlations between populations. The simulation component of our study demonstrated that the integrated approach yields more precise parameter estimates and can better distinguish competing between hypotheses relative to standard abundance models. Because the integrated food web model uses more data than conventional methods this improved performance was not surprising; however, we were surprised by the substantial degree of improvement in the integrated

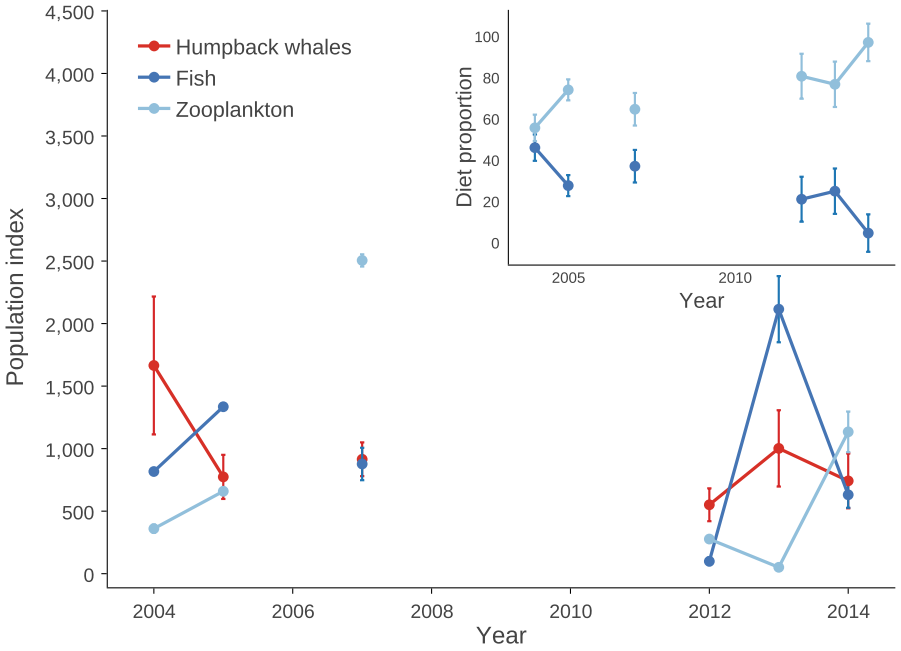

FIGURE 3 Estimated abundances of humpback whales and their prey from 2004 to 2014. Points denote mean population index estimates, error bars are one standard error from the mean. Proportional diets of whales (inset) are estimated using stable isotopes, thus, are expressed in terms of assimilated biomass. Each point in the inset gives the posterior mean diet estimate and error bars are one posterior standard deviation from the mean

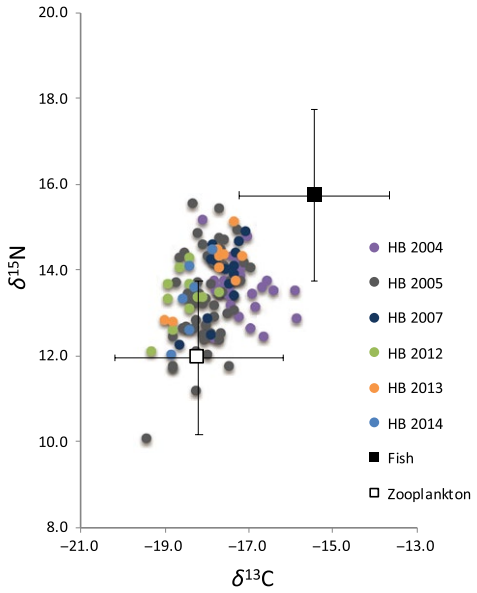

FIGURE 4 Isotope values ($\delta^{13}C$, $\delta^{15}N$) derived from the skin of humpback whales and their prey (corrected for isotopic discrimination). Each colour denotes a different sampling year and error bars denote 2 standard deviations

models for datasets with low sample size and low process variance or moderate sample sizes with high process variance (Figure 1). Our empirical example highlighted how incorporating diet information can resolve parameters that cannot be precisely estimated using abundance data (Figure 5).

Based on the results of our stable isotope analysis, around 25% of the humpback whale diet is composed of fish, though this can vary from over 40% in some years to under 5% in others (Figure 3). Previous diet estimates, calculated using stable isotope mixing models, found a larger proportion of fish in humpback whale diets (Witteveen et al., 2012; Wright, 2014). We attribute this discrepancy to different analytical procedures. For instance we used skin discrimination factors for marine mammals that fed on these food sources (fish and krill), rather than those associated with other tissues and foods. We also structured our mixing models differently than past studies by grouping sampled foods into two main food sources whereas Witteveen et al. (2012) estimated the diets of whales using 2-isotope systems and either 5 or 9 sources.

Although we applied the best analytical practices available in our analysis of whale diets, several limitations may have influenced the results of our case study. First, our model did not explicitly account for the migratory life history of whales. Stable isotopes from food acquired in the winter breeding ground could be influencing the measurements made in Alaska if the isotopic turnover time is on the long end of the estimated range (between 7 and 60 days). In addition, we did not include any direct interactions between fish and zooplankton due to the constraint imposed by having a small sample size. Finally, our analysis assumed that the isotope values of whale's prey did not significantly vary through time. It is known that the isotope values of fishes can vary considerably from year to year, sometimes as much as up to 2% in nitrogen and carbon (Kurle, Sinclair, Edwards, & Gudmundson, 2011). Accounting for such variation will be a significant step in refining the estimates obtained here. Thus, while we do not consider our models sufficiently sophisticated for making accurate predictions of system dynamics in this particular case, our analysis showed that integrative food web models do have significant advantages over standard abundance approaches.

We focused this study on three-species trophic interactions. When applying integrated food web models to larger food webs, stable isotope methods may be unable to uniquely estimate the dietary proportions of generalist consumers (Hopkins & Kurle, 2016). This nonestimability occurs when the number of sources exceeds the

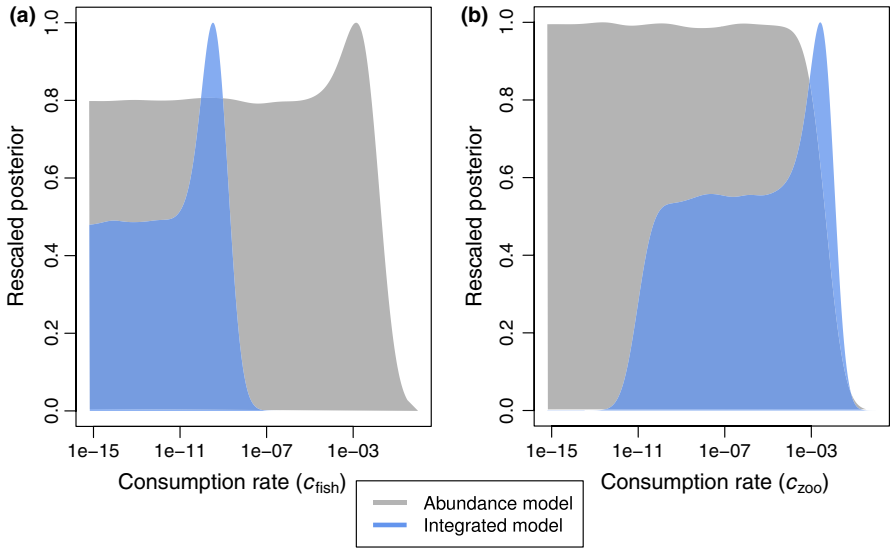

FIGURE 5 Posterior distributions of capture rates between humpback whales and fish (a) and zooplankton (b). Abundance model in grey, integrated model in blue. Posteriors are rescaled for comparability

number of isotope tracers commonly used in ecology (^{2}H, ^{15}O, ^{13}C, ^{15}N and ^{34}S) by more than one (Phillips & Gregg, 2003). Including informative priors in the mixing model (Chiaradia, Forero, McInnes, & Ramírez, 2014) or using prey abundance data to weight source estimates (Yeakel et al., 2011) have both been used to circumvent this analytical limitation. Another promising method is to supplement stable isotopes with fatty acid data, a technique that can extend the number of ecological tracers for systems with many dietary sources (Galloway et al., 2015).

As a general rule of thumb for designing integrated multispecies studies, we advise sampling both abundance and tissues at a frequency defined by the population with the fastest turnover. This study design will generate datasets with sufficient fluctuations in density that the response to predation can be observed without increasing effort by surveying populations that have not had time to respond to the effects of predation. In cases where the stable isotopes are being collected retroactively, e.g., through museum specimens, we suggest starting with a sensitivity analysis of the multispecies abundance model to determine which interactions are the most critical to answering your scientific question. Then place most effort on collecting and analysing the appropriate tissues to inform those interactions.

We believe that integrated food web models show promise for ecologists interested in studying new facets of multispecies dynamics. The ability of ecological tracers to detect differences in consumption at the individual level could lead to new models that explore the impacts of group, or even individual heterogeneity on food web dynamics. For example integrated data models could be used to explore the heterogeneity of diet over the life history of individuals. Diet heterogeneity may play a substantial role in compartmentalizing feeding interactions and thus buffering the propagating effects of a single population going extinct (Stouffer & Bascompte, 2011) and thus in determining community stability (Ferguson, Taper, Guy, & Syslo, 2012; May, 2001), though there is currently very little data available to test this hypothesis.

It is difficult to accurately determine the functional response without experiments (e.g., Arditi, Perrin, & Saiah, 1991) or extensive behavioural field studies (e.g., Fryxell, Mosser, Sinclair, & Packer, 2007; Novak & Wootton, 2008). However, the functional response determines a number of key ecosystem properties such as whether trophic cascades occur and how systems will respond to enrichment (Arditi & Ginzburg, 2012). Here, we show that combining existing data sources using integrated methods is one way forwards for accurately parameterizing complex, empirical food web dynamics. New methods to directly observe ecological interactions may allow ecologists to accurately model the functional response and lead to new insights into the role of predation in the maintenence of biodiversity.

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AUTHORS' CONTRIBUTIONS

J.M.F. and J.B.H. conceived the study; J.M.F. led the analysis and wrote the first draft of the manuscript. J.B.H. contributed substantial

revisions and performed the stable isotope analysis. B.H.W. provided data and feedback on the manuscript.

DATA ACCESSIBILITY

Data and code for analysis of the humpback whales and their prey is available from Dryad Digital Repository https://doi.org/10.5061/dryad.5q136q2 (Ferguson, 2018).

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Additional supporting information may be found online in the Supporting Information section at the end of the article.

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