

Exploring the isotopic niche: isotopic variance, physiological incorporation, and the temporal dynamics of foraging

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2 ABSTRACT

3 Consumer foraging behaviors are dynamic, changing in response to prey availability, seasonality,
4 competition, and even the physiological states of the consumers. The isotopic composition of
5 a consumer is a product of these factors as well as the isotopic ‘landscape’ of its prey, i.e. the
6 isotopic mixing space. Stable isotope mixing models are used to back-calculate the most likely
7 proportional contribution of a set of prey to a consumer’s diet based on their respective isotopic
8 distributions, however they are disconnected from ecological process. Here we build a mechanistic
9 framework that links the ecological and physiological processes of an individual consumer to
10 the isotopic distribution that describes its diet, and ultimately to the isotopic composition of its
11 own tissues, defined as its ‘isotopic niche’. By coupling these processes, we systematically
12 investigate under what conditions the isotopic niche of a consumer changes as a function of
13 both the geometric properties of its mixing space and foraging strategies that may be static or
14 dynamic over time. Results of our analytical derivations reveal general insight into the conditions
15 that impact isotopic niche width as a function of consumer specialization on prey, as well as its
16 ability to transition between diets over time. We show analytically that moderate specialization
17 on isotopically unique prey can serve to maximize a consumer’s isotopic niche width, while
18 temporally dynamic diets will tend to result in peak isotopic variance during dietary transitions. We
19 demonstrate the relevance of our theoretical findings by examining a marine system composed of
20 nine invertebrate species commonly consumed by sea otters. In general, our analytical framework
21 highlights the complex interplay of mixing space geometry and consumer dietary behavior in
22 driving expansion and contraction of the isotopic niche. Because this approach is established on
23 ecological mechanism, it is well-suited for enhancing the ecological interpretation, and uncovering
24 the root causes, of observed isotopic data.

25 **Keywords:** Isotopic niche, Trophic niche, Mixing space, Dietary variation, Specialization, Prey switching

1 INTRODUCTION

26 Consumer foraging behaviors are dynamic, often resulting in variable diets that change over time and space
27 as a function of environmental conditions, the densities of consumers and available resources, and even
28 the physiological states of individual foragers, to name a few. Understanding how diets change, and to
29 what extent different conditions promote or inhibit specific changes, is both a challenging theoretical and
30 empirical problem in ecology, but is essential for elucidating the adaptive nature of complex ecological
31 systems.

32 The comparison of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) stable isotope values of a consumer with respect
33 to its potential prey is a commonly utilized approach to quantify diet composition. The carbon and
34 nitrogen isotopic composition of a consumer represents that of the food it eats, but is offset by predictable
35 amounts, often called trophic discrimination factors, that are mediated by consumer physiology (????).
36 The isotopic composition of a consumer thus reflects 1) the proportional contribution of different prey to
37 the consumer's diet (Moore and Semmens, 2008; Parnell et al., 2010), and 2) the isotopic composition of
38 its prey, collectively described as the isotopic, or prey, mixing space (Phillips, 2001; Phillips and Koch,
39 2002; Newsome et al., 2007).

40 The isotopic niche of a consumer is a low-dimensional specification of the 'Hutchinsonian niche'
41 (Hutchinson, 1957), an n-dimensional hypervolume that defines all biotic and abiotic requirements needed
42 for a species to exist. The isotopic niche is also generally derived from both biotic and abiotic processes,
43 but in contrast to the large and ultimately immeasurable construct of the n-dimensional hypervolume,
44 isotopic niches are defined exactly as a consumer's isotopic variance with a dimension determined by the
45 number of isotope systems employed (Bearhop et al., 2004; Newsome et al., 2007, 2012; Martínez del Rio
46 et al., 2009; Jackson et al., 2011). It is the width, or spread of this distribution that correlates to the breadth
47 of the isotopic niche. Although the isotopic niche can be the result of many ecological and environmental
48 factors that influence the flow of elements through biological systems (Araújo et al., 2007), when it is
49 primarily driven by consumer-resource interactions, the isotopic niche is synonymous with the trophic
50 niche as defined by Bearhop et al. (2004). Changes in the size of the isotopic niche have been shown to
51 relate to ecosystem fragmentation (Layman et al., 2007), evolutionary diversification (?), changes in food
52 availability (Lehmann et al., 2015), and even individual responses to seasonal environments (Martínez del
53 Rio et al., 2009), however a systematic understanding of how different sources of variability influence the
54 isotopic niche is lacking.

55 Both the consumer's dietary strategy as well as the isotopic mixing space contribute different sources of
56 variability that are reflected in the isotopic composition of the consumer. For example, a consumer could be
57 an obligate specialist on a single prey, such that its dietary variability is extremely low, in which case the
58 isotopic mean and variability of the consumer's tissues will reflect that of its targeted prey. In contrast, the
59 consumer could be a generalist, or intermediate specialist on certain prey such that the variability in its diet
60 as well as the isotopic variability of its prey contributes to its own isotopic composition. Thus, the isotopic
61 composition of a consumer is not only a reflection of what the consumer eats, but is also determined by the
62 mixing space over which it integrates isotope values, and the amount of time over which a particular tissue
63 integrates dietary inputs.

64 The isotopic niche is generally defined with respect to the isotopic variance of a population (Araújo et al.,
65 2007, 2009; Fink et al., 2012), however population-level variance is itself an artifact of the individual-
66 level distributions from which the population is composed (Bolnick et al., 2007; Araújo et al., 2011).
67 An important step in understanding how the isotopic niche changes in response to different consumer
68 foraging strategies is to examine how individual-level variation contributions to observed isotopic variability.
69 Individual-level variability, in particular that variability resulting from temporal changes in diet, has large
70 implications for the population (???). For example, populations with greater individual-level variability
71 have been shown to exhibit greater stability (Bolnick et al., 2011), and in certain cases can increase the
72 likelihood of species coexistence (?). Changes in individual diet through time is frequently measured via
73 stable isotope analysis of metabolically inert, temporally-integrating tissues such as hair, whiskers, claws,
74 or even growth layers in teeth (Koch et al., 1995; Matthews and Mazumder, 2004; Sponheimer et al., 2006;
75 Post, 2008; Newsome et al., 2009; Yeakel et al., 2009; Hopkins III and Kurle, 2015).

76 Once physiologically-mediated isotopic discrimination between a consumer and its food has been
77 accounted for, the isotopic niche is a direct reflection of the proportional contribution of different prey
78 resources to the consumer's diet. Isotope mixing models, which originally used a bootstrapping framework
79 (Phillips and Gregg, 2003; Phillips et al., 2005) and now employ Bayesian methods (Moore and Semmens,
80 2008; Parnell et al., 2010; Hopkins and Ferguson, 2012; Parnell et al., 2013), are used to reconstruct
81 the probability distribution that describes the contribution of different prey; mixing models can only be
82 solved exactly if the number of potential prey resources are less than or equal to the number of isotope
83 systems used plus one. These tools are forensic in nature, and can be used to back-calculate consumer
84 diets across a range of isotopically distinct prey with differing stoichiometries (Hopkins III and Kurle,
85 2015), to quantify intra- and inter-population niche variability (Sennens et al., 2009), to reconstruct diets
86 of extinct taxa (Yeakel et al., 2013), and even combined with process-based models that are designed to
87 constrain contribution-to-diet estimates based on known mechanistic relationships between species (Ogle
88 et al., 2014).

89 A conceptually divergent, yet parallel, strategy is to consider the inter-related effects of ecological
90 interactions and the concomitant integration of stable isotope values, and how these factors combine to
91 result in the isotopic composition of a consumer. In this way, the consumer's isotopic distribution can
92 be forward-integrated through time based on the mechanistic linkages between its foraging strategy, its
93 ability to find and acquire prey, and the isotopic landscape (mixing space) over which its diet is composed.
94 This general perspective has been applied to investigate properties of the isotopic niche for cases of fixed
95 (non-varying) diets (Araújo et al., 2007, 2009), and with respect to experimental systems where consumers
96 are forced to switch between unique prey (Fink et al., 2012). However, such a process-based framework has
97 not been directly linked to consumer foraging behaviors, prey availability, or other ecological considerations
98 such that the combined impacts of ecologically-mediated dietary variation and mixing space geometry on
99 the isotopic niche can be assessed.

100 Here we build a mechanistic framework that links the ecological and physiological processes of an
101 individual consumer to the isotopic distribution that describes its diet, and ultimately to the isotopic
102 composition of its own tissues. By coupling these processes, we are able to systematically investigate under
103 what conditions the isotopic niche of a consumer changes as a function of both geometric properties of
104 its mixing space, and alternative foraging strategies. We show that the isotopic variance of a consumer's
105 diet (and by extension the width of its isotopic niche) is expected to be a concave parabolic function with
106 respect to prey specialization, such that it possesses a peak variance, though the appearance of this peak
107 is contingent on mixing space geometry. We demonstrate the potential importance of these findings by

108 examining a prey mixing space for sea otters (*Enhydra lutris*), which are known to possess high dietary
109 individuality (?Tinker et al., 2008; Newsome et al., 2009, 2015).

110 We then extend our framework to explore how a consumer's isotopic niche responds to temporally
111 dynamic diets. We examine an example of a switch between two probabilistic diets that oscillates between,
112 for example, seasons, and show analytically that the maximum expected isotopic niche width occurs during
113 the transitions between diets. Determining how different sources of variability emerge from ecological,
114 behavioral, and geometric drivers is important for interpreting the meaning of concepts such as the isotopic
115 niche. Moreover, integrating these different sources of variation into a statistical process-based framework
116 lends itself particularly well to hypothesis-testing aimed at uncovering the root causes of observed isotopic
117 data. We hope that our approach is a step towards assessing how the isotopic niche may change due to
118 more complex foraging behaviors and even population dynamics, and we expand on these ideas in the
119 Discussion.

2 METHODS & ANALYSIS

120 We begin by establishing a forward-integration approach for modeling the incorporation of stable isotopes
121 from multiple resources into a consumer's tissues. This new methodology provides an analytical link
122 between the mechanistic drivers of foraging and the distribution of stable isotope values describing a
123 consumer's tissues over time. Using this framework, we aim to 1) examine how certain dietary behaviors,
124 such as prey specialization and different modes of dietary variation, impact the isotopic variance of
125 consumer tissues, and 2) show how these methods can be expanded to include foraging behaviors that
126 themselves are temporally dynamic, changing over seasons or years. Accordingly, our general goal is to
127 reveal how both ecological and geometric factors can influence the expansion and contraction of isotopic
128 variability, thus aiding ecological interpretation of the 'isotopic niche'.

129 Deriving the within-individual isotopic niche width

130 There are many ways to statistically summarize the integration of prey by a consumer species, however
131 in order to establish a mechanistic link between foraging and the consumer's isotopic composition, we
132 follow the proceeding heuristic foraging mechanic. We assume that a consumer encounters and consumes
133 resources in proportion to the encounter rate of each prey; prey that are encountered more frequently
134 are assumed to be consumed more frequently. An alternative approach could incorporate preferences
135 (Chesson, 1983) or even state-dependence (Mangel and Clark, 1988; Clark and Mangel, 2000; Mangel,
136 2014), and we will briefly address these considerations in the Discussion. As prey are encountered and
137 consumed, the prey's isotope values are incorporated into the consumer's tissues weighted by the prey-
138 specific proportional contribution to diet. The resulting distribution that describes the dietary input of
139 multiple prey (each with isotope values that are independently and Normally distributed) is a mixed Normal
140 distribution with weights determined by the prey's proportional contribution to diet. This proportional
141 contribution is itself a random variable drawn from a Dirichlet density (a multivariate Beta distribution)
142 that serves as a probabilistic description of the consumer's dietary input (Ainsworth et al., 2010). The
143 following section details our probabilistic determination of the consumer's isotopic composition. We focus
144 our attention on the variability of the isotopic distribution describing the consumer's diet, which scales
145 directly with the consumer's own isotopic distribution, which is itself equivalent to the isotopic niche
146 (Bearhop et al., 2004; Newsome et al., 2007). Here and henceforth, we assume that the isotope ratios under
147 consideration follow dietary pathways such that the isotopic niche is synonymous with the trophic niche
148 (Bearhop et al., 2004).

149 A consumer encounters each prey at a frequency determined by a Poisson process with parameter ψ_i ,
 150 which determines the number of encounters $M_i = m_i$ between time 0 and time t , with the frequency
 151 distribution

$$f_{M_i}(m_i|\psi_i) = e^{-\psi_i t} \frac{(\psi_i t)^{m_i}}{m_i!}. \quad (1)$$

152 Here and henceforth, we use the general function $f(\cdot)$ to denote different frequency distributions, as well
 153 as uppercase notation to describe stochastic variables, and lowercase notation to describe specific values of
 154 stochastic variables. If we assume that encounter rates are variable, such that some prey are more patchily
 155 distributed than others, we can treat $\Psi_i = \psi_i$ as a random variable with a Gamma density

$$f_{\Psi_i}(\psi_i|c, a_i) = \frac{c^{a_i}}{\Gamma(a_i)} e^{-c\psi_i} \psi_i^{a_i-1}. \quad (2)$$

156 Here, a_i is the dispersion parameter, which is proportional to the encounter rate, and c scales with the
 157 time between encounters (Mangel, 2006; Ainsworth et al., 2010; Yeakel et al., 2014). If we integrate
 158 across all possible values of ψ_i , we obtain the Negative Binomial density with mean encounter rate a_i/c
 159 and coefficient of variation $1/\sqrt{a_i}$ (Hilborn and Mangel, 1997). Following the derivation described by
 160 Ainsworth et al. (2010), if we define the proportional contribution of prey to a consumer's diet to scale
 161 with the encounter rate, such that

$$p_i = \frac{\psi_i}{\sum_{j=1}^n \psi_j}, \quad (3)$$

162 then the random variable $P_i = p_i$ where $P_i \in \mathbf{P}$ and $p_i \in \mathbf{p}$, and note that we allow boldface
 163 type to denote vectors of variables. From Eq. 3, it follows that the vector describing the proportional
 164 contributions to diet \mathbf{P} follows a Dirichlet distribution (Johnson, 1960) with density

$$f_{\mathbf{P}}(p_1, \dots, p_n|a_1, \dots, a_n) = \frac{\Gamma(\sum_{i=1}^n a_i)}{\prod_{i=1}^n \Gamma(a_i)} \prod_{i=1}^n p_i^{a_i-1}, \quad (4)$$

165 where $\Gamma(\cdot)$ is the gamma function (cf. Mangel, 2006). As such, the expected proportional contribution of a
 166 prey i to the consumer's diet has the expectation $E\{P_i\} = a_i/a_0$ where $a_0 = \sum_i a_i$, and variance

$$V\{P_i\} = \frac{a_i(a_0 - a_i)}{a_0^2(a_0 + 1)}. \quad (5)$$

167 In this paper we consider the case where resources are plentiful and feeding is regular, and we draw a
 168 single prey i with probability p_i for inclusion to the consumer's diet.

169 Describing the dietary behavior of a consumer as a Dirichlet distribution provides a flexible and powerful
 170 framework to investigate how different foraging strategies influence a consumer's isotopic niche. For
 171 example, a pure generalist consumer would have a Dirichlet distribution with parameters $a_i = 1$ for all prey
 172 $i = 1, \dots, n$, such that the marginal distribution for P_i is close to uniform with expectation $E\{P_i\} = 1/n$.
 173 Because we have assumed that the proportional contribution of a prey to the consumer's diet scales with the

174 prey's encounter rate, this would be analogous to a system where a consumer is equally likely to encounter
 175 the same number of any prey. In contrast, an obligate specialist would have a Dirichlet density that is
 176 spiked for a given prey k , such that the single parameter $a_k \gg 1$, while $a_{i \neq k} = 1$. The use of a Dirichlet
 177 distribution is also at the heart of Bayesian isotope mixing models (Moore and Semmens, 2008; Parnell
 178 et al., 2010; Hopkins and Ferguson, 2012; Parnell et al., 2013), which assume a Dirichlet prior and enable
 179 the input of alternative dietary information to inform isotopic data.

180 If the stable isotope ratios for each of the potential prey follow independent Normal distributions, and the
 181 dietary behavior of the consumer has a Dirichlet density, the resultant density that describes the isotopic
 182 distribution of a consumer's diet $f_Z(Z = z)$ is a mixed Normal distribution, with weights given by \mathbf{p}
 183 drawn from the Dirichlet. Given that the isotopic means and variances for prey i are denoted by μ_i and σ_i^2 ,
 184 respectively, this density can be written as

$$f_Z(z|\mathbf{a}, \boldsymbol{\mu}, \boldsymbol{\sigma}) = \left(\sum_{i=1}^n p_i \frac{1}{\sqrt{2\pi\sigma_i^2}} e^{-\frac{(z-\mu_i)^2}{2\sigma_i^2}} \right) f_{\mathbf{P}}(\mathbf{p}|\mathbf{a}), \quad (6)$$

185 with the expectation

$$\text{E}\{Z\} = \sum_{i=1}^n \frac{a_i}{a_0} \mu_i, \quad (7)$$

186 Accordingly, the isotopic mean of the consumer's diet is a weighted average of the isotopic means of its
 187 potential prey, where weights are determined by the outcome of the Dirichlet random variable.

188 Of more interest to us here is the variance of Z , which will allow us to analytically determine the isotopic
 189 niche width of the consumer as a function of its dietary behavior and the mixing space of its prey. We find
 190 that

$$\text{V}\{Z\} = \sum_{i=1}^n \frac{a_i}{a_0} (\sigma_i^2 + \mu_i^2) - \frac{a_i^2 \mu_i^2}{a_0^2} - \sum_{i \neq j} \frac{a_i a_j \mu_i \mu_j}{a_0^2}. \quad (8)$$

191 Although the form of Eq. 8 is not intuitive, we emphasize that - over different dietary behaviors that shape
 192 the Dirichlet distribution and for different isotopic mixing spaces - it is this equation that governs the
 193 expansion or contraction of the consumer's isotopic niche width, and therefore of chief ecological interest.

194 The isotopic variance of the consumer's diet $\text{V}\{Z\}$ can be simplified by considering a specific set of
 195 dietary behaviors. Here we examine how $\text{V}\{Z\}$ is influenced by generalist vs. specialist consumer diets,
 196 as well as the role of general mixing space geometries, in determining consumer isotopic niche width. It
 197 is important to note that specialism, as discussed here defines the degree to which a consumer's diet is
 198 dependent on a single prey resource, ranging from $s = 1/n$ (obligate generalization) to $s = 1$ (obligate
 199 specialization). It is thus conceptually different than 'individual specialization' defined as the proportional
 200 variance of an individual relative to that of its population (Within-Individual Component / Total Niche
 201 Width, or WIC/TNW; Roughgarden, 1979), and often the variable of interest in other studies examining
 202 properties of the isotopic niche (Araújo et al., 2007, 2009, 2011; Layman et al., 2011).

If a generalist consumer alters its diet to include more of a certain prey k relative to the others, the Dirichlet distribution that defines its dietary behavior goes from $a_i = 1$ for all $i = 1, \dots, n$ to $a_{i \neq k} = 1$ for $i = 1, \dots, n$, with $a_k > 1$. As specialization increases, the Dirichlet parameter corresponding to the targeted prey k increases to a value much higher than one (pure specialization is obtained only at the limit $a_k \rightarrow \infty$). Thus, we can assume that $a_i = 1$ for all $i \neq k$, and $a_k = (n - 1)s_k/(1 - s_k)$, where s_k denotes specialization on prey k . We can thus substitute $a_0 = (n - 1)/(1 - s_k)$ and $p_i = a_i/a_0 = (1 - s_k)/(n - 1)$ for all $i \neq k$, and $a_k/a_0 = s_k$. We can then rewrite Eq. 8 as

$$V\{Z\} = \frac{1 - s_k}{n - 1} \sum_{i \neq k}^n (\sigma_i^2 + \mu_i^2) + s_k(\sigma_k^2 + \mu_k^2) - \left(\frac{1 - s_k}{n - 1} \sum_{i \neq k}^n \mu_i + s_k \mu_k \right)^2, \quad (9)$$

and note that, independent of the prey mixing space (a function of μ_i and σ_i^2 for prey $i = 1, \dots, n$), the isotopic variance of the consumer's diet will always be a concave parabolic function over s_k . With respect to the size of the consumer's isotopic niche width, this means that there can be a peak variance for a value of s_k intermediate to pure generalization ($s_k = 1/n$) and pure specialization ($s_k = 1$).

The peak variance \hat{s}_k , which describes the maximum isotopic variance of the consumer, may or may not fall between $s_k = 1/n$ and $s = 1$, and is only of ecological interest if it does. The peak variance can be solved analytically by setting the derivative of Eq. 9 with respect to s_k equal to zero, and solving for s_k , which results in

$$\hat{s}_k = \frac{A(1 - n) + B(n - 1)^2 + 2C(C - Dn + D)}{2(C - Dn + D)^2}, \quad (10)$$

where $A = \sum_{i \neq k}^n (\sigma_i^2 + \mu_i^2)$, $B = (\sigma_k^2 + \mu_k^2)$, $C = \sum_{i \neq k}^n \mu_i$, and $D = \mu_k$.

Determination of the peak variance allows us to predict where the consumer's isotopic niche is expected to be maximized as a function of specialization on different prey. Although here we have focused on the special case where a consumer targets a single prey, one can rewrite the equation for the consumer's isotopic niche width with respect to increasing specialization on any number or combination of prey in the mixing space. For example, in the case where a consumer specializes on two prey (e.g. two species of crab), one would rewrite Eq. 8 in terms of both s_k (specialization on prey k) and s_l (specialization on prey l), resulting in a concave parabolic plane in dimensions s_k and s_l . Determining the maximum variance would then entail taking the derivative of Eq. 8 with respect to both s_k and s_l . In dimensions higher than 2, the process would be the same, with the goal of finding the maximum variance over a hyperplane with a number of dimensions determined by the number of prey on which the consumer is preferentially targeting. Because specializing on multiple prey does not introduce anything conceptually unique, we consider only the case of a single-prey specialist.

The Dynamics of Isotopic Incorporation

We have established a framework for analytically calculating the distribution of isotope values that characterizes a consumer's diet, composed of multiple, isotopically distinct prey. The dietary behavior of the consumer is a function of a single Dirichlet distribution, which is assumed not to change over time, although we will relax this assumption in the next section. Over long timescales the dietary distribution of the consumer is static, with a fixed mean and variance. Over short timescales, the consumer's diet varies

237 as Eq. 5, while its final isotopic distribution has a variability emerging from the combined effects of the
 238 Dirichlet and the mixed Normal distribution describing the prey mixing space (Eq. 8).

239 As the consumer acquires and consumes its prey, the isotopic composition of its diet is incorporated
 240 into its tissues. The timescale of physiological incorporation is based on the turnover rate of consumer
 241 tissues, which on the fast end can occur within days to weeks (e.g. blood plasma), and on the slow end
 242 occur over years (e.g. bone) (Tieszen et al., 1983), and can be estimated via controlled feeding studies
 243 (Kurle, 2009; ?; Kim et al., 2012). Although the physiological details are not well understood, isotopic
 244 incorporation can be modeled using either single- or multi-compartmental approaches (Cerling et al., 2006;
 245 Martínez del Rio and Anderson-Sprecher, 2008). In a single compartment framework, isotope ratios are
 246 ingested with food, and directly incorporated into consumer tissues at a tissue-specific rate. In multiple
 247 compartment frameworks, it is assumed that incorporation occurs over multiple body pools, the turnover of
 248 each potentially occurring at different rates. Though an assumption of multi-compartmental incorporation
 249 can provide better statistical fit with experimental data (Cerling et al., 2006; Kurle, 2009; Carleton et al.,
 250 2008), the physiological processes that drive incorporation of isotope ratios from one compartment to
 251 the other are not well understood (Martínez del Rio and Anderson-Sprecher, 2008), and for many tissues
 252 single-compartment models fit as well or better than multi-compartment models (Kurle, 2009).

253 In this next section, we assume that the ingested isotope ratios are incorporated into consumer body
 254 tissues directly, moderated by the rate of incorporation λ , which is treated as a free parameter. Here we
 255 consider only a single compartment model, such that isotope ratios are directly shuttled to consumer tissues
 256 at rate λ ; we note, however, that functions for multi-compartment models could be used instead, though we
 257 do not expect large qualitative differences in results (cf. Fig. 1 in Martínez del Rio and Anderson-Sprecher,
 258 2008). For simplicity, we assume that time is scaled such that a single time step corresponds to a single
 259 foraging bout. Moreover, we assume that the consumer is incorporating prey of smaller size than itself,
 260 such that $0 < \lambda < 1$. Thus, we aim to determine the isotopic composition of the consumer X_c as a function
 261 of its diet, the isotopic mixing space, and λ . We note 1) that the isotopic composition of the consumer
 262 could represent its carbon ($\delta^{13}\text{C}$) or nitrogen ($\delta^{15}\text{N}$) isotope value, and our proceeding derivations work
 263 equivalently for both, and 2) that all trophic discrimination factors are assumed to have been accounted for,
 264 such that X_c directly reflects the consumer's diet. In a completely deterministic framework, the isotopic
 265 composition of the consumer over time t can be written as an ordinary differential equation, where

$$\frac{d}{dt}X_c(t) = \lambda \sum_{i=1}^N p_i \mu_i - \lambda X_c(t). \quad (11)$$

266 However, we must also take into account the stochastic effects described in the previous section, including
 267 the variation associated with the consumer's diet and the isotopic variation associated with each prey. We
 268 account for these stochastic effects by describing changes in the consumer's isotopic distribution with the
 269 stochastic differential equation

$$dX_c(t) = \lambda \left(E\{Z\} dt + \sqrt{V\{Z\}} dW \right) - \lambda X_c(t) dt. \quad (12)$$

270 where dW is the increment of Brownian motion. This stochastic differential equation describes an Ornstein-
 271 Uhlenbeck process, which is a stochastic process that has a steady state variance around the mean (Mangel,
 272 2006). Because the time interval dt is infinitesimal at the continuous limit, the consumer's isotopic

273 distribution will have a Normal distribution. In this case, if the initial isotopic values of the consumer at
 274 time $t = 0$ is $X_c(0)$, the expectation and variability of X_c at time t are

$$\begin{aligned} E\{X_c(t)\} &= E\{Z\} + (X_c(0) - E\{Z\})e^{-\lambda t}, \\ V\{X_c(t)\} &= \frac{\lambda V\{Z\}}{2} (1 - e^{-2\lambda t}). \end{aligned} \quad (13)$$

275 where $E\{Z\}$ and $V\{Z\}$ are as defined in Eqns. 7 and 8. One can observe that as t increases, the exponential
 276 part of $E\{X_c(t)\}$ and $V\{X_c(t)\}$ go to zero, such that $E\{X_c(t)\} \rightarrow E\{Z\}$, and $V\{X_c(t)\} \rightarrow \lambda V\{Z\}/2$. In
 277 other words, the expectation of the consumer's isotopic distribution will equilibrate to that of its diet, while
 278 its variance will always be less than the variance of its diet by a factor of $\lambda/2$. Variance decreases as the
 279 rate of incorporation decreases due to the consumer averaging its isotopic value over more prey (because
 280 the tissue is turning over more slowly), and this serves to average out fluctuations in the consumer's diet.

281 Our static model is defined by a consumer's diet that varies instantaneously over a given parameterization
 282 of $f_Z(z)$. This is relevant for organisms that have a consistently varying diet over time, however most
 283 organisms have diets that undergo large, qualitative changes over longer periods time. In such cases, the
 284 Dirichlet distribution that characterizes diet during one small temporal interval will be different than the
 285 Dirichlet distribution characterizing diet during another interval far apart in time. Such a shift might be
 286 due to seasonal, ontogenetic, or demographic changes in the consumer or its prey base over the course
 287 of months, or years, depending on the timescale of interest. In the following section, we will relax the
 288 assumption that diet is characterized by a single Dirichlet distribution, thus generalizing our formulation of
 289 consumer isotopic dynamics as a function of time.

290 The random variable of interest is now $Z(t)$, which is the trajectory defining the isotopic distribution of
 291 the consumer's diet over time. Solving for $X(t)$, we find

$$\begin{aligned} E\{X(t)\} &= X(0)e^{-\lambda t} + \lambda e^{-\lambda t} \int_{s=0}^t e^{\lambda s} E\{Z(s)\} ds, \\ V\{X(t)\} &= \lambda^2 e^{-2\lambda t} \int_{s=0}^t e^{2\lambda s} V\{Z(s)\} ds. \end{aligned} \quad (14)$$

292 By defining the temporal dynamics of diet $Z(t)$ and the incorporation rate λ , we can thus analytically
 293 determine the isotopic mean and variance of the consumer's tissues.

3 RESULTS

294 We have provided an analytical solution for the mean and variance of the consumer's isotope distribution
 295 as a function of its diet and the prey mixing space. By formulating these solutions in terms of consumer
 296 generalization and specialization (Eq. 9), we make three observations: 1) the variance of the isotopic
 297 distribution of the consumer's diet, $V\{Z\}$, which scales to its isotopic niche width, is concave parabolic
 298 (Fig. 1); 2) whether and to what extent $V\{Z\}$ demonstrates measurable nonlinearity depends in part on the
 299 geometry of the mixing space; 3) the peak variance over the generalization-specialization continuum is the

300 consumer's maximum isotopic niche width. This point may or may not exist at a value intermediate to an
301 obligate generalist and obligate specialist.

302 The nonlinear nature of the consumer's isotopic niche width as a function of its specialization on certain
303 prey (or combinations of prey) is driven almost entirely by the geometry of the prey mixing space. One can
304 gain some intuitive understanding of this nonlinearity by considering the following example, illustrated in
305 Fig. 1. In a three-prey system, where all prey have equal isotopic means and variances, a consumer that
306 ranges from generalization on all three prey to specialization on a single prey will likewise have isotopically
307 equivalent diets. As the mean isotope value of the targeted prey is moved away from the others, such that its
308 offset from the mixing space centroid (the center of the mixing space; ?Newsome et al., 2012) is increased,
309 the variance function displays increasing nonlinearity. For a skewed mixing space, where one prey source
310 has a very different isotope composition than the rest (e.g. a mixing space consisting of terrestrial foods vs.
311 a marine subsidy; ?), if the consumer incorporates isotopes from all three sources in equal proportions (a
312 generalist), it will have relatively higher isotopic variance than if its prey exhibited a less skewed mixing
313 space geometry. The skewness of the mixing space increases with the offset of the targeted prey from
314 the mixing space centroid as shown in Fig. 1. As the consumer integrates this isotopically unique prey
315 in greater proportions, the heterogeneity of incorporated isotope values will increase, serving to increase
316 the consumer's isotopic variability. The isotopic variability will then decline as the consumer begins
317 specializing on the atypical prey, and if it is consuming this prey exclusively, the isotopic variability of its
318 diet will reflect the isotopic variability of its prey exactly. The concave parabolic nature of the isotopic
319 variability of the consumer's diet can thus be explained by heterogeneous incorporation of isotope ratios
320 over an skewed, or asymmetric, mixing space.

321 Understanding what dietary strategy or mixing space geometry can maximize the isotopic niche width
322 of the consumer's diet will serve to help ecologists determine what mechanisms - ecological or statistical
323 - may be driving patterns in isotope data, or whether these mechanisms can be decoupled at all. Our
324 analytical solution for peak variance over dietary specialization on prey k , \hat{s}_k , reveals that maximum
325 isotopic niche width can, but doesn't always, fall in $s_k \in [1/n, 1]$, with bounds denoting exclusive prey
326 generalization or specialization, respectively. If the peak lies outside of this region, changes in isotopic
327 variance as specialization on a targeted prey is increased will appear monotonic or even linear.

328 Although the specific nature of \hat{s}_k will depend strongly on mixing space geometry, we can elucidate
329 certain key attributes that will determine the general nature of where this value falls. For mixing space
330 geometries where the targeted prey has higher than average variance, \hat{s}_k will tend to lie towards prey
331 specialization ($s_k > 0.5$), however the offset of the mean value of the targeted prey from the mixing space
332 centroid will quickly push \hat{s}_k to $s_k \rightarrow 0.5$ (Fig. 2A,B). In contrast, if the targeted prey has lower than
333 average variance, \hat{s}_k will tend to lie towards prey generalization ($s_k < 0.5$; Fig. 2B,C). As before, if the
334 offset of the targeted prey's mean value increases, $\hat{s}_k \rightarrow 0.5$. In both cases, if the mean value for the
335 targeted prey is close to the mixing space centroid, the maximum isotopic variance for the consumer could
336 lie in any region.

337 Temporally variable diets

338 The equilibrial solution to our stochastic differential equation (Eq. 13) reveals that the isotopic variability
339 of the consumer scales to diet as a factor of $\lambda/2$. As the incorporation rate decreases, such that the turnover
340 time is longer, the isotopic variability of the consumer declines. This is due to the consumer averaging its
341 tissues over a greater number of foraging bouts. Moreover, we observe that as the consumer transitions

342 from some initial isotopic state $X_c(0)$ to diet, the variance of the consumer's isotopic values equilibrate
 343 twice as fast as the mean value.

344 If the consumer's diet is itself variable over time, we do not expect its isotopic composition to equilibrate
 345 as it would in a controlled feeding study (Eq. 14). For example, the consumer might adopt one diet during
 346 the wet season, and another during the dry season, such that it oscillates between the two throughout the
 347 year. We consider a composite diet with an isotopic distribution $\mathbb{Z}(t) \sim f_{\mathbb{Z}}(t)$ that dynamically oscillates
 348 between two subdiets, which we will refer to as 'seasonal diets' with frequency ω . We note that $1/\omega$ in
 349 this context corresponds to the 'dietary correlation time' of Fink et al. (2012). Seasonal diets have random
 350 variables Z_1 and Z_2 , each distributed according to Eq. 6, though they have different underlying Dirichlet
 351 distributions – encoding which prey the consumer targets during each season with frequency distributions
 352 f_{P_1} and f_{P_2} – while the isotopic distributions of prey are assumed to be constant over time. We can thus
 353 describe the composite diet as a mix of the seasonal diets characterized by weights that oscillate over time,
 354 and this determines the contribution of each seasonal dietary strategy to the whole. We define $\mathcal{U}(t)$ to be
 355 the proportional contribution of Z_1 to the composite diet $\mathbb{Z}(t)$ over time, such that it can vary between zero
 356 (no incorporation of Z_1) to unity (complete reliance on Z_1). The frequency distribution for the composite
 357 diet is thus

$$f_{\mathbb{Z}(t)} = \mathcal{U}(t)f_{Z_1} + (1 - \mathcal{U}(t))f_{Z_2}. \quad (15)$$

358 If we do not specify the type of oscillation that drives changes in diet over time, the expectation and
 359 variance for the isotopic distribution of the composite diet over time are thus

$$\begin{aligned} E\{\mathbb{Z}(t)\} &= \mathcal{U}(t)E\{Z_1\} + (1 - \mathcal{U}(t))E\{Z_2\}, \\ V\{\mathbb{Z}(t)\} &= \mathcal{U}(t)V\{Z_1\} + (1 - \mathcal{U}(t))V\{Z_2\} + \mathcal{U}(t)(1 - \mathcal{U}(t))(E\{Z_1\} - E\{Z_2\})^2, \end{aligned} \quad (16)$$

360 where the isotopic mean of the composite diet is averaged over both seasonal diets, weighted by the
 361 proportional inclusion of each. In the wet/dry season example, the consumer could either shift gradually
 362 from its wet season diet to its dry season diet if $\mathcal{U}(t)$ is smooth, or shift abruptly if $\mathcal{U}(t)$ is discontinuous.

363 Dietary transitions between seasons tend to be gradual, even if the start/end of a given season is abrupt
 364 (??). To understand how a temporally oscillating diet affects the isotopic variance of the composite diet, we
 365 consider the smooth oscillation $\mathcal{U}(t) = 1/2 + 1/2 \sin(\omega t)$, such that the proportional contribution of Z_1
 366 oscillates with frequency ω (Fig. 3A). Substituting $\mathcal{U}(t)$ into Eq. 16 provides the solution to a sinusoidally
 367 varying diet, with expectation and variance

$$\begin{aligned}
 E\{\mathbb{Z}(t)\} &= \frac{E\{Z_1\} + E\{Z_2\}}{2} + \frac{E\{Z_1\} - E\{Z_2\}}{2} \sin(\omega t), \\
 V\{\mathbb{Z}(t)\} &= \overbrace{\frac{V\{Z_1\} + V\{Z_2\}}{2} + \frac{1}{2} \left(\frac{E\{Z_1\} - E\{Z_2\}}{2} \right)^2}^{\alpha_V} \\
 &\quad + \overbrace{\frac{V\{Z_1\} - V\{Z_2\}}{2} \sin(\omega t)}^{\beta_V} + \overbrace{\frac{1}{2} \left(\frac{E\{Z_1\} - E\{Z_2\}}{2} \right)^2}^{\gamma_V} \sin\left(2\omega t + \frac{\pi}{2}\right).
 \end{aligned} \tag{17}$$

368 where we have combined the non-oscillating components of the variance into three parameters α_V , β_V ,
 369 and γ_V for notational efficiency.

370 We gain three key insights from the solution for the expectation and variance of the composite diet. 1)
 371 As would be expected, the central tendency of the composite diet is the average of the mean values for
 372 each subdiet, while the amplitude of oscillations is driven entirely by the difference in the mean values of
 373 each subdiet; 2) the time-averaged variance (denoted by $\langle \cdot \rangle_t$) is simply $\langle V\{\mathbb{Z}(t)\} \rangle_t = \alpha_V$, which is only
 374 impacted by the average variance between the seasonal diets and the difference in the mean isotope values
 375 between the seasonal diets (Fig. 4); 3) the oscillating component shows that the composite dietary variance
 376 has a modified frequency, as well as an offset, meaning that the maximal variance of the consumer's
 377 composite diet generally occurs during the transition from one diet to the other (Fig. 3B). Together, these
 378 results reveal that if the consumer's diet is varying continuously over time between two seasonal diets, both
 379 the averaged variance, as well as the difference in the mean isotope values of the seasonal diets – directly
 380 reflecting the heterogeneity of prey mixing space geometry – will serve to increase the time-averaged
 381 variance of the consumer's diet, and by extension the isotopic variance of the consumer itself.

382 Less intuitively, we observe that the consumer's peak variance, or niche width, as measured by the
 383 variance of its composite diet, occurs not during the exclusive adoption of its subdiets, but during the
 384 transition between the two, and this peak variance is driven exclusively by the difference in means
 385 between seasonal diets. As the seasonal diets become more heterogeneous in isotopic space, the greater the
 386 consumer's peak variance during the transition, and this occurs because it is sampling between two dietary
 387 strategies that are isotopically distinct. We can directly observe this by considering a transition between
 388 two diets with a) different means and the same variances, and b) the same means and different variances.
 389 In the former case, the peak variance of the composite diet occurs during the transition (Fig 3B); in the
 390 latter case, because the diets have the same mean isotope value, the peak occurs not during the transition,
 391 but when the consumer adopts the diet with the greater variance, which in our example would occur at the
 392 height of the season (Fig 3C).

393 The isotopic composition of a consumer $X_c(t)$ during a single dietary shift is governed by a single
 394 timescale of physiological origin: the rate of incorporation λ (Eq. 13). However, a seasonally shifting diet
 395 that is driven by oscillating foraging strategies introduces an additional ecological timescale that will affect
 396 $X_c(t)$, determined by the frequency of diet switching ω (Fig. 5A). Depending on the turnover rate of the
 397 tissue of interest and how often the consumer shifts its diet, the ratio of these timescales ω/λ will impact
 398 how the isotopic mean and variance of the consumer changes over time. For the case of a sinusoidally
 399 varying diet, we can solve for $X_c(t)$ directly, such that

$$\begin{aligned} V\{X_c(t \gg 0)\} = & \alpha_V \frac{\lambda}{2} + \beta_V \frac{\lambda^2}{\sqrt{(2\lambda)^2 + \omega^2}} \sin(\omega t - \theta_1) \\ & + \gamma_V \frac{\lambda^2}{2\sqrt{\lambda^2 + \omega^2}} \sin(2\omega t + \theta_2). \end{aligned} \quad (18)$$

400 where the offsets θ_1 and θ_2 are $\tan^{-1}(\omega/2\lambda)$ and $\tan^{-1}(\lambda/\omega)$, respectively. As in the case of a single
 401 diet Z , the time-averaged variance is scaled by the incorporation rate as $\alpha_V \lambda / 2$. Moreover, we observe
 402 that the consumer's isotopic composition lags behind changes in diet, such that an isotopic shift in the
 403 consumer's tissues is observed after the actual foraging shift. This lag involves both θ_1 and θ_2 , however
 404 these offsets play different roles in contributing to the lag for different mixing space geometries. When the
 405 isotopic means of the seasonal diets are similar, the lag is mostly due to θ_1 ; when the means are different
 406 and the variances are similar, the lag is mostly due to θ_2 ; when both the isotopic means and variances of
 407 the seasonal diets are different, both contribute significantly to the lag.

408 As shown in Fig. 5, we observe that 1) the lag between the transition and the peak variance of the
 409 consumer increases with decreasing λ (i.e. increasing timescale of incorporation), and 2) the amplitude
 410 of the variance of $X_c(t)$ decreases with increasing ω (i.e. decreasing timescale of ecological switching).
 411 The first result is not surprising, as it mirrors the role of λ in the static diet example. The second result
 412 is less intuitive: in words, as the consumer shifts its diet more frequently, there is still a peak variance
 413 during dietary transitions, though with diminishing amplitude, and this would make it more difficult to
 414 measure (Fig 5B). This is due to the consumer slowly integrating isotopes into its tissues from both diets,
 415 thus averaging across diet-switching events, thus dampening fluctuations. Accordingly, the decrease in
 416 the amplitude of isotopic variance of the consumer's tissue is an averaging effect, where the timescale of
 417 incorporation is much larger than the timescale of dietary switching.

4 DISCUSSION

418 We have established a forward-integration approach towards understanding how the isotopic distribution of
 419 an individual consumer evolves due to ecological, physiological, and geometric factors. Our framework
 420 introduces mechanistic links between the ecological foraging dynamics of a consumer, the physiological
 421 constraints that dictate incorporation, and the more abstract effects of mixing space geometry. We focus
 422 our efforts on building an analytical framework to understand how the isotopic variance of an individual –
 423 its isotopic niche width – changes as a function of different foraging strategies that are both probabilistic
 424 and dynamic over time. We consider two foraging scenarios: 1) *static strategy*: probabilistic consumption
 425 of multiple prey, the proportions of which are on average constant over time, and 2) *dynamic strategy*:
 426 probabilistic consumption of multiple prey whose relative contribution to consumer's diet varies over time.
 427 The former example is most relevant for consumers inhabiting environments where resource availability
 428 is stable (reliable), whereas the latter is more appropriate for consumers that prey switch between two
 429 qualitatively different subdiets.

430 Our primary findings concern whether and to what extent the peak isotopic variance of the consumer,
 431 or maximum isotopic niche width, is realized under different, but definable, conditions with respect to
 432 static and dynamic foraging scenarios. When the consumer exhibits a static foraging strategy, the isotopic
 433 variance of its diet is tied directly to its prey specialization and the skewness of the isotopic mixing

space. We show that as the mixing space becomes more skewed, there is an increasing likelihood that the peak variance will occur at intermediate specialization (where a single prey accounts for ca. 50% of the consumer's diet; Figs. 1,2). When the consumer exhibits a dynamic, yet smoothly varying foraging strategy, we show that the peak variance occurs during the transition from one diet to another, and is offset by a lag that is a function of both its incorporation rate and the timescale over which it shifts between diets (Fig. 3). Below we show that these findings are relevant beyond theory by examining an empirical sea otter mixing space, and discuss areas where additional realism can be incorporated to gain further ecological insight into the isotopic niche.

442 The isotopic niche: generalization vs. specialization

443 To demonstrate the empirical relevance of the nonlinear nature of $V\{Z\}$, we examine a prey-rich marine
444 system near San Simeon and Monterey Bay, California, composed of nine invertebrate species commonly
445 consumed by sea otters (Tinker et al., 2008). In this system, all potential prey resources have unique
446 isotopic means and variances (Fig. 6), including multiple species of sea urchins and crab, clams, abalone,
447 mussels, and snails. We can investigate how alternatively targeting each prey species alters the isotopic
448 variance of a sea otter's diet across different degrees of specialization by modifying the underlying Dirichlet
449 distribution (i.e. by increasing a_k for each species individually, while holding $a_{i \neq k} = 1$; Fig. 7A). We
450 determined the existence of strong nonlinearity in the isotopic variance of diet for 44% of prey species (Fig.
451 7B). For targeted prey exhibiting nonlinear variance (including mussels, snails, purple sea urchins, and
452 kelp crabs), the maximum isotopic variance was found in the region $s \leq 0.5$.

453 The message that we take from the sea otter example is relatively straightforward: for a given prey mixing
454 space, a consumer's dietary variability – where the consumer's tissues scale in proportion to its diet by a
455 factor of $\lambda/2$ – will be a function of both mixing space geometry, as well as its dietary strategy, and these
456 effects can be confounding. Despite this, we are able to establish certain predictions for the consumer's
457 isotopic niche width as a function of diet: as the consumer incorporates moderate amounts of isotopically
458 unique prey into its diet, its variance will be expected to increase. Knowledge of the interplay between
459 mixing space geometry and a consumer's dietary strategy, and its consequent effect on the isotopic variance
460 of diet, is particularly important for characterizing consumers based exclusively on isotopic variance. For
461 example, without knowledge of these relationships, a highly variable consumer might be interpreted as a
462 dietary generalist, whereas it might be able to achieve a similarly high or higher variance by moderately
463 focusing its foraging activities on a single prey species with an isotopic distribution far from the mixing
464 space centroid.

465 The isotopic niche over time

466 We gain additional insight into the factors influencing consumer isotopic variability by considering
467 dynamic diets, where the consumer oscillates between different foraging strategies over time. We considered
468 a simple sinusoidal oscillation for $U(t)$, the proportional contribution of diet 1 to the composite diet over
469 time $Z(t)$. The subdiets from which the composite diet is composed can be thought of as 'seasonal diets'.
470 Our analytical results showed that the peak variance of the composite diet occurred during the transition
471 between seasonal diets. Importantly, this is not due to any particular mixing space geometry, but a general
472 result that will always occur, as long as the diets are isotopically distinct (each with a unique mean and
473 variance), and the transition is smooth such that a consumer gradually shifts between different diets, as
474 opposed to an abrupt, discontinuous diet switch.

475 Although the peak variance of $\mathbb{Z}(t)$ is entirely due to ecological diet shifts rather than mixing space
476 geometry, the latter does play a role in determining the mean value (time average) of $V\{\mathbb{Z}(t)\}$. The effect of
477 mixing space geometry on the time-averaged variance of the composite diet is determined by α_V , which is
478 a function of 1) the average variance of the subdiets from which \mathbb{Z} is composed, and 2) the mean difference
479 between the two subdiets (see Eq. 18). As either of these factors increase, the average variance of the
480 composite diet increases, setting the baseline from which the peak dietary variance fluctuates (Fig. 4). We
481 also observed that as the frequency of dietary transitions increased relative to the rate at which the consumer
482 integrates dietary isotopes into its tissues, the consumer's isotopic variance exhibited lower amplitude as it
483 fluctuated between the different variances of its diet (Fig. 5). This occurs because the greater transition
484 frequencies serve to average variance of the two diets within its tissues. Fink et al. (2012) found a similar
485 dynamic when they derived an analytical solution for the variance of a consumer population transitioning
486 between two prey.

487 An interesting observation that we gain from exploring a sinusoidal dietary shift is that the variance
488 peak observed during dietary transitions is dependent on the smoothness of the transition. In fact, it is the
489 transition mid-point, at $\mathcal{U}(t) = 0.5$, where the composite diet is pulled equally from each seasonal diet,
490 and this serves to maximize the isotopic heterogeneity of the mixture (the consumer). Thus, when foraging
491 strategies are dynamic, it is the point of maximum isotopic heterogeneity that results in peak isotopic
492 variance of the diet. This is analogous to the cause of peak dietary variance in the static example, where
493 specialization on prey resources with greater isotopic offsets from the mixing space centroid maximizes
494 isotopic heterogeneity, resulting in a variance peak.

495 An extreme alternative to a smooth dietary transition would be one that is discontinuous, as depicted by a
496 step-function, or square wave (Fig. 8A). Such an instantaneous dietary shift is not ecologically unrealistic;
497 e.g. both brown bears and gray wolves abruptly shift their diet to salmon during salmon runs (??), as
498 do predators on other prey populations exhibiting localized boom-bust dynamics such as locusts, krill,
499 jellyfish, and sardines (??). Because there is no point during a sharp, discontinuous transition that serves to
500 mix subdiets, the variance of the composite diet does not peak in response. Instead, both the expectation
501 and the variance of the composite diet incorporates this step function behavior, transitioning to reflect the
502 shifts between different diets. Because the isotope ratios associated with diet are incorporated gradually
503 into the consumer's tissues, both the mean and the variance of the consumer will adopt a sawtooth-like
504 dynamic (Fig. 8A,B), where they begin to asymptote to the expectation and variance of the subdiets, but
505 are reverted abruptly at the dietary switch. We note that, as in the static example, the isotopic variance of
506 the consumer approaches the variance of its diet twice as fast as its expectation (cf. Eq. 13).

507 Population dynamics and state-dependent foraging

508 We presented a simple dynamic-switching framework, where a consumer oscillates between two different
509 diets over time to explore its effect on its isotopic niche. In reality, a consumer's dietary strategy might be
510 shifting constantly over time, in response to a constantly changing environment. One potentially important
511 extension of our framework could incorporate a population dynamic underlying the availability of potential
512 resources (and by extension the consumer's diet) in a continuous, more complex, and ecologically justified
513 manner. Our original formulation of the Dirichlet distribution that describes the consumer's diet was
514 established on the relationship between the random variables describing the proportional contribution of
515 prey to diet ($P_i = p_i$) and its encounter rate ($\Psi_i = \psi_i$), where $p_i = \psi_i / \sum_j \psi_j$, and this was assumed to
516 have a static distribution over time. However, if the prey are fluctuating in accordance to an underlying
517 population dynamic (for example, determined by a system of differential equations), the encounter rate

518 of each prey would itself be a function of time. By relating the expectation and/or variance of Ψ_i to the
519 density of prey, the parameterization of the Dirichlet can be directly coupled to changes in population
520 densities, thus mechanistically incorporating population dynamics into predictions of a consumer's isotopic
521 composition.

522 Furthermore, the relationship between p_i and ψ_i explicitly assumes passive foraging between the consumer
523 and its potential prey, and this holds for our original static (single diet) example, our shifting diet example,
524 and would hold for the example above where the Dirichlet changes in response to an underlying population
525 dynamic. Although this is not a bad starting point, and may be a perfectly reasonable assumption for a filter
526 feeder that consumes resources indiscriminately, it is not a reliable assumption for most organisms that
527 may rank prey based on intrinsic traits (e.g., energetic yield, handling/processing time). Instead, a more
528 complex relationship between p_i and the attributes of the consumer's prey, and perhaps attributes of the
529 consumer itself, could be used to determine the parameterization of the Dirichlet distribution defining the
530 consumer's diet over time.

531 For example, our framework implicitly assumes that there is a steady state influx of prey biomass to
532 match the metabolic expenses of the consumer. In other words, prey are chosen in accordance to the
533 Dirichlet distribution, but it is assumed that each foraging bout contributes equally to the consumer's
534 diet, and that the consumer always finds a meal. In reality, the success of a given foraging bout is not
535 certain, and there is some risk of not finding any prey at all (?); in such a case, the consumer would resort
536 to metabolizing its own tissues (??). Such a dynamic would directly impact the rate of incorporation by
537 altering the proportional contribution of newly consumed isotopes to the turnover of the consumer's body
538 tissues. Moreover, the foraging decisions that a consumer makes are often a function of its energetic state
539 (?Yeakel et al., 2014), which changes as it successfully or unsuccessfully finds and acquires its prey (?).
540 Such state-dependent foraging may be difficult to treat analytically, but could be explored numerically, and
541 this approach would be useful for hypothesis testing, particularly when one is interested in comparing the
542 effects of different foraging strategies on the statistical properties of the consumer's isotopic composition.

543 From individuals to populations

544 Finally, the framework that we have presented has focused entirely on the individual, in particular on
545 how the isotopic variance of an individual consumer changes in response to different ecological and
546 physiological factors as well as aspects of the isotope mixing space it utilizes. Most ecological applications
547 using stable isotope analysis operate at the level of the population, although there is a rich literature
548 of efforts that use stable isotope analysis to understand sources of isotopic variation at the level of the
549 individual (Koch et al., 1995; Matthews and Mazumder, 2004; Sponheimer et al., 2006; Post, 2008;
550 Newsome et al., 2009; Yeakel et al., 2009; Newsome et al., 2012; Hopkins III and Kurle, 2015).

551 Understanding how variance percolates from prey to the individual consumer is a necessary first step
552 for understanding sources of isotopic variation at population level. Such considerations quickly become
553 complex, as there are scenarios when the isotopic variance of an individual is or is not closely coupled to
554 the variance of the population. For example, if individuals within a population have similar means and -
555 for simplicity - equal variances, then the variance of the population will scale linearly with the variance
556 of the individuals (Fig. 9A,B). This relationship highlights an important message: when individuality is
557 low, the variance of the population is entirely explained by the variance of the individuals; this means that
558 the results that we have presented for a consumer individual are expected to scale directly to that of the
559 population. However, if the individuals within a population have very different means and relatively small

560 variances, then there will not be a significant relationship between population-level and individual-level
561 variation (Fig. 9C,D).

562 We can imagine different individual-population relationships occurring within a 2-D state-space defined
563 by individuality on one axis and specialization on the other. At the extremes, a population could consist
564 of 1) obligate specialists with low individuality where all individuals specialize on the same resource, 2)
565 obligate specialists with high individuality where all individuals specialize on different resources, and
566 3) obligate generalists with low individuality where all individuals are generalists; an obligate generalist
567 with high individuality cannot exist in this context. These potential end-members are discussed at length
568 in Bearhop et al. (2004) and Fink et al. (2012). As we have seen in the above analyses, the variation of
569 individuals is driven by a complex interplay between mixing space geometry, consumer foraging behaviors,
570 and physiological incorporation. How these different population-level end-members might shape both
571 individual and population-level isotopic distributions is an important question, though the answers will
572 likely harbor additional complexities. For example, isotopically similar individuals with low variances
573 imply that all individuals are consuming similar things, in similar quantities, such that individuality is low,
574 though our results show that low isotopic variance need not indicate specialization or generalization *per se*
575 (cf. Figs 1,7). Accounting for individual variation in dietary proclivities over time is bound to complicate
576 interpretation further.

577 Conclusions

578 There are many sources of variation that contribute to a consumer's isotopic composition. These sources
579 include the geometry of the prey mixing space, the foraging behaviors of the consumers, as well as temporal
580 changes in the environment that might alter the ability of the consumer to find, acquire, and consume its
581 prey. Along with physiological incorporation of isotopes into consumer tissues, these factors serve to drive
582 the temporal evolution of the isotopic distribution, or isotopic niche, of the consumer. By coupling the
583 isotopic variance of this distribution to mechanistic relationships between the consumer and its diet, as
584 well as the isotopic mixing space of the system, we have presented a systematic exploration of the factors
585 that cause the isotopic niche to both expand and contract. Incorporating the effects of population dynamics
586 and/or more complex foraging strategies will enable hypothesis testing of different ecological mechanisms
587 to generate the isotopic distributions that are observed in nature. We hope that such a forward-integrating
588 approach, alongside the use of tools such as mixing models to back-calculate dietary composition, will
589 serve to expand and enhance the ecological interpretation of isotopic data.

DISCLOSURE/CONFLICT-OF-INTEREST STATEMENT

590 The authors declare that the research was conducted in the absence of any commercial or financial
591 relationships that could be construed as a potential conflict of interest.

AUTHOR CONTRIBUTIONS

592 JDY, UB, EAES, and SDN conceived the idea. JDY and UB designed the statistical framework and
593 conducted the analyses. EAES and SDN contributed empirical data. All authors contributed equally to
594 drafting and writing the manuscript.

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REFERENCES

- 600 Ainsworth, C. H., Kaplan, I. C., Levin, P. S., and Mangel, M. (2010). A statistical approach for estimating
599 fish diet compositions from multiple data sources: Gulf of California case study. *Ecol. Appl.* 20,
601 2188–2202
- 603 Araújo, M. S., Bolnick, D. I., and Layman, C. A. (2011). The ecological causes of individual specialisation.
604 *Ecol. Lett.* 14, 948–958
- 605 Araújo, M. S., Bolnick, D. I., Machado, G., Giaretta, A. A., and dos Reis, S. F. (2007). Using $\delta^{13}\text{C}$ stable
606 isotopes to quantify individual-level diet variation. *Oecologia* 152, 643–654
- 607 Araújo, M. S., Bolnick, D. I., Martinelli, L. A., Giaretta, A. A., and dos Reis, S. F. (2009). Individual-level
608 diet variation in four species of Brazilian frogs. *J. Anim. Ecol.* 78, 848–856
- 609 Bearhop, S., Adams, C. E., Waldron, S., Fuller, R. A., and Macleod, H. (2004). Determining trophic niche
610 width: a novel approach using stable isotope analysis. *J. Anim. Ecol.* 73, 1007–1012
- 611 Bolnick, D., Svanback, R., Araújo, M., and Persson, L. (2007). Comparative support for the niche variation
612 hypothesis that more generalized populations also are more heterogeneous. *Proc. Natl. Acad. Sci. USA*
613 104, 10075
- 614 Bolnick, D. I., Amarasekare, P., Araújo, M. S., Bürger, R., Levine, J. M., Novak, M., et al. (2011). Why
615 intraspecific trait variation matters in community ecology. *Trends Ecol. Evol.* 26, 183–192
- 616 Carleton, S. A., Kelly, L., Anderson-Sprecher, R., and Martínez del Rio, C. (2008). Should we use one-, or
617 multi-compartment models to describe ^{13}C incorporation into animal tissues? *Rapid Commun. Mass Sp.*
618 22, 3008–3014
- 619 Cerling, T. E., Ayliffe, L. K., Dearing, M. D., Ehleringer, J. R., Passey, B. H., Podlesak, D. W., et al. (2006).
620 Determining biological tissue turnover using stable isotopes: the reaction progress variable. *Oecologia*
621 151, 175–189
- 622 Chesson, J. (1983). The Estimation and Analysis of Preference and Its Relationship to Foraging Models.
623 *Ecology* 64, 1297
- 624 Clark, C. W. and Mangel, M. (2000). *Dynamic state variable models in ecology: methods and applications*
625 (Oxford University Press, USA)
- 626 Fink, P., Reichwaldt, E. S., Harrod, C., and Rossberg, A. G. (2012). Determining trophic niche width: an
627 experimental test of the stable isotope approach. *Oikos* 121, 1985–1994
- 628 Hilborn, R. and Mangel, M. (1997). *The ecological detective: Confronting models with data* (Princeton:
629 Princeton University Press)
- 630 Hopkins, J. B. and Ferguson, J. M. (2012). Estimating the diets of animals using stable isotopes and a
631 comprehensive bayesian mixing model. *PLoS ONE* 7, e28478
- 632 Hopkins III, J. B. and Kurle, C. M. (2015). Measuring the realized niches of animals using stable isotopes:
633 from rats to bears. *Methods Ecol Evol*, 1–12
- 634 Hutchinson, G. E. (1957). Concluding remarks. In *Cold spring harbor symposium on quantitative biology*
635 (Concluding remarks)
- 636 Jackson, A. L., Inger, R., Parnell, A. C., and Bearhop, S. (2011). Comparing isotopic niche widths among
637 and within communities: SIBER - Stable Isotope Bayesian Ellipses in R. *J. Anim. Ecol.* 80, 595–602
- 638 Johnson, N. L. (1960). An Approximation to the Multinomial Distribution: Some Properties and
639 Applications. *Biometrika* 47, 93
- 640 Kim, S. L., Martínez del Rio, C., Casper, D., and Koch, P. L. (2012). Isotopic incorporation rates for shark
641 tissues from a long-term captive feeding study. *J. Exp. Biol.* 215, 2495–2500
- 642 Koch, P., Heisinger, J., Moss, C., Carlson, R., Fogel, M., and Behrensmeyer, A. (1995). Isotopic tracking
643 of change in diet and habitat use in African elephants. *Science* 267, 1340

- 644 Kurle, C. M. (2009). Interpreting temporal variation in omnivore foraging ecology via stable isotope
645 modelling. *Functional Ecology* 23, 733–744
- 646 Layman, C. A., Araújo, M. S., Boucek, R., Hammerschlag-Peyer, C. M., Harrison, E., Jud, Z. R., et al.
647 (2011). Applying stable isotopes to examine food-web structure: an overview of analytical tools.
648 *Biological Reviews*, no–no
- 649 Layman, C. A., Quattrochi, J. P., Peyer, C. M., and Allgeier, J. E. (2007). Niche width collapse in a resilient
650 top predator following ecosystem fragmentation. *Ecol. Lett.* 10, 937–944
- 651 Lehmann, D., Mfune, J. K. E., Gewers, E., Brain, C., and Voigt, C. C. (2015). Individual variation of
652 isotopic niches in grazing and browsing desert ungulates. *Oecologia*, 1–14
- 653 Mangel, M. (2006). *The theoretical biologist's toolbox: Quantitative methods for ecology and evolutionary
654 biology* (Cambridge: Cambridge University Press)
- 655 Mangel, M. (2014). Stochastic dynamic programming illuminates the link between environment,
656 physiology, and evolution. *B. Math. Biol.* 77, 857–877
- 657 Mangel, M. and Clark, C. W. (1988). *Dynamic modeling in behavioral ecology* (Princeton: Princeton
658 University Press)
- 659 Martínez del Rio, C. and Anderson-Sprecher, R. (2008). Beyond the reaction progress variable: the
660 meaning and significance of isotopic incorporation data. *Oecologia* 156, 765–772
- 661 Martínez del Rio, C., Sabat, P., Anderson-Sprecher, R., and Gonzalez, S. P. (2009). Dietary and isotopic
662 specialization: the isotopic niche of three *Cinclus* ovenbirds. *Oecologia* 161, 149–159
- 663 Matthews, B. and Mazumder, A. (2004). A critical evaluation of intrapopulation variation of $\delta^{13}\text{C}$ and
664 isotopic evidence of individual specialization. *Oecologia* 140, 361–371
- 665 Moore, J. W. and Semmens, B. X. (2008). Incorporating uncertainty and prior information into stable
666 isotope mixing models. *Ecol. Lett.* 11, 470–480
- 667 Newsome, S., Yeakel, J. D., Wheatley, P. V., and Tinker, M. T. (2012). Tools for quantifying isotopic niche
668 space and dietary variation at the individual and population level. *J. Mammal.* 93, 329–341
- 669 Newsome, S. D., Martinez del Rio, C., Bearhop, S., and Phillips, D. L. (2007). A niche for isotopic ecology.
670 *Front. Ecol. Environ.* 5, 429–436
- 671 Newsome, S. D., Tinker, M., Monson, D., Oftedal, O., Ralls, K., Staedler, M., et al. (2009). Using stable
672 isotopes to investigate individual diet specialization in California sea otters (*Enhydra lutris nereis*).
673 *Ecology* 90, 961–974
- 674 Newsome, S. D., Tinker, M. T., Gill, V. A., Hoyt, Z. N., Doroff, A., Nichol, L., et al. (2015). The interaction
675 of intraspecific competition and habitat on individual diet specialization: a near range-wide examination
676 of sea otters. *Oecologia*, 1–15
- 677 Ogle, K., Tucker, C., and Cable, J. M. (2014). Beyond simple linear mixing models: process-based isotope
678 partitioning of ecological processes. *Ecol. Appl.* 24, 181–195
- 679 Parnell, A. C., Inger, R., Bearhop, S., and Jackson, A. L. (2010). Source partitioning using stable isotopes:
680 coping with too much variation. *PLoS ONE* 5, e9672
- 681 Parnell, A. C., Phillips, D. L., Bearhop, S., Semmens, B. X., Ward, E. J., Moore, J. W., et al. (2013).
682 Bayesian stable isotope mixing models. *Environmetrics* 24, 387–399
- 683 Phillips, D. L. (2001). Mixing models in analyses of diet using multiple stable isotopes: a critique.
684 *Oecologia* 127, 166–170
- 685 Phillips, D. L. and Gregg, J. W. (2003). Source partitioning using stable isotopes: coping with too many
686 sources. *Oecologia* 136, 261–269
- 687 Phillips, D. L. and Koch, P. (2002). Incorporating concentration dependence in stable isotope mixing
688 models. *Oecologia* 130, 114–125

- 689 Phillips, D. L., Newsome, S. D., and Gregg, J. W. (2005). Combining sources in stable isotope mixing
690 models: alternative methods. *Oecologia* 144, 520–527
- 691 Post, D. M. (2008). Individual variation in the timing of ontogenetic niche shifts in largemouth bass.
692 *Ecology* 84, 1298–1310
- 693 Roughgarden, J. (1979). *Theory of population genetics and evolutionary ecology: an introduction*. (New
694 York: Macmillan)
- 695 Semmens, B. X., Ward, E. J., Moore, J. W., and Darimont, C. T. (2009). Quantifying inter-and intra-
696 population niche variability using hierarchical Bayesian stable isotope mixing models. *PLoS ONE* 4,
697 e6187
- 698 Sponheimer, M., Passey, B. H., de Ruiter, D. J., Guatelli-Steinberg, D., Cerling, T. E., and Lee-Thorp, J. A.
699 (2006). Isotopic evidence for dietary variability in the early hominin *Paranthropus robustus*. *Science*
700 314, 980–982
- 701 Tieszen, L. L., Boutton, T. W., Tesdahl, K. G., and Slade, N. A. (1983). Fractionation and turnover of
702 stable carbon isotopes in animal tissues: Implications for $\delta^{13}\text{C}$ analysis of diet. *Oecologia* 57, 32–37
- 703 Tinker, M. T., Bentall, G., and Estes, J. A. (2008). Food limitation leads to behavioral diversification and
704 dietary specialization in sea otters. *Proc. Natl. Acad. Sci. USA* 105, 560–565
- 705 Yeakel, J. D., Dominy, N. J., Koch, P. L., and Mangel, M. (2014). Functional morphology, stable isotopes,
706 and human evolution: a model of consilience. *Evolution* 68, 190–203
- 707 Yeakel, J. D., Guimarães Jr, P. R., Bocherens, H., and Koch, P. L. (2013). The impact of climate
708 change on the structure of Pleistocene food webs across the mammoth steppe. *Proc. Roy. Soc. B* 280,
709 20130239–20130239
- 710 Yeakel, J. D., Patterson, B. D., Fox-Dobbs, K., Okumura, M., Cerling, T., Moore, J., et al. (2009).
711 Cooperation and individuality among man-eating lions. *Proc. Natl. Acad. Sci. USA* 106, 19040–19043

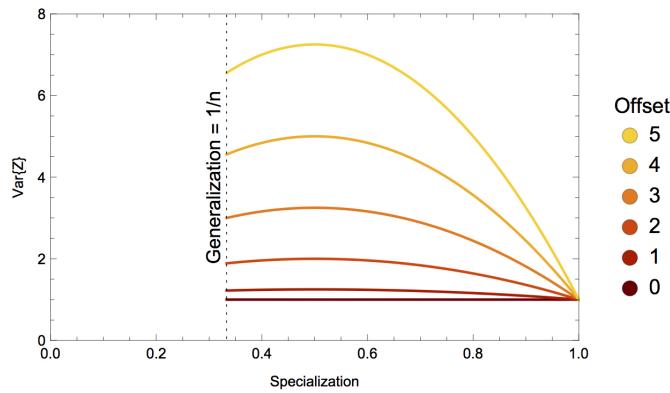


Figure 1. Variance of the isotopic distribution of a consumer's diet, $V\{Z\}$, with respect to specialization on a single prey, s_k . This illustrative example shows a three-prey system with prey means $\{-15, -15 + \text{offset}, -15\}$ and equal variances; colors depict specialization on prey 2 with a mean isotope value that is a function of some offset amount. As the offset of the targeted prey increases, so does the nonlinearity of $V\{Z\}$.

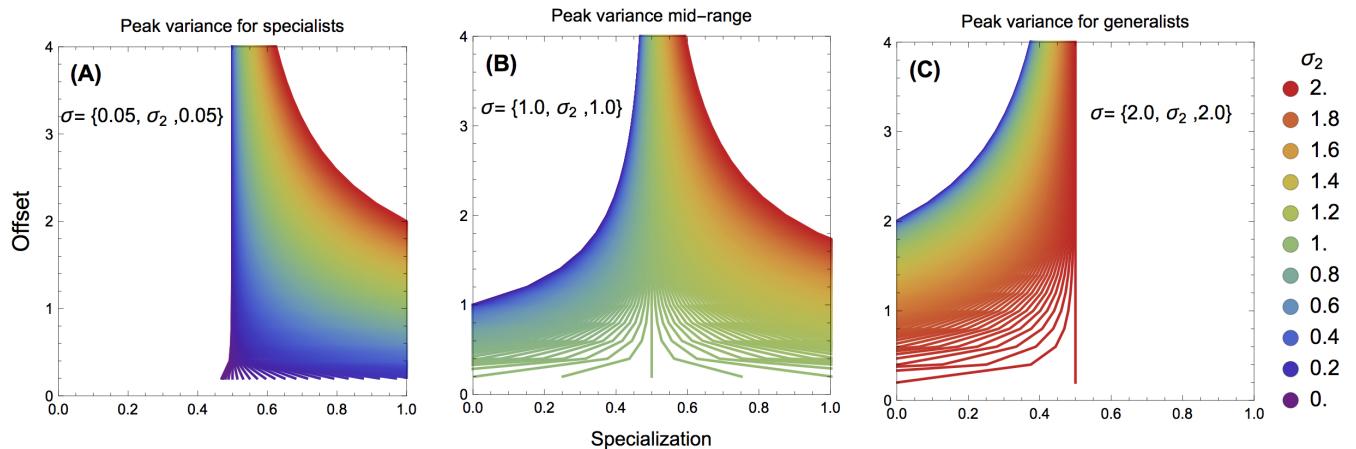


Figure 2. Maximal consumer isotopic variance \hat{s}_k over the specialization index s as a function of mixing space geometry. (A) and (B) If the targeted prey has a higher than average isotopic variance, the maximum consumer niche width will lie towards consumer specialization. (B) and (C) If the targeted prey has a lower than average isotopic variance, the maximum consumer niche width will lie towards consumer generalization. (A), (B), and (C) as the mean offset of the targeted prey is farther from the centroid of the mixing space, the maximal consumer isotopic niche width tends towards $s = 0.5$.

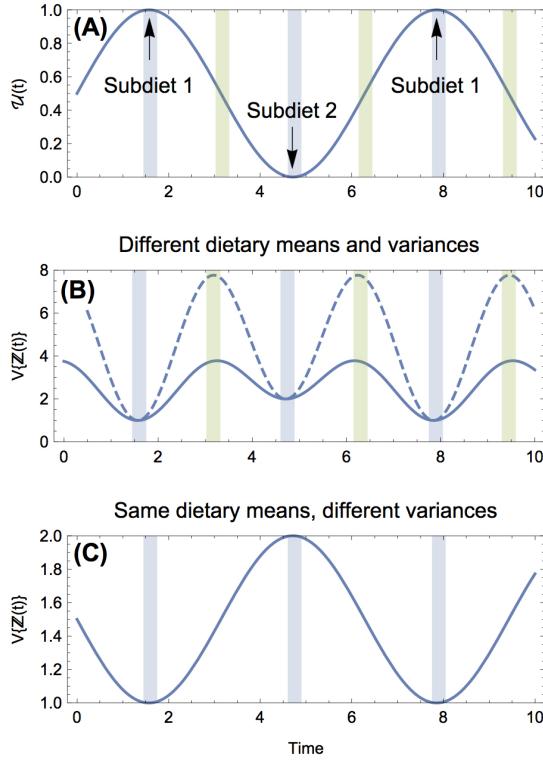


Figure 3. (A) The proportional contribution of Diet 1 to the composite diet \mathbb{Z} over time. (B) The isotopic variance of the composite diet $V\{\mathbb{Z}(t)\}$ when subdiets 1 and 2 have different means and variances. The peak variance occurs during the dietary transitions (green shading), whereas the troughs reflect the variances of subdiet 1 and 2, respectively (blue shading). (C) The isotopic variance of the composite diet $V\{\mathbb{Z}(t)\}$ when subdiets 1 and 2 have the same means but different variances. When the subdiets have the same means, $V\{\mathbb{Z}(t)\}$ oscillates to reflect the respective variances of the subdiets, and does not exhibit peak variance during the dietary transition.

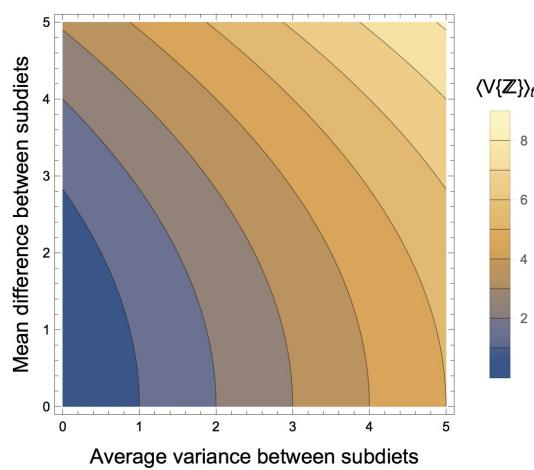


Figure 4. Components of the mixing space that affects the time-averaged variance of the composite diet, $\langle V\{\mathbb{Z}\} \rangle_t$. As the average variance between the subdiets increases, the time-averaged variance of the composite diet increases. As the difference in the isotopic means of the subdiets increase, the time-averaged variance of the composite diet increases, though at a slower rate.

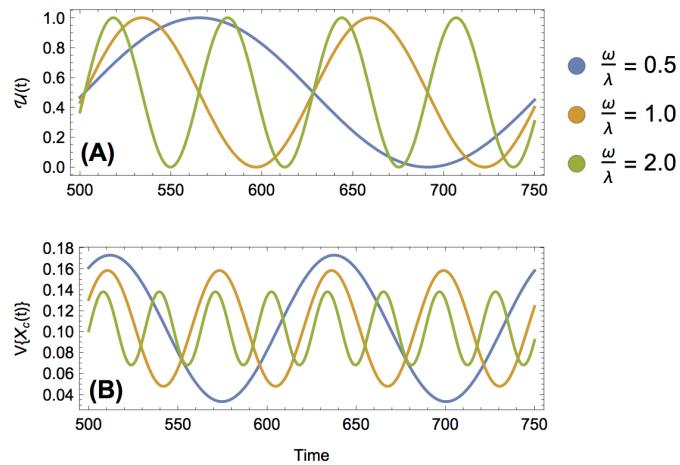


Figure 5. (A) A sinusoidally varying diet, where $\mathcal{U}(t) = 1/2 + 1/2 \sin(\omega t)$ for increasing values of ω , or equivalently, decreasing timescales of dietary switching. (B) The isotopic variance of a consumer over time $V\{X_c(t)\}$ across increasing values of ω relative to the consumer's incorporation rate λ . As the timescale of diet switching decreases relative to the timescale of isotopic incorporation, the amplitude of isotopic variance decreases due to increased isotopic averaging over faster shifts in diet.

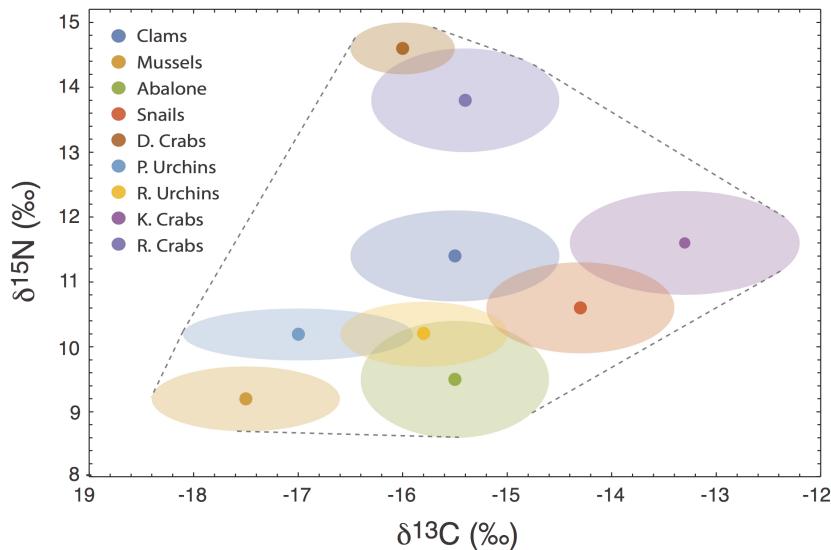


Figure 6. The isotopic mixing space ($\delta^{13}\text{C}$ vs. $\delta^{15}\text{N}$) for a sea otter consumer near San Simeon and Monterey Bay, California, composed of nine commonly consumed invertebrate species. Units are per-mil (‰).

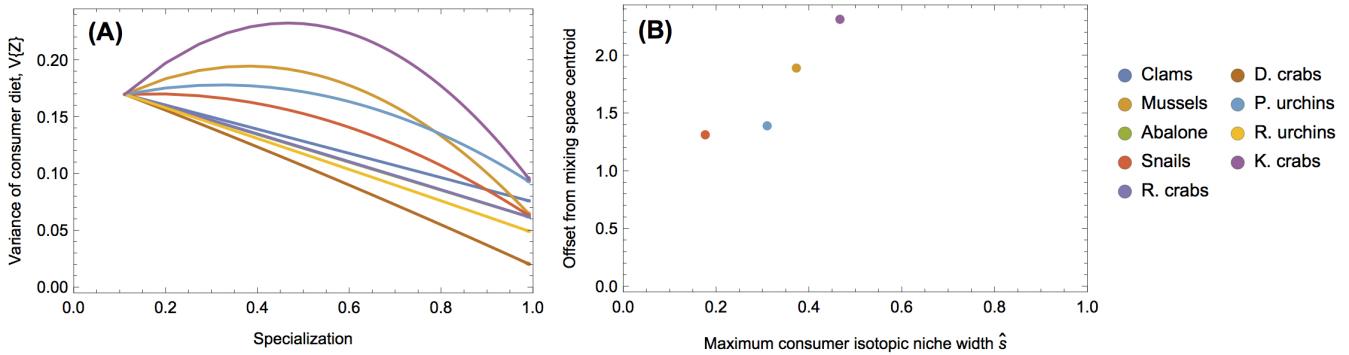


Figure 7. **(A)** Predicted variance in $\delta^{13}\text{C}$ of sea otter diets over different degrees of specialization on each prey in the system (colors). **(B)** Calculated maximum consumer niche width values as a function of specialization and the offset of the prey isotopic mean from the mixing space centroid.

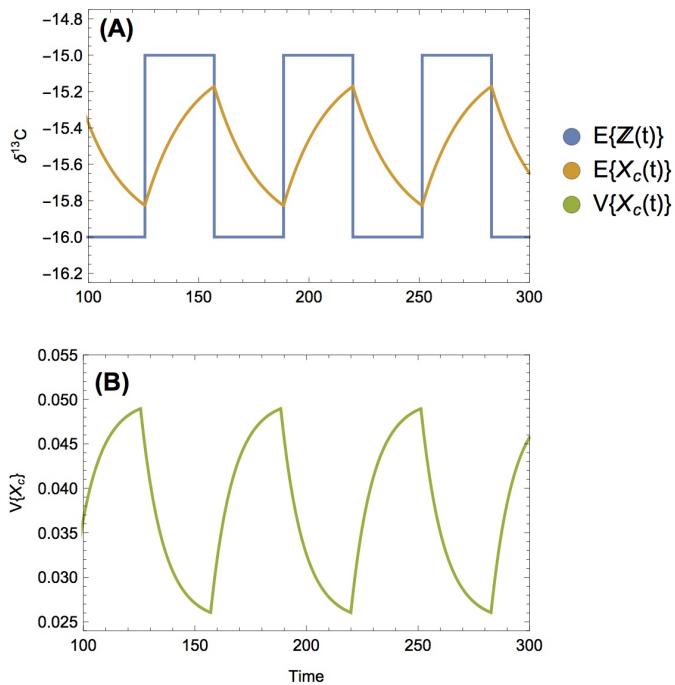


Figure 8. **(A)** The mean isotopic value of the composite diet over time $E\{\bar{Z}(t)\}$ when diet-switching is discontinuous, following a square wave pattern, where subdiets have a mean $\delta^{13}\text{C}$ value of -15 and -16, respectively. The mean isotopic value of the consumer over time $E\{X_c(t)\}$ is observed to abruptly change directions when its diet transitions, asymptotizing towards (but not reaching) the isotopic mean of its current diet. **(B)** Consumer isotopic variance $V\{X_c(t)\}$ follows a similar trajectory over time, asymptotizing towards (but not reaching) the isotope variance of its current diet. When diets follow a discontinuous switching dynamic, the peak variance does not appear at the transition, as it does when the diet switching is smooth.

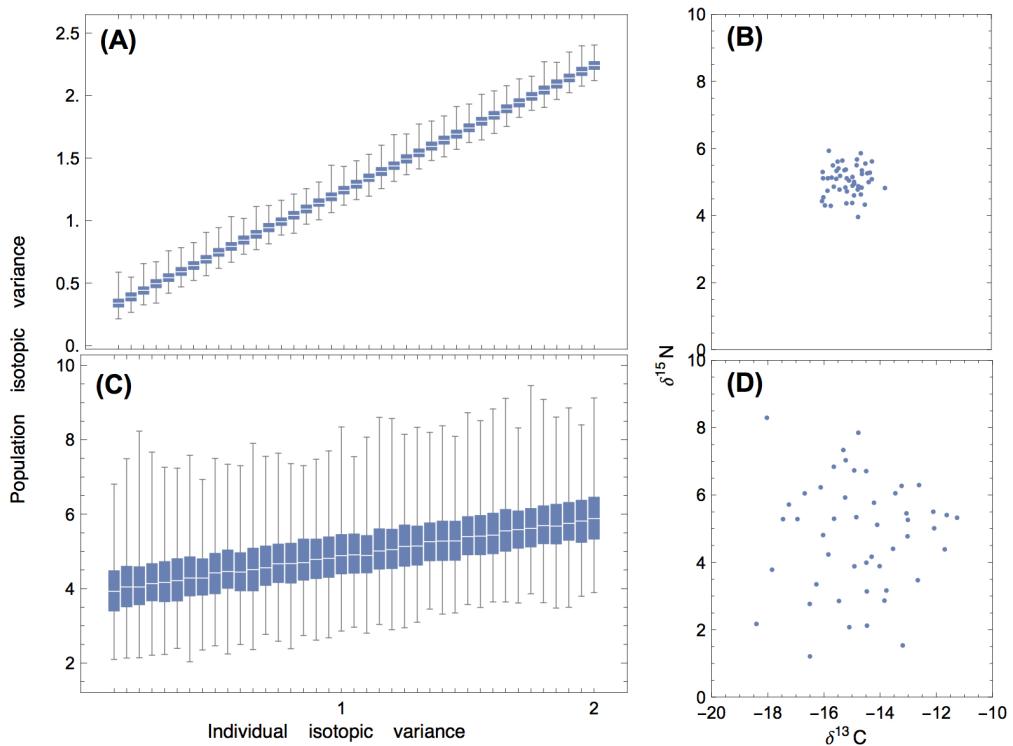


Figure 9. Population isotopic variance vs. individual isotopic variance where mean isotope values of individuals are randomly drawn from a Normal distribution (50 individuals per population; 1000 replicates), and individuals are assumed to have the same variance. (A) and (B) When the mean values of individuals are randomly drawn from a normal distribution with low variance, there is a linear relationship between individual-level and population-level isotopic variance. (C) and (D) When the mean values of individuals are randomly drawn from a normal distribution with high variance, the relationship becomes masked by noise.