Hitting the moving target: modelling ontogenetic shifts with stable isotopes reveals the importance of isotopic turnover

Eric Hertz1*, Marc Trudel1,2, Rana El-Sabaawi1, Strahan Tucker2, John F. Dower1, Terry D. Beacham2, Andrew M. Edwards1,2 and Asit Mazumder1

1Department of Biology, University of Victoria, PO Box 3020, Station CSC, Victoria, BC Canada, V8W 3N5; and 2Pacific Biological Station, Fisheries and Oceans Canada, 3190 Hammond Bay Road, Nanaimo, BC Canada, V9T 6N7

Summary

1. Ontogenetic niche shifts are widely prevalent in nature and are important in shaping the structure and dynamics of ecosystems. Stable isotope analysis is a powerful tool to assess these shifts, with δ15N providing a measure of trophic level and δ13C a measure of energy source.

2. Previous applications of stable isotopes to study ontogenetic niche shifts have not considered the appreciable time lag between diet and consumer tissue associated with isotopic turnover. These time lags introduce significant complexity into field studies of ontogenetic niche shifts.

3. Juvenile Chinook salmon (Oncorhynchus tshawytscha) migrate from freshwater to marine ecosystems and shift their diet from feeding primarily on invertebrates to feeding primarily on fish. This dual ontogenetic habitat and diet shift, in addition to the long time lag associated with isotopic turnover, suggests that there is potential for a disconnect between the prey sources that juvenile salmon are consuming, and the inferred prey sources from stable isotopes.

4. We developed a model that considered ontogenetic niche shifts and time lags associated with isotopic turnover, and compared this ‘ontogeny’ model to one that considered only isotopic turnover. We used a Bayesian framework to explicitly account for parameter uncertainty.

5. Data showed overwhelming support for the ontogeny model relative to the isotopic turnover model. Estimated variables from best model fits indicate that the ontogeny model predicts a much greater reliance on fish prey than does the stomach content data. Overall, we found that this method of quantifying ontogenetic niche shifts effectively accounted for both isotopic turnover and ontogenetic diet shifts; a finding that could be widely applicable to a variety of systems.

Key-words: Bayesian, Chinook salmon, niche, ontogeny, trophic level

Introduction

Ontogenetic niche shifts, shifts in diet or habitat with increasing size or age, are widely prevalent in nature (Werner & Gilliam 1984; Rudolf & Lafferty 2011). The implications of these shifts can be dramatic for food webs: ontogenetic niche shifts may alter population and community dynamics (de Roos & Persson 2013), and even determine the structure (Persson et al. 2003), function (Rudolf & Rasmussen 2013) and stability of ecosystems (Rudolf & Lafferty 2011). Furthermore, the functional differences between different life stages of a single species can exceed the differences between species (Rudolf & Rasmussen 2013). Some ontogenetic niche shifts are discrete, as in the case with a salamander shifting diet from aquatic to terrestrial prey after metamorphosis (Davic 1991; Rudolf & Lafferty 2011). However, ontogenetic niche shifts can also occur gradually, such as deposit-feeding polychaetes grad-
usually shifting their diet from diatoms to macroalgae or saltmarsh grasses (Hentschel 1998).

Ontogenetic niche shifts have been typically studied using stomach content analysis (e.g. Graham et al. 2007; but see Rudolf et al. 2014). Stomach contents are a taxonomically detailed snapshot of diet, but may be biased by differences in digestibility among prey items, may not reflect assimilated diets, and do not capture temporal shifts. Increasingly, stable isotope analysis (SIA) is being paired with stomach contents to allow greater temporal resolution (Post 2003). Stable isotope ratios of nitrogen (δ^15N) provide an indicator of trophic level, as δ^15N undergoes a trophic enrichment of 3.4%o (±1.0%o SD) (Post 2002), though the value of this enrichment may depend on the δ^15N of diet (Caut, Angulo & Courchamp 2009; Hussey et al. 2014). Stable isotope ratios of carbon (δ^13C) undergo a more conservative trophic enrichment of 0–1%o and thus better represent the basal resource pool (Post 2002; Miller, Brodeur & Rau 2008). Therefore, a more complete picture of the resource utilization of an organism can be made by observing both stomach contents and stable isotopes.

In using SIA to study ontogeny, researchers often analyse δ^15N and δ^13C separately against body size (Graham et al. 2007; Authier et al. 2012). However, simultaneously analysing δ^15N and δ^13C allows a better understanding of shifts in isotopic niche space (Layman et al. 2007; Turner, Collyer & Krabbenhoft 2010). Discrete ontogenetic niche shifts can be measured in bivariate δ^15N-δ^13C space (Turner, Collyer & Krabbenhoft 2010), but this method requires discrete groups of organisms (e.g. juvenile and adult). Recent developments have also allowed bivariate modelling of continuous (i.e. gradual) ontogenetic shifts, for example by adding size as a covariate in Bayesian mixing models such as mixSIAR (Francis et al. 2011; Stock & Semmens 2013), or by using multivariate hierarchical models (Reum, Hovel & Greene 2015). However, these previous applications of stable isotopes to gradual ontogenetic niche shifts ignored the often-significant time lag between diet and consumer tissue. Laboratory studies have indicated that an organism can take weeks to years to equilibrate with a new diet, depending on tissue (Vand Zanden et al. 2015). Thus, due to these lag effects, there can be a significant disconnection between the isotopes of prey consumed and the isotopes of the predator. These time lags introduce significant, underappreciated complexity into the study of ontogenetic niche shifts in field studies: if not considered, niche shifts could be missed.

The migration of juvenile Chinook salmon (Oncorhynchus tshawytscha) from freshwater to marine ecosystems is a case where an approach that considers both ontogenetic niche shifts and the time lag associated with isotopic turnover is needed. In the ocean, juvenile Chinook salmon shift their diet from foraging on invertebrates to feeding mainly on fish as they increase in size (Brodeur 1991; Hertz et al. 2015b). Hence, in addition to shifting their habitat between freshwater and the marine environment, they also shift their diet from invertebrates to fish. The dual ontogenetic habitat and diet shift, in addition with the long time lag associated with the isotopic turnover of dorsal muscle tissue (~1 month; Heady & Moore 2013), indicates that there is the strong potential for a disconnect between the prey sources that juvenile salmon are actively consuming, and the inferred prey from SIA. Because it is hypothesized that early marine diet is important to overall survival rates (Daly, Brodeur & Weitkamp 2009), being able to characterize ontogenetic niche shifts accurately would be useful in conservation and fisheries management contexts.

Here, we develop a model that simultaneously considers the processes of isotopic turnover and shifting diet (Fig. 1). We use juvenile Chinook salmon to compare this ontogeny model to a model based only on growth and metabolism (isotopic turnover model). We determine whether the ontogeny model is able to replicate the diet shift seen in juvenile Chinook salmon, and we test whether diet-dependent discrimination factors are supported by this model. We also compare ontogeny model predictions to stomach contents to test whether the dietary resource contribution of stomach contents diverges from that calculated from stable isotopes, due to the time lag of isotopic turnover.

Materials and methods

We developed a model, based on first principles, to account for ontogenetic shifts and the time lag associated with isotopic turnover. We parameterized this model using data collected from trawl surveys conducted off of the west coast of Vancouver Island (WCVI) in British Columbia, Canada. The model consumer was juvenile Chinook salmon, while prey groups were invertebrates and forage fish. We used a Bayesian approach for model fits to explicitly account for parameter uncertainty.

THE MODEL

By considering the change in weight between sampling periods, as well as the initial isotopic ratio, the change of a stable isotope δ_y for isolate i (where i is N for nitrogen and C for carbon) and for individual j = 1, 2, 3…, n following a discrete diet or habitat shift can be described using a growth-based turnover model as (Fry & Arnold 1982).

\[ \delta_y = \delta_{y0} + (\delta_{yB} - \delta_{y0}) \cdot \left( \frac{w_f}{w_i} \right)^{\gamma}, \quad \text{eqn 1} \]

where δ_{yB} is the stable isotope ratio prior to the diet or habitat shift, δ_{y0} is the stable isotope ratio when the consumer is equilibrated with its new diet, w_f is the initial weight, w_i is the final weight and γ is the isotopic turnover. Generally, δ_{y0} and γ are the parameters that are fitted using this model, while the other variables (δ_{yB}, δ_{y0}, w_f and w_i) are measured, either on an individual or population level. In this model, isotopic turnover is entirely due to growth dilution when \( c = -1 \), and to both growth
and metabolism when $c_j < -1$ (Fry & Arnold 1982). This weight-based turnover model accounts for individual variation in growth and may be more suitable to field conditions than time-based turnover models (Buchheister & Latour 2010). We refer to this as our ‘isotopic turnover model’. A single compartment was used to model the dynamic of each isotope, with a single rate constant per isotope (Martinez Del Rio & Anderson-Sprecher 2008). Given that the turnover of muscle tissue may be best described with a one compartment model in salmon (Heady & Moore 2013), this assumption should not impact results. While, as far as we know, multicompartiment models have yet to be extended to weight-based turnover models, a multicompartiment model should be relatively simple to implement with the model presented here, if necessary [e.g. by altering eqn (1) following Martinez Del Rio & Anderson-Sprecher (2008)].

The fully equilibrated stable iso-sotope ratio $\delta_{iso}$ (for isotope $i$ and individual $j$) of an organism feeding on a mixture of prey can be determined using a linear mixing model as

$$\delta_{iso} = \sum_{m=1}^{M} \beta_{jm} (\delta_{im} + \mu_{im}),$$  \hspace{1cm} eqn 2

where for prey item $m = 1, 2, ..., M$, $\delta_{im}$ is the stable isotope ratio, $\mu_{im}$ is the trophic discrimination factor and $\beta_{jm}$ is the proportion of prey item $m$ in the diet. This model assumes that the nutrient composition, energy density and stoichiometry of the prey items are similar.

For a consumer that undergoes a gradual ontogenetic niche shift as it grows, $\delta_{iso}$ is not fixed but is a moving target (function of consumer weight) until the consumer’s diet stabilizes. In the simplest case of a diet shift occurring between two prey items, we have

$$\beta_{j1} + \beta_{j2} = 1,$$  \hspace{1cm} eqn 3

with $\beta_{j1}$ and $\beta_{j2}$ dependent on the weight of consumer $j$. Hence, substituting eqn (3) into eqn (2), we get

$$\delta_{iso} = \beta_{j2} (\delta_{i2} + \mu_{i2}) + [1 - \beta_{j2}] (\delta_{i1} + \mu_{i1}).$$  \hspace{1cm} eqn 4

Because $\beta_{j1}$ and $\beta_{j2}$ are constrained by zero and one, the logistic function is well suited to model diet changes with weight:

$$\beta_{j2} = \frac{k}{1 + e^{(b - w_j)/s}} ,$$  \hspace{1cm} eqn 5

where $k$ is the maximum contribution of prey source 2 in the diet of the consumer, and $b$ and $s$ are scaling parameters, with $b$ indicating the inflection point and $s$ is the rate at which the asymptote is reached. This function assumes that the proportion of each prey item increases (in the case of $\beta_{j2}$) and decreases (in the case of $\beta_{j1}$) monotonically with consumer size $w_j$ (Fig. 1).

For simplicity, the trophic discrimination factor is generally assumed to be constant ($\mu_{i1} = \mu_{i2}$) in SIA applications (Cabana & Rasmussen 1996; Post 2002). However, recent analyses indicate that the trophic discrimination factors of consumers varies inversely with the isotopic ratio of their diet for both $\delta^{15}N$ and $\delta^{13}C$ ($\mu_{i1} \neq \mu_{i2}$) (Caut, Angulo & Courchamp 2009; Hussey et al. 2014). To test whether there is support for diet-dependent discrimination factors in this model, we let $\theta_i$ equal $\mu_{i2} - \mu_{i1}$ and substitute $\delta_{iso}$ from (4) and (5) into (1) to give

$$\delta_{ij} = \delta_{i0} (w_j / w_{j0})^{\theta_i} + \left[ \frac{k}{1 + e^{(b - w_j)/s}} \right] (\alpha_{i2} - \alpha_{i1}) + \alpha_{i1} + \mu_{i1}$$  \hspace{1cm} eqn 6

We used eqn (6) to model the ontogenetic shift in diet of juvenile Chinook salmon from invertebrates to forage fish during their early marine life, and to determine whether the discrimination factor of juvenile Chinook salmon varied with diet source. We call this the ontogeny model – the equation for nitrogen ($i = N$) and for carbon ($i = C$) are fitted simultaneously, with the parameters $k$, $b$ and $s$ shared between the two equations. Thus, for $n$ individuals, we have $2n$ equations, with a total of 13 unknown parameters to be estimated in this case (namely $c_j$, $k$, $b$, $s$, $\alpha_{i1}$, $\alpha_{i2}$, $\theta_i$ and $\mu_i$). While we limited our analyses to two prey sources here, the model could be extended to $i + 1$ prey sources, with the form of eqn (5) also able to be altered.

**SAMPLE COLLECTION AND MODEL PARAMETERIZATION**

Chinook salmon from the WCVI migrate to the ocean in late May after rearing in freshwater for a few months (Trudel et al. 2007). These stocks tend to reside off the WCVI until their second summer at sea (Trudel et al. 2009; Tucker et al. 2011, 2012), reducing the confounding effects of large-scale migration seen in other salmon stocks and species (e.g. Tucker et al. 2009).

The $\delta_{ij}$ values were from juvenile Chinook salmon sampled in fall 2000–2009 ($n = 555$) (Tucker et al. 2011, 2012). A rope trawl was towed behind a research vessel for 30 min at ~5 knots (9.8 km h$^{-1}$). Up to 30 juvenile Chinook salmon were taken from each tow. These fish were measured, weighed ($w_j$) and then frozen.
individually at −20 °C. DNA microsatellite variation was used to assess stock composition (Beacham et al. 2006; Tucker et al. 2011, 2012) and only fish with a high probability of originating from WCVI (>80%) were retained for the analyses conducted in this study. The majority (482/555) of these retained fish were caught within inlets and sounds rather than open shelf waters (Fig. S1, Supporting information). The fish from 2000 to 2009 were grouped together due to low sample size, especially of large fish, in many years. The annual variation in isotopes, and implications on survival, will be examined in a subsequent paper.

The full model parameterization is outlined in Table S1. Briefly, the two diet sources were zooplankton and forage fish, based on previous research on the ontogeny of Chinook salmon using stomach contents (Brodeur 1991; Hertz et al. 2015b). Zooplankton samples were taken either via oblique tows taken at 1–2 knots (2000–2001) or vertical bongo tows (two 58-cm Nitex nets) to 150 m or within 10 m of the ocean floor (2002–2009). The smallest size fraction (0.25–1.0 mm) was used for SIA, as there was better spatial coverage of these sites, and there is a strong correlation between the isotopes of the 0.25–1.0 and 1.0–1.7 mm size fractions (El-Sabaawi et al. 2012). This suggests that small zooplankton may be a reasonable indicator of the isotopic signature of the larger prey items that comprise a greater proportion of diet.

Previous analyses have shown spatial and interannual differences in WCVI zooplankton isotopes (El-Sabaawi et al. 2012). As such, we averaged the summer (June–July) and fall (October–November) zooplankton samples across all years and areas to obtain an average overall zooplankton value. Furthermore, while there was the greatest coverage of zooplankton sampling on the outer shelf of WCVI, salmon were primarily caught within inlet and sound habitats, which may have a slightly different isotopic composition. We thus reparameterized models using only zooplankton sampled within protected inlet and shelf habitats (where salmon were primarily caught), and then using only zooplankton sampled on the outer shelf (where sampling coverage was greatest), to see whether this would impact model fits.

Pacific Herring (Clupea pallasii) was used as the forage fish end-member in the model. While the taxonomic details of the prey consumed by WCVI Chinook salmon are at a very coarse level (e.g. fish and amphipods) and not broken down to the species level, it is likely that most of the prey fish consumed are herring, as it is the dominant forage fish in the WCVI catch data and has been noted in the stomachs of the fish analysed here. Furthermore, herring have generally similar isotopic ratios to other possible fish prey off WCVI (M. Trudel, unpublished data), suggesting that they may be reasonably representative of the forage fish community. Pacific Herring were sampled in conjunction with juvenile Chinook salmon in 2005. Finally, our sampling does not result in specific values of δ15N or δ13C for sample or standard (δ15N standard: atmospheric nitrogen; δ13C standard: Vienna Peedee Belemnite). An internal standard showed a standard deviation of ~0.2‰. Since differences in sample lipids can affect δ13C, all juvenile Chinook salmon and prey items with a C : N ratio >3.5 were mathematically lipid-corrected following Post et al. (2007).

Stomach contents were removed, weighed and pooled by tow in the laboratory for identification. Prey were identified under a dissecting microscope to the lowest possible taxonomic resolution and were pooled into seven major categories (Fig. S2). The percent contribution of each prey item was expressed as an average volume per fish within a tow, and then all tow results were averaged within regions, years and seasons, to prevent individual tow with larger catches overwhelming any particular region or year category.

**STABLE ISOTOPE ANALYSIS**

Samples varied slightly in their preparation for SIA (oven-dried whole fish vs. freeze-dried dorsal muscle), so where necessary, we mathematically corrected samples (Fig. S3). Samples were ground, packed into tin capsules and run on a Thermo Delta IV Isotope Ratio Mass Spectrometer (University of Victoria). Stable isotope ratios are expressed in the delta notation

$$\delta^{15}N \text{ or } \delta^{13}C = \left[ \frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right] \times 1000,$$

**eqn 7**

where $R$ is 15N : 14N or 13C : 12C for sample or standard ($\delta^{15}N$ standard: atmospheric nitrogen; $\delta^{13}C$ standard: Vienna Peedee Belemnite). An internal standard showed a standard deviation of ~0.1‰. Since differences in sample lipids can affect $\delta^{13}C$, all juvenile Chinook salmon and prey items with a C : N ratio >3.5 were mathematically lipid-corrected following Post et al. (2007).

**BAYESIAN MODELLING**

Bayesian approaches have been applied to a wide variety of stable isotope questions to explicitly consider the often-significant uncertainty associated with analyses in complex ecological systems (Moore & Semmens 2008; Francis et al. 2011). Furthermore, Bayesian models allow the use of prior information to inform parameter distributions (Stock & Semmens 2013). For our model application, we wanted to determine how the $\delta_{ij}$ values of juvenile Chinook salmon would change with isotopic turnover and shifting diet according to eqn (6). To compare this ontogeny model to a null, isotopic turnover model that did not consider ontogeny, we also fit a model using eqn (1) to the data; that is, $\delta_{ij}$ is fixed rather than dependent on prey as in eqn (6). For the isotopic turnover model (1), we used diffuse priors for $\delta_{ij}$ and $c_i$ of $\sim$ Normal(0, 1 × 106), representing a mean of 0 and standard deviation of $1 \times 10^6$. We treated $\delta_{00}$ and $w_0$ as point estimates (Table S1).

For the ontogeny model (6), we used some diffuse priors because of a lack of prior information and to see whether the data contain enough information for the model to replicate patterns seen in stomach content data. To use as priors for the general shape of a logistic function (i.e. $b$ and $s$ in eqn 5) between per cent piscivory and weight, we reviewed the publications of juvenile and subadult Chinook salmon from near our study area that reported the proportion of fish in stomach and weight (seven studies: Brodeur & Pearcy 1990; Brodeur 1991; Schabetsberger et al. 2003; Miller & Brodeur 2007; Daly, Brodeur & Weitkamp 2009; Duffy et al. 2010; Beamish et al. 2012). When necessary, length was converted to weight after Trudel et al. (2005). We also included the stomach contents reported in this study (binned to facilitate comparison). We fit eqn (5) to these combined data to determine the parameters of $b$ and $s$ using nonlinear regression via the function nls in R (R Core Team 2012). These estimates and their standard errors resulted in priors $b$ = Normal(1, 0.5) and $s$ = Normal(4, 50).

Since $f$ is constrained by [0,1], we used a diffuse beta distribution for $f$, namely $f = \text{Beta}(1, 1)$ where both shape parameters are 1.

For the remainder of the ontogeny model, $\delta_{00}$ and $w_0$ were fixed based on data (Table S1). For $c_i$ we used a diffuse prior,
Ontogenetic shifts and stable isotopes

$\mathcal{N} \sim \text{Normal}(0, 10^4)$. Since $\theta_0 = \mu_2 - \mu_1$ is usually assumed to be zero, but often may be between 0 and 1 for adjacent trophic levels (Caut, Angulo & Courchamp 2009; Hussey et al. 2014), we used a prior of $\theta_0 \sim \text{Normal}(0, 1)$. The priors for $\mu_1$ and $\mu_2$ were taken from literature values (Post 2002) where $\mu_1 = \text{Normal}(3.4, 1)$ and $\mu_2 = \text{Normal}(0.4, 1.3)$. The priors for $\alpha_1$ and $\alpha_2$ came from field samples and were $\alpha_1 \sim \text{Normal}(-18.9, 0.9)$ and $\alpha_2 \sim \text{Normal}(-16.7, 1.8)$, respectively. $\psi_0$ had a prior of $\text{Normal}(9.4, 0.6)$ while $\psi_0$ had a prior of and $\text{Normal}(12.9, 0.5)$. Error terms for models were $\text{Gamma}(0.001, 0.001)$ where $r$ and $\mu$ are 0.001 (McCarthy 2007). To summarize, diffuse priors were used for $k$, $c_i$ and the error term, while the rest of the priors were based on data. All priors were normal distributions with the exception of $b$ and the error term, which were beta and gamma, respectively.

Gibbs sampling, a randomized Markov chain Monte Carlo algorithm, was used via openBUGS (Thomas et al. 2006) with the R2OpenBugs package (Sturtz, Ligges & Gelman 2005). Following a burn-in phase of 3000, with a thinning of 100, we sampled 10,000 values for two chains. Using the CODA package (Plummer et al. 2006), Gelman diagnostics were calculated to assess model convergence (Gelman & Rubin 1992) – values substantially above 1 indicate a lack of convergence. We compared the isotopic turnover model with the ontogeny model using deviance information criterion (DIC; Spiegelhalter et al. 2002), an information criteria comparable to AIC that is commonly used in Bayesian statistics. All analysis was performed in the statistical language $\text{R}$ (version 2.15.1; R Core Team 2012). Code for analysis is provided in Appendix S1.

To compare Bayesian model fits to the data from stomach contents, we converted stomach content estimates of contributions of the two different prey sources to expected stable isotope ratios using eqn (4). Here, $\beta_2$ (proportion of fish) was assessed at each consumer weight according to the data in Fig. S2, while the rest of the parameters come from Table S1.

Results

Stable Isotopes in Prey

All prey samples had a $C : N$ ratio $> 3.5$, so were mathematically lipid-corrected. The isotopic ratio of the initial prey source, zooplankton, averaged across all years and areas was $9.4\%_{\text{on}}$ ($\pm 0.6\%_{\text{on}}$ SD) for $\delta^{15}N$ and $-18.9\%_{\text{on}}$ ($\pm 0.9\%_{\text{on}}$) for $\delta^{13}C$ (Table S2). The average zooplankton sampled at the shelf had $\delta^{15}N$ and $\delta^{13}C$ of $9.3\%_{\text{on}}$ and $-19.1\%_{\text{on}}$, respectively, which were slightly depleted relative to stations located in inlets and sounds (Table S2). The second diet source, Pacific Herring, was sampled at four inside stations ($n = 21$) in 2005. The $\delta^{15}N$ for herring was $12.9\%_{\text{on}}$, and the $\delta^{13}C$ was $-16.7\%_{\text{on}}$ (Table S1). Neither $\delta^{15}N$ nor $\delta^{13}C$ of herring showed a relationship with size ($P > 0.05$).

Since Pacific Herring were only sampled in 2005, we wanted to check whether the baseline zooplankton isotopes in 2005 were anomalous. We found that the zooplankton in 2005 were slightly depleted in $\delta^{13}C$ relative to the mean from all other years combined, but not significantly so (2005: $-19.4\%_{\text{on}}$ 2000–2004, 2006–2009: $-19.0\%_{\text{on}}$; $t$-test: $t_{(480)} = 0.06$). The zooplankton in 2005 ($9.8\%_{\text{on}}$) were significantly enriched in $\delta^{15}N$ relative to the mean from all other years combined ($9.3\%_{\text{on}}$; $t$-test: $t_{(480)} = 0.002$).

Consumer Stable Isotopes

Juvenile Chinook salmon experienced a rapid shift in their $\delta^{15}N$ and $\delta^{13}C$ with increasing size (Fig. 2). $\delta^{15}N$ of salmon ranged from $8.7\%_{\text{on}}$ to $16.5\%_{\text{on}}$ (up from an initial value of $\delta^{15}N = 8.1\%_{\text{on}}$) and increased rapidly as size increased from 12 to 50 g (Fig. 2). $\delta^{15}N$ plateaued at 15 g, when size reached c. 75 g (Fig. 2). $\delta^{13}C$ ranged from $-20.9$ to $-14.1\%_{\text{on}}$, 158 out of 555 juvenile Chinook salmon had $C : N$ ratios $> 3.5$ and were mathematically lipid-corrected. Compared to $\delta^{15}N$, there appeared to be wider variation in $\delta^{13}C$. A similar trend between size and $\delta^{13}C$ was seen, with a rapid shift in isotopic values as size increased from 12 g to 50 g, and with a plateau near $-16\%_{\text{on}}$ reached when size approached 100 g (Fig. 2).

Yearly differences in isotope values did not appear to be the cause of the large variation in isotope values, as all years generally followed the same trend (Figs S4 and S5). Due to interannual differences in timing of sampling, the plateau is not reached in all years, precluding fitting models to each year separately. Splitting the data by conservation unit (CU) did not appreciably change the model fitting, except for the Northwest Vancouver Island CU, where small size-at-capture meant the dietary plateau in isotope values was not reached (Figs S6 and S7).

Bayesian Models

All models showed satisfactory evidence for model convergence, with point scale reduction factors ranging from 1.00 to 1.02. Models indicated a rapid diet shift that occurred up to c. 100 g. For $\delta^{15}N$, the general fit of the ontogeny model matched the data well, but the isotopic turnover model appeared to predict high $\delta^{15}N$ at weights above 150 g, which did not agree with the limited data at larger weights (Fig. 2). For $\delta^{13}C$, the general fit of the ontogeny model showed the general pattern seen in the data, but the isotopic turnover model appeared to under-predict the $\delta^{13}C$ of juvenile Chinook salmon at large sizes (Fig. 2). Splitting zooplankton by collection location did not appreciably change model fits, so we report only the combined zooplankton model data.

The combined DIC of the isotopic turnover models (2983) was much higher than that of the combined ontogeny model (2954) indicating overwhelming support for the ontogeny model (Tables 1 and 2). The median posterior estimates of $\mu_d$ (the trophic discrimination factor) were 4.14 (2.50, 5.85; lower, upper 95% credible interval) and 0.63 (−1.54, 2.83) for $\delta^{15}N$ and $\delta^{13}C$, respectively (Table 2; Fig. S11). 0 (the difference between discrimination factors for different prey items) for $\delta^{15}N$ and $\delta^{13}C$ were both slightly above 0 (Table 2), but the 95% credible intervals overlapped with 0 for both isotopes suggesting little support for diet-dependent discrimination factors.
Modelled estimates of the stable isotope ratios of juvenile Chinook salmon from the stomach contents over-predicted $\delta^{15}N$ values at small (<40 g) and large (>110 g) sizes (Fig. 2). Stable isotope estimates from the stomach contents model for $\delta^{13}C$ did not closely reflect what is seen in consumers (Fig. 2).

**Discussion**

In this study, we used SIA to model a gradual ontogenetic niche shift in a migratory species in the field. Our analyses indicated that the ontogeny model predicted juvenile Chinook salmon isotope ratios better than a simple turnover-based model. We found that using stomach content data to predict the isotopic ratios of juvenile Chinook salmon was ineffective without considering the time lag associated with isotopic turnover. Our modelling also suggested that there were no differences in isotopic fractionation between the two diet sources. Finally, the stable isotope data indicated a higher reliance on fish prey than did the stomach contents. Although we tested our model on juvenile salmon, our approach combining isotopic turnover and ontogenetic niche shifts is applicable to a wide range of systems and will provide critical information on ontogeny of organisms across ecosystems.

**Implications for Salmon Ontogenetic Niche Shifts**

Juvenile Chinook salmon consume a diverse diet, with significant dietary contributions coming from a variety of taxonomic categories with varying trophic levels (Fig. S2). Although diets of salmon are much more diverse than our

---

Table 1. Summary of median and model selection results from isotopic turnover model fit (eqn 1). Lower and upper 95% credible intervals are in parentheses. $\delta_{\text{initial}}$ is the equilibrium consumer value. $c_i$ is the isotopic turnover

| Isotope | $\delta_{\text{initial}}$ | $c_i$ | DIC |
|---------|----------------|-------|-----|
| C       | $-1.59 (0.15)$ | $1 (0.10)$ | $1471$ |
| N       | $23.4 (20.1, 29.9)$ | $-0.17 (0.23, 0.11)$ | $1512$ |
| Overall |                   |       | $2983$ |
model accounts for, the model makes accurate predictions even when considering only two prey categories. General fits of the ontogeny model are good for both $\delta^{15}N$ and $\delta^{13}C$, and the DIC support of this model relative to the isotopic turnover model indicates the importance of considering ontogenetic niche shifts in this situation. Our comparison of stable isotope models to diet contributions estimated from stomach contents further indicates the importance of considering the time lag associated with isotopic turnover in ontogeny studies: at small and large sizes, the contribution of fish is overestimated by the stomach content data, possibly due to these lag effects. Alternatively, since stomach contents are only a snapshot model accounts for, the model makes accurate predictions even when considering only two prey categories. General fits of the ontogeny model are good for both $\delta^{15}N$ and $\delta^{13}C$, and the DIC support of this model relative to the isotopic turnover model indicates the importance of considering ontogenetic niche shifts in this situation. Our comparison of stable isotope models to diet contributions estimated from stomach contents further indicates the importance of considering the time lag associated with isotopic turnover in ontogeny studies: at small and large sizes, the contribution of fish is overestimated by the stomach content data, possibly due to these lag effects. Alternatively, since stomach contents are only a snapshot...
of diet, part of this discrepancy may also be due to a sampling effect.

Previous studies have found an inverse relationship between diet isotopic ratio and discrimination factor (Caut, Angulo & Courchamp 2009; Hussey et al. 2014). In our study, we found little evidence of this process occurring, as the credible intervals for \( \theta \), overlapped with zero for both \( \delta^{15}N \) and \( \delta^{13}C \) models. Thus, over the range of isotopic ratios in this study, there was little evidence to suggest a difference between the discrimination factors between diet sources.

The isotopic turnover \( (c_1) \) was considerably lower than \(-1\), suggesting that the isotopic turnover was slower than had it been due to growth alone (Buchheister & Latour 2010). The mechanisms underlying this are unclear, though this finding does indicate that, as expected for quickly growing organisms, growth effects of turnover overwhelm the metabolic turnover of isotopes (Buchheister & Latour 2010; Weidel et al. 2011). Setting \( c_1 \) to \(-1\) significantly reduced model fits (results not shown), suggesting that while these variables are important in allowing effective model fits, it is possible that the isotopic equilibrium values of \( \delta^{15}N \) and \( \delta^{13}C \) were not well enough defined to allow for accurate fitting of these parameters.

The posterior diet shift predicted by the isotope model was similar to stomach content data, though the isotope model predicts a higher degree of piscivory. One explanation is that juvenile Chinook salmon assimilate more of different prey items would be altered by this differential assimilation.

**SOURCES OF ERROR AND FUTURE STUDIES**

Due to sample sizes, we combined multiple years and areas. Thus, interannual variation in a number of parameters could cause some of this variation. Zooplankton isotopes show seasonal and interannual differences (El-Sabaawi et al. 2012; Table S2), though since forage fish also feed on zooplankton, any changes in zooplankton isotopes should also be reflected in forage fish. Since isotopic turnover rate is related to size (Weidel et al. 2011; Vander Zanden et al. 2015), and juvenile Chinook salmon generally consume fish that are less than half their fork length (Duffy et al. 2010), turnover rates of prey will likely also be appreciably faster, minimizing potential for prey turnover lag effects.

When relationships between isotope ratios and size were plotted with only 1 year and one stock in one area, there was still large unexplained variation (Fig. S8). This suggested that local, smaller-scale variation was underlying much of the overall variation. Individual-level diet specialization could cause these differences (Araujo et al. 2007), and this could be the result of niche partitioning due to intraspecific competition (Lafferty, Belant & Phillips 2015). Contrastingly, juvenile Chinook salmon may be using similar resources, but with slightly different isotopic ratios due to local differences in nutrient utilization (Rau, Ohman & Pierrot-Bults 2003) or productivity of phytoplankton (Laws et al. 1995; Miller, Brodeur & Rau 2008). Factors intrinsic to the salmon themselves may also play a role, with nutritional status (Hertz et al. 2015a) and growth rate (Trueman, McGill & Guyard 2005) both noted to affect isotope ratios. Overall, the factors underlying local variability remain to be explored, but this variation does not change the trend observed, with a rapid ontogenetic niche shift occurring with increased size.

Even with the fewest samples at large sizes, all ontogeny models captured the asymptotic isotope ratios with some accuracy. However, the smallest fish with the lowest isotope ratios were not well predicted by the model. This may be due to an additional shift that juvenile Chinook salmon make from freshwater to estuarine/nearshore residence. Chinook salmon spend weeks to months in these nearshore areas (Maier & Simenstad 2009; Marin Jarrin & Miller 2013), feeding somewhat on terrestrial-derived nutrients from insects (Duffy et al. 2010). Then salmon move offshore where they become accessible to our sampling gears. Thus, these smallest salmon may be recent migrants into the study area, and still represent the isotopic composition of the nearshore food web that they migrated from.

**GENERAL MODEL APPLICATIONS**

A model such as the one we propose is important for migratory species that change diet soon after changing habitats or simply those that experience an ontogenetic niche shift that is gradual relative to the turnover time of the tissue studied. For these species, the isotopic baseline is a moving target until they come to equilibrium with their diet (~100 g for salmon in this study). The approach we used is more biologically plausible than previous field studies of ontogenetic niche shifts, as our approach is based on first principles, unlike some previous numerical approaches (e.g. Hammerschlag-Peyer et al. 2011). Furthermore, our method did not require splitting data into arbitrary body size bins, which is ideal because binning reduces information from the data, and binned results can...
depend on the bin size used. More broadly, this approach is useful for tracing ontogeny in animals that are not amenable to stomach content analysis (e.g. squid; Miller et al. 2013) or those where destructive sampling for stomach contents is not possible due to conservation or other concerns (e.g. Bowhead Whales, Balaena mysticetus; Pomerleau et al. 2012).

Quantitative, continuous models, such as the one outlined here, are a useful approach that effectively approximates the complexity of trophic dynamics in nature since ontogenetic niche shifts are widely prevalent, and species' niches are dynamic (Werner & Gilliam 1984). Assuming that there is no ontogenetic shift occurring when there actually is one could lead to misleading results, especially because due to the long turnover time associated with some tissues, a discrete ontogenetic niche shift can sometimes resemble a gradual one (e.g. Heady & Moore 2013).

CONCLUSION

The development of models for ontogenetic niche shifts has undergone two separate trajectories in laboratory and field studies. In laboratory experiments, the isotopic ratios of diet can be directly controlled, allowing for the development of models to directly determine rates of isotopic turnover and discrimination (Fry & Arnold 1982; Buchheister & Latour 2010). In field studies, however, researchers deal with unknown variability in isotopic ratios of diet, isotopic turnover and discrimination values. Thus, to date, the models concerning ontogenetic niche shifts in the field have been more qualitative in nature (e.g. Graham et al. 2007). By applying laboratory approaches to field studies, our approach has allowed for novel insights in the field application of isotopes.

Inferences of diet from stable isotope studies critically depend on the assumption that an organism is at equilibrium with sampled diet (Post 2002; Buchheister & Latour 2010). However, due to the time lag associated with isotopic turnover, an organism undergoing an ontogenetic niche shift will not reach equilibrium with diet until well after the shift is complete. The assumption of equilibrium is rarely tested and can confound interpretation of isotopic data. By modelling the isotopes as a function of both isotopic turnover and ontogeny, we are better able to understand the overall diet, and more effectively model trophic dynamics in nature.

Acknowledgements

We thank Mary Thiess, Tyler Zubkowski, Yeongha Jung, John Morris and Shapna Mazumder for help with sample collection and processing. We also thank the captains and crews of the CCGS W.E. Ricker for field support. Thanks to Trevor Davies, Julia Baum and James Robinson for discussion and analytical support. We thank Daniel Schindler and four anonymous reviewers for helpful comments on earlier versions of this manuscript. Research was funded by an NSERC Strategic Grant to AM, JFD and MT, NSERC Discovery Grant to AM, and Bonnville Power Administration support to MT and Fisheries and Oceans Canada.

Data accessibility

Data are available from the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.pp75d (Hertz et al. 2016).

References

Araújo, M.S., Bolnick, D.I., Machado, G., Giaretta, A.A. & Dos Reis, S.F. (2007) Using δ13C stable isotopes to quantify individual-level diet variation. Oecologia, 152, 643-654.

Authier, M., Martin, C., Ponchon, A., Steelandt, S., Bentaleb, I. & Guinet, C. (2012) Breaking the sticks: a hierarchical change-point model for estimating ontogenetic shifts with stable isotope data. Methods in Ecology and Evolution, 3, 281–290.

Beacham, T.D., Candy, J.R., Jonsen, K.L., Supernault, J., Weiklo, M., Deng, L. et al. (2006) Estimation of stock composition and individual identification of Chinook salmon across the Pacific Rim by use of microsatellite variation. Transactions of the American Fisheries Society, 135, 861-888.

Beamish, R.J., Neville, C., Sweeting, R. & Lange, K. (2012) The synchronous failure of juvenile Pacific salmon and herring production in the Strait of Georgia in 2007 and the poor return of sockeye salmon to the Fraser River in 2009. Marine and Coastal Fisheries, 4, 463-414.

Brodeur, R.D. (1991) Ontogenetic variations in the size and type of prey consumed by juvenile coho, Oncorhynchus kisutch, and chinook, O. tschawytscha. salmon. Environmental Biology of Fishes, 30, 303–315.

Brodeur, R.D. & Peary, W.G. (1990) Trophic relations of juvenile Pacific salmon off the Oregon and Washington coast. Fishery Bulletin, 88, 617–636.

Buchheister, A. & Latour, R.J. (2010) Turnover and fractionation of carbon and nitrogen stable isotopes in tissues of a migratory coastal predator, summer flounder (Paralichthys dentatus). Canadian Journal of Fisheries and Aquatic Sciences, 67, 445-461.

Cabana, G. & Rasmussen, J.B. (1996) Comparison of aquatic food chains using nitrogen isotopes. Proceedings of the National Academy of Sciences of the United States of America, 93, 10844-10847.

Caut, S., Angulo, E. & Courchamp, F. (2009) Variation in discrimination factors (ΔN2 and Δ13C): the effect of diet isotopic values and applications for diet reconstruction. Journal of Applied Ecology, 46, 443-453.

Chiaradia, A., Forero, M.G., McInnes, J.C. & Ramirez, F. (2014) Searching for the true diet of marine predators: incorporating Bayesian priors into stable isotope mixing models. PLoS One, 9, e92665.

Daly, E.A., Brodeur, R.D. & Weitkamp, L.A. (2009) Ontogenetic shifts in diets of juvenile and subadult Coho and Chinook salmon in coastal marine waters: important for marine survival? Transactions of the American Fisheries Society, 138, 1420-1438.

Davic, R.D. (1991) Ontogenetic shift in diet of Desmognathus quadramacu- latus. Journal of Herpetology, 25, 108–111.

Davis, N.D., Myers, K.W. & Ishida, Y. (1998) Caloric value of high-seas salmon prey organisms and simulated salmon ocean growth and prey consumption. North Pacific Anadromous Fish Commission Bulletin, 1, 146–162.

Duffy, E.J., Beauchamp, D.A., Sweeting, R.M., Beamish, R.J. & Brennan, J.S. (2010) Ontogenetic diet shifts of juvenile Chinook salmon in nearshore and offshore habitats of Puget Sound. Transactions of the American Fisheries Society, 139, 803–823.

El-Sabaawi, R., Trudel, M., Mackas, D.L., Dower, J.F. & Mazumder, A. (2012) Interannual variability in bottom-up processes in the upstream range of the California Current system: an isotopic approach. Progress in Oceanography, 106, 16–27.

Francis, T.B., Schindler, D.E., Holtgrieve, G.W., Larson, E.R., Scheuereell, M.D., Semmens, B.X. et al. (2011) Habitat structure determines resource use by zooplankton in temperate lakes. Ecology Letters, 14, 364–372.

Fry, B. & Arnold, C. (1982) Rapid 13C/12C turnover during growth of brown shrimp (Penaeus aztecus). Oecologia, 54, 200–204.

Gelman, A. & Rubin, D.B. (1992) Inference from iterative simulation using multiple sequences. Statistical Science, 7, 457–472.

Graham, B.S., Grubbs, D., Holland, K. & Popp, B.N. (2007) A rapid ontogenetic shift in the diet of juvenile yellowfin tuna from Hawaii. Marine Biology, 150, 647-658.

Hammerschlag-Peyer, C.M., Yeager, L.A., Araújo, M.S. & Layman, C.A. (2011) A hypothesis-testing framework for studies investigating ontogenetic niche shifts using stable isotope ratios. PLoS One, 6, e21704.
Heady, W.N. & Moore, J.W. (2013) Tissue turnover and stable isotope clocks to quantify resource shifts in anadromous rainbow trout. *Oecologia*, 172, 21–34.

Hentschel, B.T. (1998) Intraspecific variations in δ13C indicate ontogenetic diet changes in deposit-feeding polychaetes. *Ecology*, 79, 1357–1370.

Hertz, E., Trudel, M.K. & Mazumder, A. (2015a) Effects of fasting and nutritional restriction on the isotopic ratios of nitrogen and carbon: a meta-analysis. *Ecology and Evolution*, 5, 4829–4839.

Hertz, E., Trudel, M., Brodeur, R.D., Daly, E.A., Eisner, L., Farley, E.V., et al. (2015b) Continental-scale variability in the feeding ecology of juvenile Chinook salmon along the coastal Northeast Pacific Ocean. *Marine Ecology Progress Series*, 537, 247–263.

Hertz, E., Trudel, M., El-Sabaawi, R., Tucker, S., Beacham, T.D. et al. (2016) Data from: Hitting the moving target: modelling ontogenetic shifts in largemouth bass. *Dryad Digital Repository*. http://dx.doi.org/10.5061/dryad.pp75d.

Hussey, N.E., MacNeil, M.A., McMeans, B.C., Olin, J.A., Dudley, S.F., Cliff, G. et al. (2014) Rescaling the trophic structure of marine food webs. *Ecology Letters*, 17, 239–250.

Lafferty, D.J., Belant, J.L. & Phillips, D.L. (2015) Testing the niche variation hypothesis with a measure of body condition. *Oikos*, 124, 732–740.

Laws, E.A., Popp, B.N., Bidigare, R.R., Kennicutt, M.C. & Macko, S.A. (1995) Dependence of phytoplankton carbon isotopic composition on growth rate and [CO2] model- theoretical considerations and experimental results. *Geochimica et Cosmochimica Acta*, 59, 1131–1138.

Layman, C.A., Arrington, D.A., Montagna, C.G. & Post, D.M. (2007) Can stable isotope ratios provide for community-wide measures of trophic structure? *Ecology*, 88, 42–48.

Maier, G.O. & Simenstad, C.A. (2009) The role of marsh-derived macroedritus to the food webs of juvenile Chinook salmon in a large altered estuary. *Estuaries and Coasts*, 32, 984–998.

Marin Jarrin, J.R. & Miller, J.A. (2013) Sandy beach surf zones: an alternative nursery habitat for 0-age Chinook salmon. *Estuarine, Coastal and Shelf Science*, 135, 220–230.

Martinez Del Rio, C. & Anderson-Sprecher, R. (2008) Beyond the reaction progress variable: the meaning and significance of isotopic incorporation data. *Oecologia*, 156, 765–772.

McCarthy, M.A. (2007) *Bayesian Methods for Ecology*. Cambridge Univ. Press, Cambridge, UK.

Miller, T.W. & Brodeur, R.D. (2007) Diets of and trophic relationships among dominant marine nekton within the northern California Current ecosystem. *Fishery Bulletin*, 105, 548–559.

Miller, T.W., Brodeur, R.D. & Rau, G. (2008) Carbon stable isotopes reveal relative contribution of shelf-slope production to the northern California Current pelagic community. *Limnology and Oceanography*, 53, 1493–1503.

Miller, T.W., Bosley, K.L., Shibata, J., Brodeur, R.D., Omori, K. & Emmett, R. (2013) Contribution of prey to Humboldt squid *Dosidicus gigas* in the northern California Current, revealed by stable isotope analyses. *Marine Ecology Progress Series*, 477, 123–134.

Moore, J.W. & Semmens, B.X. (2008) Incorporating uncertainty and prior information into stable isotope mixing models. *Ecology Letters*, 11, 470–480.

Persson, L., De Roos, A.M., Claessen, D., Byström, P., Lövgren, J., Sjögren, S. et al. (2003) Gigantic cannibals driving a whole-lake trophic cascade. *Proceedings of the National Academy of Sciences of the United States of America*, 100, 4035–4039.

Plummer, M., Best, N., Cowles, K. & Vines, K. (2006) CODA: convergence diagnosis and output analysis for MCMC. *R News*, 6, 7–11.

Pomerleau, C., Lesage, V., Ferguson, S.H., Winkler, G., Petersen, S.D. & McInnes, L.E. (2012) Annual coastal migration of juvenile Chinook salmon: a carbon isotopic perspective. *Transactions of the American Fisheries Society*, 141, 1052–1062.

Reum, J.C., Hovel, R.A. & Greene, C.M. (2015) Estimating continuous size- and sex-biased shifts in δ15N–δ13C space using multivariate hierarchical models. *Marine Biology*, 162, 469–478.

Rau, G.H., Ohman, M.D. & Pierrout-Bults, A. (2003) Linking nitrogen dynamics to climate variability off central California: a 51 year record based on N-15/N-14 in CalCOFI zooplankton. *Deep-Sea Research Part II – Topical Studies in Oceanography*, 50, 2431–2447.

Rudolf, V.H.W. & Lafferty, K.D. (2011) Stage structure alters how complexity affects stability of ecological networks. *Ecology Letters*, 14, 75–79.

Rudolf, V.H.W. & Rasmussen, N.L. (2013) Ontogenetic functional divergence: size structure of a keystone predator drives functioning of a complex ecosystem. *Ecology*, 94, 1046–1056.

Rudolf, V.H.W., Rasmussen, N.L., Dibble, C.J. & Van Allen, B.G. (2014) Resolving the roles of body size and species identity in driving functional diversity. *Proceedings of the Royal Society of London B: Biological Sciences*, 281, 20132020.

Schaefer, P.B., Cameron, A.M., Brodeur, R.D., Potts, C.L., Peterson, W.T. & Emnett, R.L. (2003) Prey selectivity and diet feeding chronology of juvenile chinook (*Oncorhynchus tshawytscha*) and coho (*O. kisutch*) salmon in the Columbia River plume. *Fisheries Oceanography*, 12, 523–540.

Spiegelhalter, D.J., Best, N.G., Carlin, B.P. & Van Der Linde, A. (2012) Bayesian measures of model complexity and fit. *Journal of the Royal Statistical Society: Series B (Statistical Methodology)*, 74, 583–639.

Stock, B.C. & Semmens, B.X. (2013) *MixSIA R GUI User Manual*, version 1.0. Available at: http://conserver.iugo-cafe.org/user/brice.semmens/MixSIA.

Sturtz, S., Ligges, U. & Gelman, A. (2005) *R2WinBUGS*: a package for running WinBUGS from R. *Journal of Statistical Software*, 12, 1–16.

Thomas, A., O’Hara, B., Ligges, U. & Sturtz, S. (2006) Making BUGS open. *R News*, 6, 12–17.

Trudel, M., Tucker, S., Morris, J.F.T., Higgs, D.A. & Welch, D.W. (2005) Indicators of energetic status in juvenile Coho salmon and Chinook salmon. *North American Journal of Fisheries Management*, 25, 370–379.

Trudel, M., Thiess, M.E., Bucher, C., Farley, E.V. Jr, MacFarlane, R.B., Casillas, E. et al. (2007) Regional variation in the marine growth and energy accumulation of juvenile Chinook salmon and Coho salmon along the west coast of North America. *American Fisheries Society Symposium*, 77, 205–232.

Trudel, M., Fisher, J., Orsi, J.A., Morris, J.F.T., Thiess, M.E., Sweeting, R.M. et al. (2009) Distribution and migration of juvenile Chinook salmon derived from coded wire tag recoveries along the continental shelf of western North America. *Transactions of the American Fisheries Society*, 138, 1369–1391.

Trueman, C.N., McGill, R.A. & Gauyard, P.H. (2005) The effect of growth rate on tissue-diet isotopic spacing in rapidly growing animals. An experimental study with Atlantic salmon (*Salmo salar*). *Rapid Communications in Mass Spectrometry*, 19, 3239–3247.

Tucker, S., Trudel, M., Welch, D.W., Candy, J.R., Morris, J.F.T., Thiess, M.E. et al. (2009) Seasonal stock-specific migrations of juvenile sockeye salmon along the west coast of North America: implications for growth. *Transactions of the American Fisheries Society*, 138, 1458–1480.

Tucker, S., Trudel, M., Welch, D.W., Candy, J.R., Morris, J.F.T., Thiess, M.E. et al. (2011) Life history and seasonal stock-specific ocean migration of juvenile Chinook salmon. *Transactions of the American Fisheries Society*, 140, 1101–1119.

Tucker, S., Trudel, M., Welch, D.W., Candy, J.R., Morris, J.F.T., Thiess, M.E. et al. (2012) Annual coastal migration of juvenile Chinook salmon: static stock-specific patterns in a highly dynamic ocean. *Marine Ecology Progress Series*, 449, 245–262.

Turner, T.F., Collyer, M.L. & Krabbenhoft, T.J. (2010) A general hypothesis-testing framework for stable isotope ratios in ecological studies. *Ecology*, 91, 2227–2233.

Vander Zanden, M.J., Clayton, M.K., Moody, E.K., Solomon, C.T. & Weidell, B.C. (2015) Stable isotope turnover and half-life in animal tissues: a literature synthesis. *PLoS One*, 10, e0116182.

Weidell, B.C., Carpenter, S.R., Kitchell, J.F. & Vander Zanden, M.J. (2011) Rates and components of carbon turnover in fish muscle: insights from biomegetics models and a whole-lake δ13C addition. *Canadian Journal of Fisheries and Aquatic Sciences*, 68, 387–399.

© 2016 The Authors. *Journal of Animal Ecology* published by John Wiley & Sons Ltd on behalf of British Ecological Society, *Journal of Animal Ecology*, 85, 681–691.
Werner, E.E. & Gilliam, J.F. (1984) The ontogenetic niche and species interactions in size structured populations. Annual Review of Ecology and Systematics, 15, 393–425.

Received 21 October 2015; accepted 8 February 2016
Handling Editor: Volker Rudolf

Supporting Information

Additional Supporting Information may be found in the online version of this article.

Table S1. Model parameterization.

Table S2. Seasonal and annual variation in isotopic composition of zooplankton collected off the west coast of Vancouver Island.

Fig. S1. Map of stock-of-origin and catch locations for juvenile Chinook salmon off the west Coast of Vancouver Island.

Fig. S2. Diet composition by major prey categories identified in the stomach contents of different tow-averaged size classes of juvenile Chinook salmon from the west coast of Vancouver Island from 2000–2009.

Fig. S3. Comparison of oven dried whole fish and freeze-dried muscle tissue for juvenile Chinook salmon.

Fig. S4. $\delta^{15}$N values and weights of juvenile Chinook separated by year.

Fig. S5. $\delta^{13}$C values and weights of juvenile Chinook separated by year.

Fig. S6. $\delta^{15}$N values and weights of juvenile Chinook separated by conservation unit.

Fig. S7. $\delta^{13}$C values and weights of juvenile Chinook separated by conservation unit.

Fig. S8. Effects of subsetting the data by year, and year and region.

Fig. S9. Posterior density plot for $\delta^{15}$N null model.

Fig. S10. Posterior density plot for $\delta^{13}$C null model.

Fig. S11. Posterior density plot for $\delta^{13}$C and $\delta^{15}$N ontogeny model.

Appendix S1. R code for Bayesian ontogeny model.