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RESEARCH ARTICLE

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Cooperative feeding in common dolphins as suggested by ontogenetic patterns in $\delta^{15}N$ bulk and amino acids

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Abstract

1. Understanding the effect of stage-specific traits on species feeding habits can reveal how natural selection shapes life strategies. Amino acid (AA) nitrogen stable isotopes ($\delta^{15}N$) provide multiple proxies of habitat baseline values and diet that can improve our understanding of species feeding strategies relative to their animal metabolism. We evaluated the effect of body length as a proxy for life stage and sex on the feeding habits of the common dolphin *Delphinus delphis delphis* using $\delta^{13}C$ and $\delta^{15}N$ in bulk tissue and AAs $\delta^{15}N$ from skin samples collected for almost two decades.
2. For bulk $\delta^{13}C$ and $\delta^{15}N$ data, we used SIBER analysis to compare isotopic niches by sex and life stage. For AA $\delta^{15}N$ data, we developed a hierarchical Bayesian model (HBM) to estimate indices of trophic status ($\Delta^{15}N$ and trophic position). The model reflected the natural hierarchical structure of AA data by partitioning variability into three sources: between laboratory replicates, within dolphins and among dolphins.
3. Estimates of $\Delta^{15}N$ based on all trophic and source AAs were more precise for each dolphin, less variable among dolphins and on average 2.4‰ higher than indices based on single trophic (Glx) and source (Phe) AAs. Precision was further increased when information was shared among individuals through random effects or regression models. Estimates of trophic position showed similar patterns. Both $\Delta^{15}N$ and $\delta^{15}N_{bulk}$ isotopic niches showed no difference by sex, suggesting that males and females have similar feeding habits and may not segregate. However, lower $\Delta^{15}N$ values for weaning calves and smaller juveniles discriminate them from adults, whereas $\delta^{15}N$ bulk isotopic niches do not. A trophic discrimination factor ($TDF_{Tro\text{-}Src}$) of 3.1‰ was required for reasonable estimates of trophic position for these dolphins.
4. Together, the lack of $\delta^{15}N$ differences between sexes, low variation between juveniles and adults and knowledge of common dolphins' social organization support intraspecific feeding cooperation as an important strategy to feed in the highly dynamic marine environment. Our study also presents an efficient way to analyse complex AA $\delta^{15}N$ data using HBM to investigate foraging behaviour in long-lived marine species difficult to study in the wild.

Rocio I. Ruiz-Cooley and Tim Gerrodette contributed equally.

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KEYWORDS
cooperative behaviour, *Delphinus*, feeding strategies, hierarchical Bayesian, isotopic niche, nitrogen stable isotopes, trophic discrimination factor, trophic position

1 | INTRODUCTION

Natural selection theory predicts that species compete for resources and space (Darwin, 1989). Under such pressure, predator and prey co-evolve and shape their feeding strategies and behavioural dynamics to capture prey or escape predation respectively (Darwin, 1989; Elton, 1927). Quantifying the trophic status of a species and its variability through life stages and physiological traits can provide insights about the feeding strategies that allow species to survive (Schoener, 1971). Traits such as body length, sex and maturity stage can be key determinants for species' energetic demands, habitat use patterns and ability to catch prey (Roughgarden, 1972). Species that change habitat during ontogenesis may encounter different prey items, competitors and even predators, and may expand or reduce their trophic niche. The feeding success of some species may be the result of competitive interactions (Darwin, 1989). Other species, however, may benefit from intra- or interspecific cooperation during which animals work together to capture prey, and avoid predation or competitors to increase feeding success (Taylor & Frank, 1996; West et al., 2007), and ultimately, their biological fitness (Clutton-Brock, 2009). Cetaceans display cooperative behaviour, but the mechanisms supporting these behaviours are relatively unknown (Benoit-Bird & Au, 2009).

Stable isotope analysis (SIA) of carbon (C) and nitrogen (N) is helpful in examining elemental cycling processes, feeding ecology of species and reconstructing food webs (Owens, 1987; Peterson & Fry, 1987; Rau, 1982). SIA has been used widely by ecologists to investigate the main prey and feeding ecology for species difficult to study, such as oceanic predators and marine mammals, because these aquatic animals spend few minutes at surface or live in remote habitats.

Quantification of bulk $\delta^{13}C$ and $\delta^{15}N$ values of cetacean tissues has revealed variability in trophic status by sex, maturity, foraging area and social structure (Marcoux et al., 2007; Ruiz-Cooley et al., 2004, 2012, 2014). The probability of the ellipse described by body tissue $\delta^{13}C$ and $\delta^{15}N$ values is proposed to represent an animal's isotopic niche (Jackson et al., 2011), which is arguably equivalent to trophic niche when isotopic variation is driven by resource interactions (Bearhop et al., 2004; Flaherty & Ben-David, 2010; Newsome et al., 2007). The $\delta^{13}C$ and $\delta^{15}N$ values are highly associated with species metabolism, nutrient requirements and therefore diet. Nutrient sources can be endogenous (e.g. during fasting), exogenous (i.e. prey) or a combination of both, which influence the degree of isotopic fractionation and isotopic routing in tissues (Martínez del Rio et al., 2009). Thus, quantifying the portion of the isotopic niche explained by diet, foraging habitat or physiology can improve our ability to understand isotopic niche overlap or separation.

The $\delta^{15}N$ analysis of individual amino acids (AAs) can separate trophic effects from habitat baseline values (primary producers) (Chikaraishi et al., 2009; McClelland & Montoya, 2002). Putatively, source AAs $\delta^{15}N$ values change little as they pass up the food chain, while trophic AAs fractionate largely with each trophic step (McClelland & Montoya, 2002). Phenylalanine (Phe) is an essential AA and is considered the most stable source AA because its isotopic fractionation is relatively low among trophic steps and taxa (McMahon & McCarthy, 2016; Nielsen et al., 2015). In contrast, glutamic acid (Glx) is the canonical trophic AA that undergoes significant isotopic fractionation with each trophic step and is fundamental for animal metabolism. Early studies proposed to calculate trophic position (TP) by incorporating AA $\delta^{15}N$ values from consumers in an equation that assumed equivalent AA isotopic fractionation among taxa and tissues (Chikaraishi et al., 2009; Popp et al., 2007). Nevertheless, AAs $\delta^{15}N$ fractionation has been shown to be variable among trophic levels, taxa, tissues and habitat (McMahon & McCarthy, 2016; Nielsen et al., 2015). Researchers have searched for the best combination of trophic and source AA pairs to estimate TP. Single AAs Glx and Phe, and weighted averages for all trophic or source AAs, have both been used, but the differences in TP estimated by these different methods have been little compared. Stochasticity associated with AA $\delta^{15}N$ data can be substantial (Nielsen et al., 2015), but has not yet been handled in a comprehensive way.

Despite caveats for calculating TP, isotopic fractionation in bulk protein tissue and AAs is linked to animal nutrition, metabolism and foraging habitat defined by the dominant primary producers in the community. Integrating data from SIA of bulk tissue and AAs can provide insights about the variability in a predator's feeding habits in relation to life stages and traits. Here, we analyse such variation by using bulk $\delta^{13}C$ and $\delta^{15}N$ and AA-specific $\delta^{15}N$ values from skin tissues collected from individual short-beaked common dolphins, *Delphinus delphis delphis*, inhabiting the Southern California Bight (SCB). The common dolphin is considered a high-trophic level generalist consumer that preys on small fish and cephalopods (Evans, 1975; Osnes-Erie, 1999; Preti, 2020). This species regularly occurs in mixed groups of males and females of hundreds to thousands of dolphins at all life stages (Chivers et al., 2016) and has been observed working together to aggregate schooling fish like anchovies and sardines (Reynoso, 1991). In a previous study, we documented strong variability in adult common dolphins' AA $\delta^{15}N$ values and proxies of relative TP ($\Delta^{15}N^{Glx\text{-}Phe} = \delta^{15}N_{Glx} - \delta^{15}N_{Phe}$ and $\Delta^{15}N^{Tro\text{-}Src} = \delta^{15}N_{Trophic} - \delta^{15}N_{Source}$) in response to environmental change over 19 years (Ruiz-Cooley et al., 2017). It remains unknown how shifts in diet composition (e.g. from optimal to suboptimal prey)

trigger different metabolic pathways resulting in AAs $\delta^{15}N$ isotopic fractionation.

In this study, we investigated the influence of body size as a proxy for life-stage and sex on isotopic niches and indices of trophic status ($\Delta^{15}N$ and TP). These indices could increase with body length if dolphins feed on prey of higher TP as they grow, or differ by sex if males and females feed on different prey items, have sex-specific energetic requirements or utilize different foraging locations. Alternatively, evidence of no isotopic differences by body size and sex would indicate similar diet and foraging habitat supporting cooperative feeding behaviour. We used stable isotope Bayesian ellipses in R (SIBER) (Jackson et al., 2011) to evaluate dolphin isotopic niches between males and females, and among life stages, and a multilevel Bayesian model to account for the different sources of heterogeneity in AA-specific $\delta^{15}N$ data. Hierarchical Bayesian models (HBM) are a flexible and powerful way to analyse ecological data (Clark et al., 2005; Gelman & Hill, 2007; Kéry & Royle, 2015). The natural hierarchical structure of stable isotope data can be realistically captured by such models, and inference is strengthened by considering all data together within a single likelihood framework (Buckland et al., 2007; Hoyle & Maunder, 2004). Moreover, uncertainty is fully propagated through the model by using probability distributions rather than point estimates and standard errors for parameters.

2 | MATERIALS AND METHODS

2.1 | Tissue samples

Skin from individual common dolphins sampled as bycatch from the large-mesh drift gillnet fishery in the SCB were collected between 1990 and 2008. All samples were stored frozen without preservative at −20°C. Standard collection and processing protocols were used to collect the biological samples and data (Jefferson et al., 1994; Norris, 1961). Sex and total body length for each dolphin were known.

2.2 | Isotope analysis

The $\delta^{15}N$ and $\delta^{13}C$ values from bulk skin tissue were obtained for 203 dolphins following standard procedures (see Supporting Information (SI)). The AA $\delta^{15}N$ values were measured from a random subsample of 30 dolphins; tissue samples were analysed at the UC-Davis stable isotope facility following protocols of Walsh et al., 2014, see Supporting Information for details. Each sample was run twice. For estimation of trophic indices, we used four source AAs that are known to track primary production (phenylalanine (Phe), methionine (Met), lysine (Lys) and tyrosine (Tyr)), and seven trophic AAs that indicate animal trophic status (aspartic acid (Asx), isoleucine (Ile), alanine (Ala), glutamic acid (Glx), leucine (Leu), proline (Pro) and valine (Val).

2.3 | Analysis of data

For bulk $\delta^{15}N$, we fitted a smoother function of weighted average values fit with the Cauchy density function to identify the pattern of variation in $\delta^{15}N$ as a function of body length. Using the postnatal growth relationship presented by Chivers et al. (2016) for this population of common dolphins, we used body length to define four life stage classes: dependent calves (70–129 cm), weaning calves (130–149 cm), juveniles (150–174 cm) and adults (175–210 cm). The $\delta^{13}C$ and $\delta^{15}N$ isotopic niche ellipse shape and size are supported by a corresponding covariance matrix in the analytical framework, while the means of $\delta^{13}C$ and $\delta^{15}N$ specify its location. Isotopic niche analysis was carried out with the SIBER package (Jackson et al., 2011) in R (R Core Team, 2020). To compare isotopic niche between sexes and among size classes, we calculated Bayesian standard ellipse area (SEA_B) and overlap proportion (Appendix 1).

2.4 | Amino acid $\delta^{15}N$

The $\delta^{15}N$ values from source and trophic AAs were obtained from a total of 21 mature individuals, 8 juveniles and 1 weaning calf. We used a HBM to partition variability: (a) between laboratory replicates, (b) among trophic and source AA values within each dolphin and (c) among individual dolphins. At the replicate level, we assumed that replicate $\delta^{15}N$ AA measurements *y* had normally distributed errors,

$$y_{ijk} \sim N\left(\mu_{ij}, \sigma_j^2\right), \tag{1}$$

where *i*, *j* and *k* are indices for individuals, AAs and replicates, respectively, and *N* indicates a normal distribution with mean μ and variance σ^2. Thus, the model estimated a mean $\delta^{15}N$ level for each AA and each animal, and a variance for each AA. Variance at this level of the model was due to variation in laboratory measurements of $\delta^{15}N$ for each AA.

At the AA level, we assumed that for each individual dolphin, the values of different trophic and source AAs were normally distributed about their respective means, that is,

$$\begin{aligned} \mu_{i,j=\text{trophic AA}} &\sim N\left(\mu_{i,\text{tro}}, \sigma^2_{\text{tro}}\right), \\ \mu_{i,j=\text{source AA}} &\sim N\left(\mu_{i,\text{src}}, \sigma^2_{\text{src}}\right). \end{aligned} \tag{2}$$

Then, a proxy of trophic status $\Delta^{15}N$ can be calculated for each animal as the difference between its trophic and source values based on all AAs

$$\Delta^{15}N_i^{\text{Tro-Src}} = \mu_{i,\text{tro}} - \mu_{i,\text{src}}, \tag{3a}$$

or based on the difference between a single trophic AA and a single source AA, such as Glx and Phe,

$$\Delta^{15}N_i^{\text{Glx-Phe}} = \mu_{i,\text{Glx}} - \mu_{i,\text{Phe}}. \tag{3b}$$

Trophic and source values $\mu_{i,\text{tro}}$ and $\mu_{i,\text{src}}$ (or $\mu_{i,\text{Glx}}$ and $\mu_{i,\text{Phe}}$) are latent (unobserved) states of each individual. Variance at this level of the

model reflected heterogeneity in the trophic and source AA values of each animal.

At the individual dolphin level, differences among animals were modelled both with and without an explanatory covariate. Without a covariate, Δ^{15}N was estimated by treating individuals as random effects (RE)

$$\begin{aligned} \Delta^{15}\mathrm{N}_i^{\mathrm{RE}} &\sim N\left(\mu_i, \sigma_{\mathrm{RE}}^2\right), \\ \mu_i &= \alpha_0 + \alpha_i, \\ \alpha_i &\sim N\left(0, \sigma_{\mathrm{re}}^2\right), \end{aligned} \tag{4}$$

where α_0 was the overall population mean and α_i was the individual effect for dolphin *i*. With a covariate *x*, Δ^{15}N was estimated with a linear model

$$\begin{aligned} \Delta^{15}\mathrm{N}_i^{\mathrm{L}} &\sim N\left(\mu_i, \sigma_L^2\right) \\ \mu_i &= \beta_0 + \beta_1 x_i \end{aligned} \tag{5}$$

and a nonlinear model (Carlin & Gelfand, 1991)

$$\begin{aligned} \Delta^{15}\mathrm{N}_i^{\mathrm{NL}} &\sim N\left(\mu_i, \sigma_{\mathrm{NL}}^2\right), \\ \mu_i &= \gamma_0 - \gamma_1 \gamma_2^{x_i}, \end{aligned} \tag{6}$$

where x_i was an individual animal property such as body length. The linear model had two parameters, intercept β_0 and slope β_1. The nonlinear model had three parameters; γ_1 and γ_2 determined the shape and rate at which the function approached the asymptote γ_0. The variances σ_{RE}^2, σ_L^2 and σ_{NL}^2 represented residual error not explained by each model. Because a previous study (Ruiz-Cooley et al., 2017) found that Δ^{15}N varied over time, we also considered each of these three models with year as a factor variable.

We used the linear model to investigate Δ^{15}N difference by sex, with x_i as a binary indicator (0 or 1). Similarly, we used the linear model with a binary indicator to calculate the probability that Δ^{15}N was different for the two dolphins <160 cm, as suggested by the nonlinear model (see Section 3). For each model, we also directly computed the difference in Δ^{15}N between the two dolphins <160 cm and the other 28 dolphins.

Trophic position TP was estimated for each dolphin with the standard equation from Chikaraishi et al. (2009)

$$\mathrm{TP}_i = \left[\left(\Delta^{15}\mathrm{N}_i - \beta\right) / \mathrm{TDF}\right] + 1, \tag{7}$$

which assumes a constant β value from the trophic minus source AA difference in primary producers (trophic level 1) and a single trophic discrimination factor (TDF) as the average change in δ^{15}N per trophic level. TP was calculated with all the different models of Δ^{15}N given in Equations 3–6. We used the estimates β = 3.4‰ (*SE* = 0.9‰) and TDF = 6.6‰ (*SE* = 1.7‰) from the meta-analysis of Nielsen et al. (2015), assuming that β and TDF were independent and had normally distributed error. Conversely, we estimated TDF by rearranging Equation 7 as

$$\mathrm{TDF}_i = \left(\Delta^{15}\mathrm{N}_i - \beta\right) / \left(\mathrm{TP} - 1\right), \tag{8}$$

and using a TP value of 4.2 for common dolphins derived from stomach content studies (Pauly et al., 1998). Pauly et al. (1998) did not provide standard errors for their TP values; we assumed *SE* = 0.1. For estimates of TDF, we excluded isotope data from the two smallest dolphins because they may not have been feeding independently.

The models were implemented in a Bayesian framework with JAGS (Plummer, 2017). After preparing the data in R, we called the jags function from R with the R2jags package (Su & Yajima, 2020; Appendix 1). Uniform priors were specified for all basic parameters. In the case of variance terms, we used uniform priors for standard deviations σ rather than variances σ^2 (Gelman, 2006). By retaining each 20th sample (thinning), the Markov Chain Monte Carlo (MCMC) samples were independent and well-mixed, and the chains converged quickly from different initial values. After burn-in phases of 500 iterations, we obtained 5,000 posterior samples for each of three MCMC chains. We used the coda package (Plummer et al., 2020) for standard diagnostics such as history and convergence of the chains, and autocorrelation and effective sample size within each chain.

We compared models with three scoring functions calculated from the posterior samples: Watanabe–Akaike (or Widely Applicable) information criterion (WAIC, Watanabe, 2010, calculated following Vehtari et al., 2017), leave-one-out information criterion (LOOIC, as calculated by the loo package, Vehtari et al., 2020) and deviance information criterion (DIC, using the 'optimism' penalty of Plummer, 2008). All three scores are improvements to the original DIC (Spiegelhalter et al., 2002), which has shortcomings (Lunn et al., 2013; Millar, 2009; Plummer, 2008). Gelman et al. (2014) noted that there is currently no consensus on the difficult problem of comparing hierarchical Bayesian models. Proportion of variance explained and degree of pooling were calculated at each level of the model (Gelman & Pardoe, 2006; Appendix 1).

We displayed marginal posterior distributions for parameters of main interest with violin plots (Adler & Kelly, 2020) as well as histograms. Uncertainty was summarized by the standard deviation (*SD*) of the posterior distribution and by the length of the shortest interval containing 95% of the mass of posterior probability (the 95% highest density interval, or HDI; Meredith & Kruschke, 2018). To integrate Δ^{15}N estimates across dolphins, we sampled from the posterior distributions of all dolphins randomly. To compare our results with a non-stochastic approach, we calculated the mean of trophic and the mean of source AA δ^{15}N values for each dolphin, and computed Δ^{15}N as the difference between them. Similarly, for Glx and Phe, we computed Δ^{15}N for each dolphin as the difference between mean Glx and mean Phe δ^{15}N values. We refer to these direct calculations as the 'observed' values.

3 | RESULTS

3.1 | SIA in bulk tissue

Body lengths ranged from 96 cm to 202 cm (*n* = 191). The mean values for the sample set were 15.9‰; 1SD (0.80) for δ^{15}N and −18.28‰;

1SD (0.71) for $\delta^{13}C$. Mean isotopic values were $\delta^{15}N = 15.98‰$ (0.85) and $\delta^{13}C = -18.17‰$ (0.60) for females ($n = 66$), and $\delta^{15}N = 15.86‰$ (0.77) and $\delta^{13}C = -18.33‰$ (0.75) for males ($n = 137$). The smoother function revealed that dependent calves had higher $\delta^{15}N$ values that gradually decreased with length by ~1.5‰ until reaching 139 cm length (Figure 1), and changed little thereafter. The isotopic niche of dependent calves, as measured by SEA, was different than the other three size classes (Figure 2a) with median overlap proportions about 0.4 (Figure 2d). Furthermore, the SEA of dependent calves was larger than other size classes (Figure 2c). Isotopic niches of males and females were similar (Figure 2b), with a median SEA overlap proportion of 0.72 (Figure 2d).

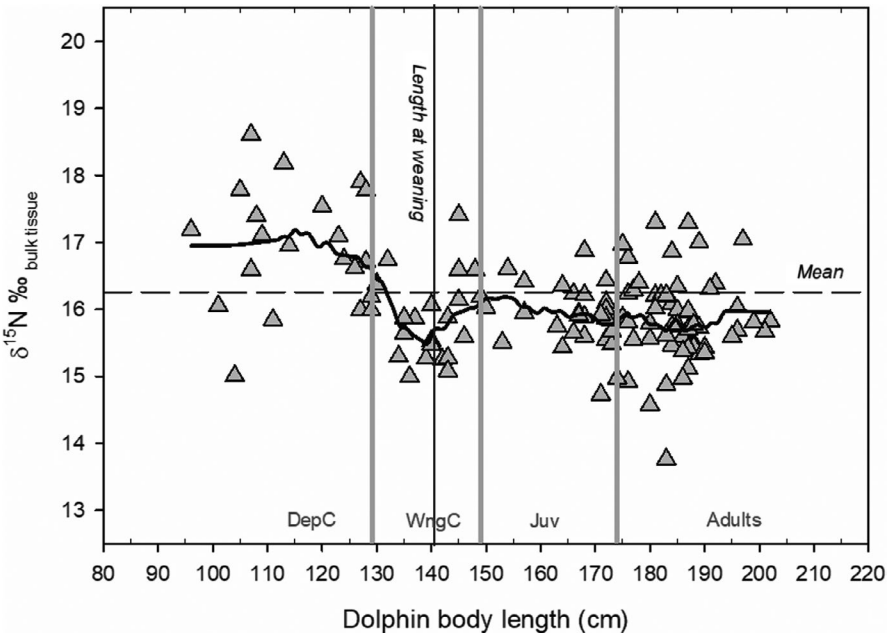

FIGURE 1 Variability in bulk $\delta^{15}N$ values by dolphin body length. The heavy line is a weighted average smoother. The thin vertical line indicates average length at independence at 140.1 cm according to Chivers et al. (2016). The horizontal dashed line indicates the mean $\delta^{15}N$ value of all data. The four life-stage classes defined for analyses are identified by vertical grey lines: DepC, dependent calves; WngC, weaning calves; Juv, juveniles and Adults

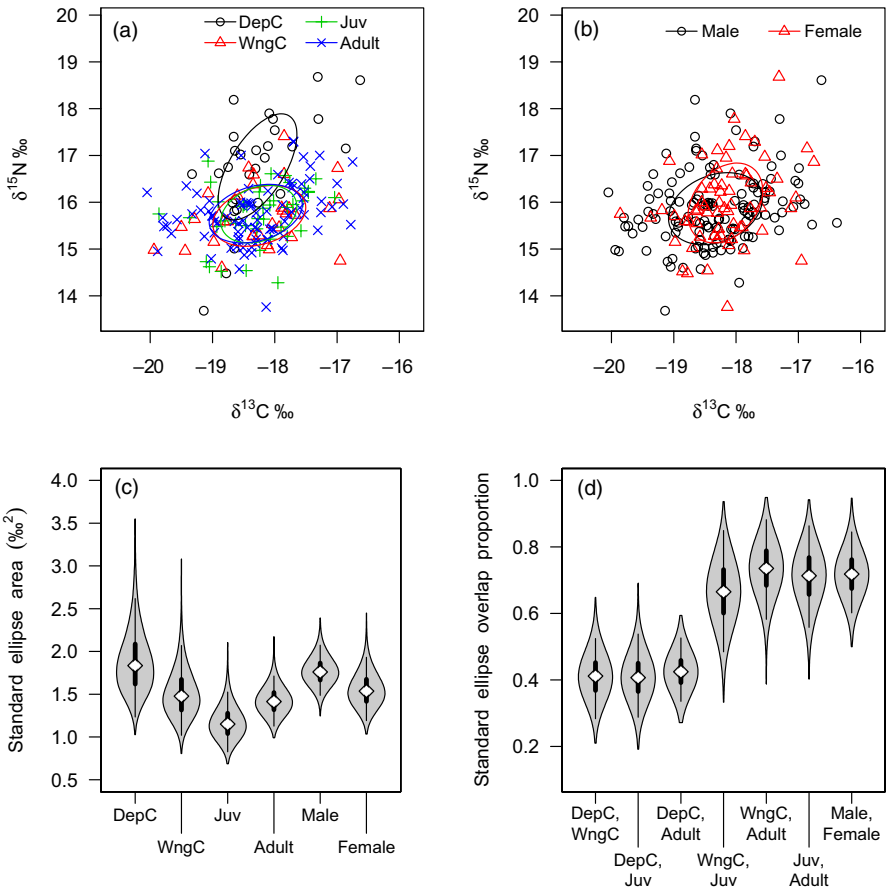

FIGURE 2 Bayesian isotopic standard ellipse analysis (SEA_B) for common dolphins. (a) Isotope biplots and standard ellipses for four size classes. (b) Isotope biplots and standard ellipses for males and females. (c) Violin plots of posterior distributions of standard ellipse areas for all size and sex classes. (d) Violin plots of posterior distributions of SEA overlap proportions for all pairs of size classes, and between males and females. Size classes are abbreviated as in Figure 1. For the violin plots, white diamonds are medians, black rectangles interquartile ranges and thin black whiskers 95% highest density intervals

3.2 | The δ^{15}AA

Median δ^{15}N values ranged from −8.7 to 26.6‰ over the 13 AAs (Figure 3). Threonine (Thr) and Glycine (Gly) had the lowest mean δ^{15}N among AAs, and were excluded as source AAs as they have been found not to belong to this group (Calleja et al., 2013). The remaining 11 AAs were divided into the standard groups of four source and seven trophic AAs (Figure 3). Most AAs had 60 samples (n = 30 dolphins, 2 replicates each), but the lab results of 8 Tyr and 6 Met samples were not usable. Mean δ^{15}N level was 23.17‰ for trophic AAs and 10.06‰ for source AAs.

Standard deviations of AA δ^{15}N replicates (σ_j, Equation 1) were mostly <1‰, but variation in laboratory measurements of Glx and Tyr were higher than other AAs (Figure 4a). SDs of trophic and source AAs (σ_{tro} and σ_{src}, Equation 2) were similar (Figure 4b). Consistent with these results, WAIC was lowest for a model with a single pooled variance at the AA level (i.e. a single variance σ^2_{AA} rather than separate variances σ^2_{tro} and σ^2_{src} in Equation 2) but separate variances σ^2_j (Equation 1) for each amino acid j at the replicate level (Appendix 2A). Consequently, we used a model with a single variance at the AA level for all further results presented below.

Trophic indices estimated using all trophic and source AAs ($\Delta^{15}N^{Tro\text{-}Src}$, Equation 3a) were less variable and generally higher in

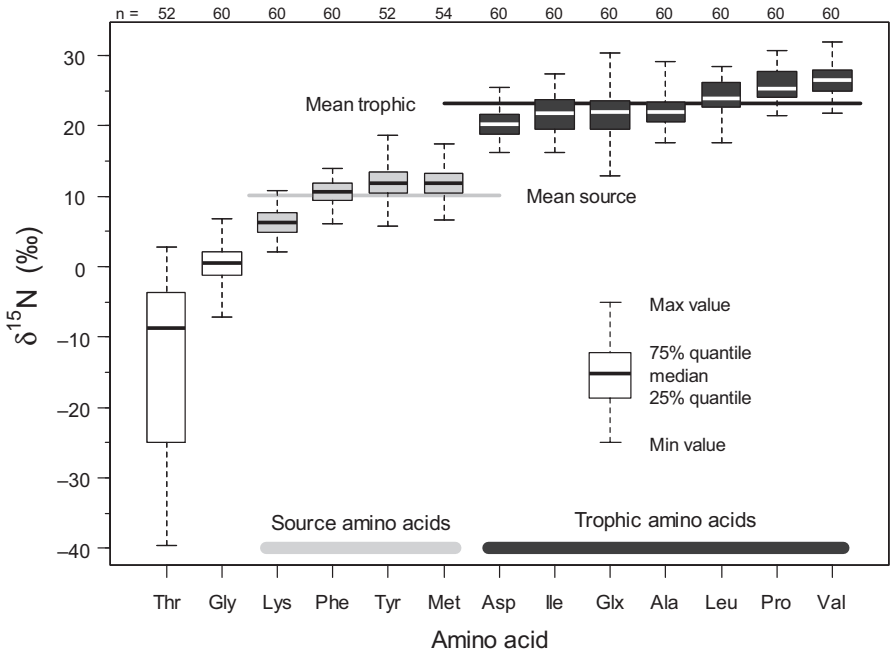

FIGURE 3 Boxplots of δ^{15}N stable isotope ratio data of 13 amino acids in skin tissue of 30 common dolphins. Sample sizes are shown at the top

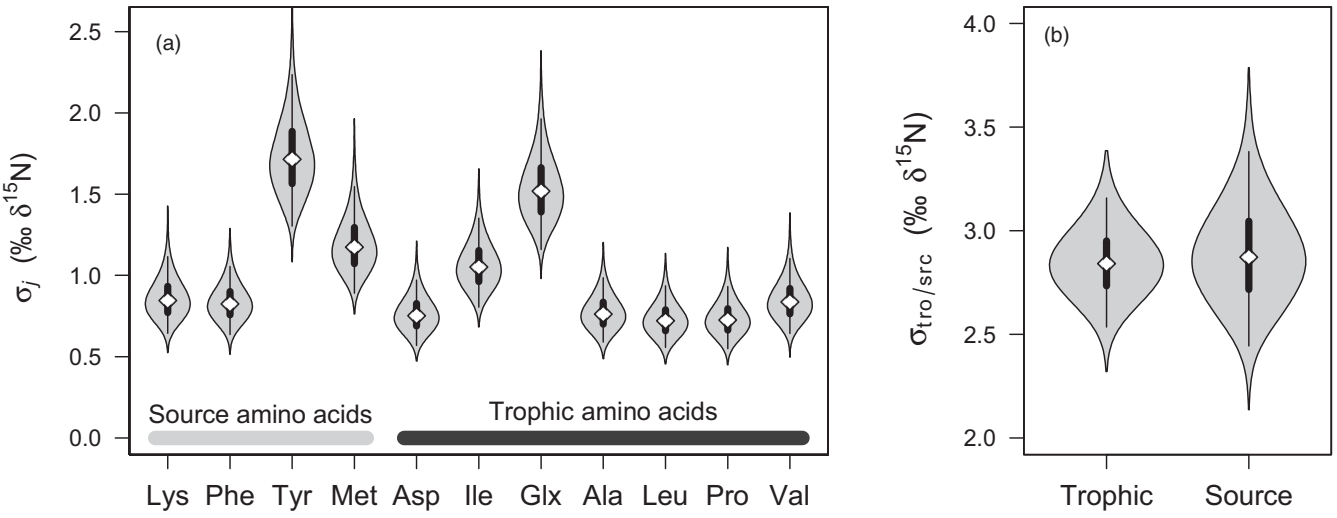

FIGURE 4 Standard deviations of (a) replicate δ^{15}N measurements of each amino acid (AA) (σ_j, Equation 1), and (b) trophic and source AAs within individual dolphins (σ_{tro} and σ_{src}, Equation 2). In (a), amino acids are ordered by median δ^{15}N value, as in Figure 3. The grey violin plots show marginal posterior probability distributions. White diamonds are medians, black rectangles interquartile ranges and thin black whiskers 95% highest density intervals

value than indices using Glx and Phe only ($\Delta^{15}N^{Glx\text{-}Phe}$, Equation 3b). Over the 30 dolphins, $\Delta^{15}N^{Tro\text{-}Src}$ ranged from 10.0 to 15.7‰, with a mean of 13.3‰, but $\Delta^{15}N^{Glx\text{-}Phe}$ ranged from 5.1 to 17.4‰, with a mean of 10.9‰ (Table 1, Figure 5a). The mean difference between $\Delta^{15}N^{Tro\text{-}Src}$ and $\Delta^{15}N^{Glx\text{-}Phe}$ was 2.4‰, but differences among individual dolphins varied widely, ranging from −3.1 to 5.9‰ (Appendix 3A). In addition, $\Delta^{15}N$ based on all trophic and source AAs (Figure 5b) was more precise than $\Delta^{15}N$ based on single AAs (Figure 5c); the mean of the lengths of the 30 HDIs was 7.4‰ for $\Delta^{15}N^{Tro\text{-}Src}$ and 10.7‰ for $\Delta^{15}N^{Glx\text{-}Phe}$ (Table 1, Appendix 3A). Similarly, estimates of TP were higher and more precise when based on all AAs rather than on Glx and Phe only (Table 1, Appendix 3B).

When the $\delta^{15}N$ data for the 30 dolphins were considered together in a random effects, linear or nonlinear model, mean estimates of $\Delta^{15}N$ were the same, 13.3% based on all AAs (Appendix 4A) and 10.9‰ based on Glx and Phe only (Appendix 4B). However, estimates of $\Delta^{15}N$ and TP for each dolphin were more precise and, among dolphins, less variable than models based on $\delta^{15}N$ values for each dolphin independently (Table 1). The nonlinear model $\Delta^{15}N^{NL}$, without year as a factor variable, had lowest WAIC, LOOIC and DIC scores (Appendix 2B). For this model (Equation 6), the range of mean posterior distributions of $\Delta^{15}N^{NL}$ ranged from 10.8 to 13.6‰, with a mean HDI of 2.4‰ (Table 1). For the corresponding model using all AAs but considering each dolphin independently (Equation 3a),

TABLE 1 Summary of estimates of trophic index $\Delta^{15}N$ and trophic position TP for 30 common dolphins using all AAs and using only Glx and Phe, and without (Equation 3) and with (Equation 6) $\delta^{15}N$ values shared across dolphins. Mean, min and max are the mean, minimum and maximum of the 30 means of the posterior distributions of the trophic index. Mean HDI is the mean length of the 30 95% highest density intervals. Eq. refers to the equations in the text for the trophic index; App. indicates the Appendix in Supporting Information with more detailed results. All units are ‰ $\delta^{15}N$

Trophic index	$\delta^{15}N$ values shared	Using all AAs				Using only Glx and Phe					
		Mean	Min	Max	Mean HDI	Mean	Min	Max	Mean HDI	Eq.	App.
$\Delta^{15}N$	No	13.3	10.0	15.7	7.4	10.9	5.1	17.4	10.7	3	3A
$\Delta^{15}N^{NL}$	Yes	13.3	10.8	13.6	2.4	10.9	6.0	13.9	6.4	6	4A,B
TP	No	2.6	2.1	3.0	2.3	2.2	1.3	3.3	2.4	3 and 7	3B
TP^{NL}	Yes	2.6	2.2	2.7	1.9	2.2	1.4	2.7	1.9	6 and 7	4C,D

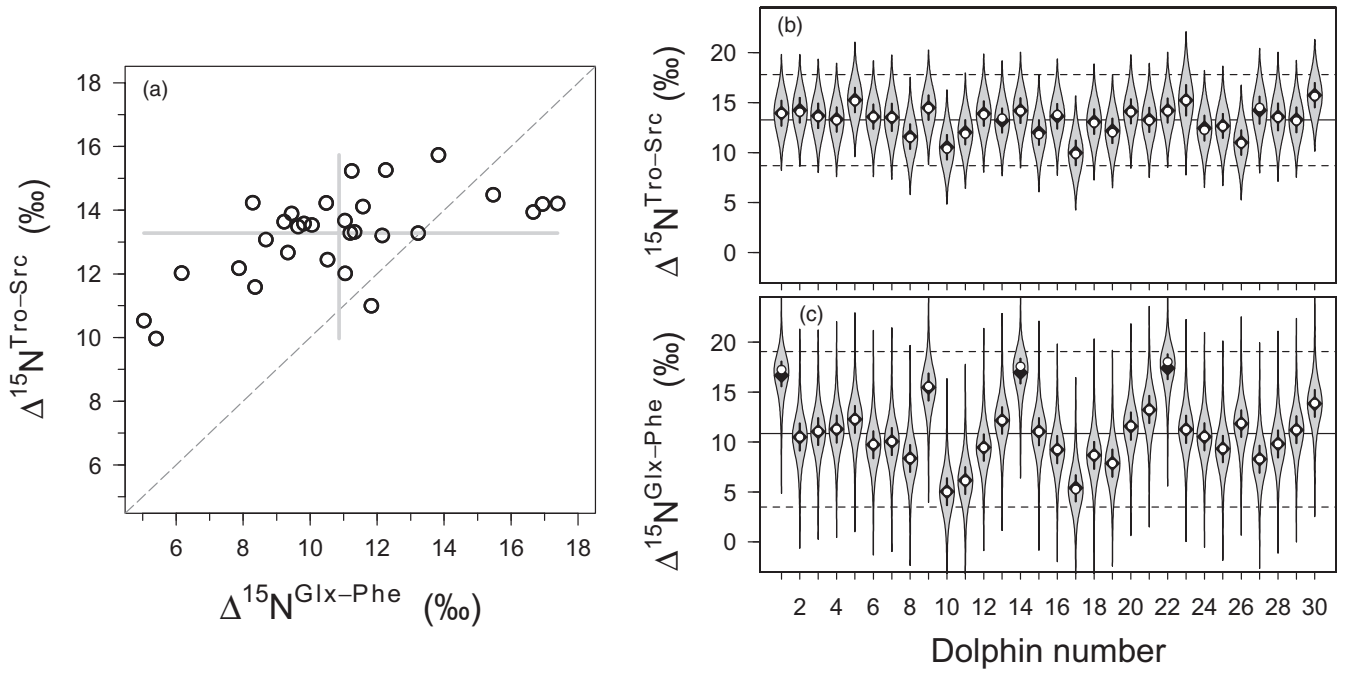

FIGURE 5 Trophic indices $\Delta^{15}N$ for common dolphins estimated as trophic AAs − source AAs ($\Delta^{15}N^{Tro\text{-}Src}$, Equation 3a) and Glx-Phe ($\Delta^{15}N^{Glx\text{-}Phe}$, Equation 3b). (a) Points are the means of individual posterior distributions, and solid grey lines are the means over all dolphins. The dashed grey line is a 1:1 relationship. The grey violin plots for (b) using all AAs and (c) using only Glx and Phe show marginal posterior probability distributions. Black diamonds are the means of the posterior distributions, thick black vertical lines the interquartile ranges and white circles the observed means. The solid horizontal line is the mean, and the dashed lines the 95% highest density interval, of the predicted trophic index over all dolphins

mean posterior distributions ranged from 10.0 to 15.7‰, with a mean HDI of 7.4‰ (Table 1).

Values of trophic position TP (Equation 7) showed similar patterns. Estimates based on all AAs were higher than estimates based on Glx and Phe alone, and estimates based on the nonlinear model, combining data across dolphins, were more precise and less variable among dolphins than estimates considering each dolphin independently (Table 1). For the nonlinear model, TP ranged from 2.2 to 2.7‰ over the 30 dolphins, with an integrated value of 2.6‰ (Table 1, Appendix 4C). Mean posterior estimates of TDF (Equation 8) ranged from 2.4 to 3.2‰, with a mean value of 3.1‰ (Appendix 4F).

Based on the length coefficient β_1 of the linear model, there was moderate support for a linear effect of body length on Δ^{15}N. The proportion of posterior density of the length coefficient $\beta_1 > 0$ was 0.87 (Figure 8a); in other words, it was about seven times (0.87/0.13) more probable that Δ^{15}N increased with length than that it did not. By usual standards (Kass & Raftery, 1995), this is moderate support. There was stronger support for the hypothesis that Δ^{15}N for the two shortest dolphins (a weaning calf (145 cm) and a juvenile dolphin (156 cm) likely <3 years old) was less than for larger animals. The proportion of posterior density of the binary predictor >160 cm was 0.93 (Figure 8b), making it 13 times more probable that Δ^{15}N was greater for the larger dolphins. There was no support for any Δ^{15}N difference by sex; posterior distributions were nearly equal for males and females (Figure 8c).

Smaller Δ^{15}N for the two shortest (and youngest) animals was visually evident from the fit of the nonlinear length model (Figure 6c), and this was confirmed by calculation of the difference. Δ^{15}N was 32 times (0.97/0.03) more likely to be smaller for the smallest dolphin (145 cm in body length) than for the 28 dolphins >160 cm, and eight times (0.89/0.11) more likely for the second smallest dolphin (156 cm; Figure 7). For the two smallest dolphins taken together, the probability that Δ^{15}N was greater for the larger dolphins was the same for the nonlinear model (0.93) as for the linear model with the binary indicator (0.93, Figure 8b).

Posterior distributions of parameters for all models are shown in Appendix 5.

4 | DISCUSSION

4.1 | Trophic indices

Given the substantial variation in AA isotopic fractionation due to different metabolic pathways, it is not surprising that estimates

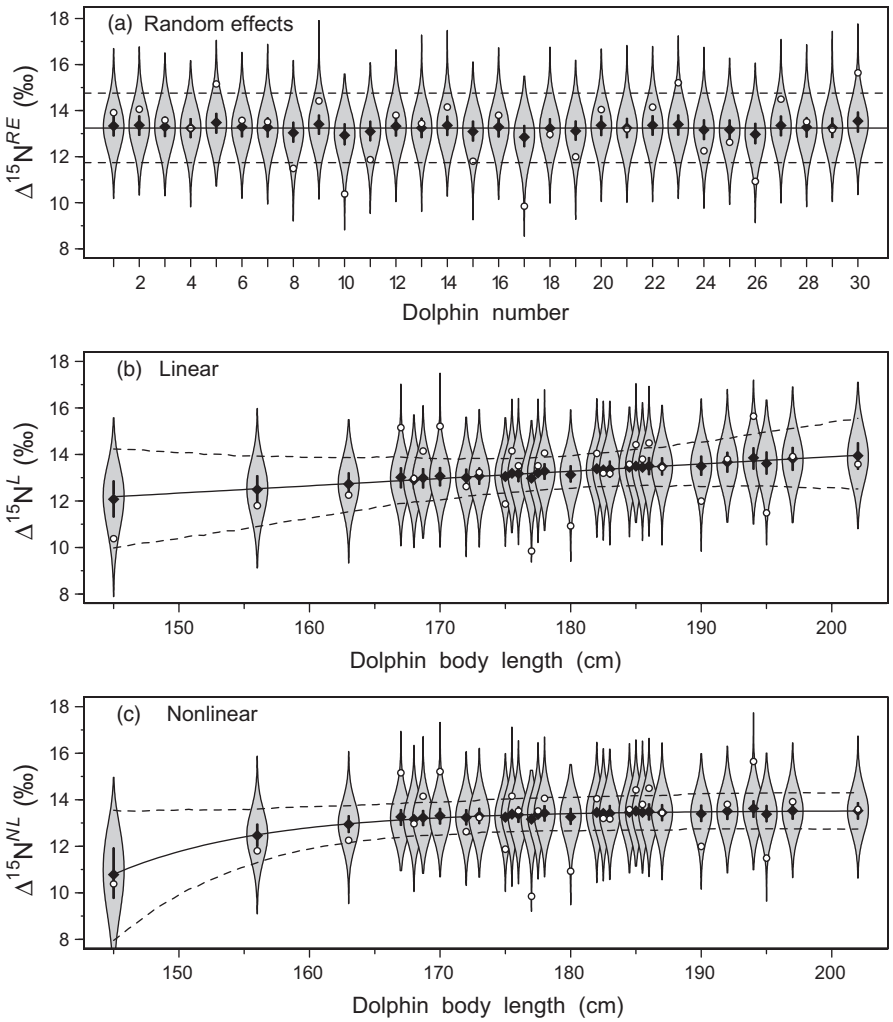

FIGURE 6 Trophic indices Δ^{15}N estimated as (a) a random effect (Equation 4), (b) a linear function of body length (Equation 5) and (c) a nonlinear function of body length (Equation 6), using all trophic and source AAs. The grey violin plots show marginal posterior probability distributions. Black diamonds are the means of the posterior distributions, thick black vertical lines the interquartile ranges and white circles the observed means. The solid horizontal line is the mean, and the dashed lines the 95% highest density interval, of the predicted trophic index

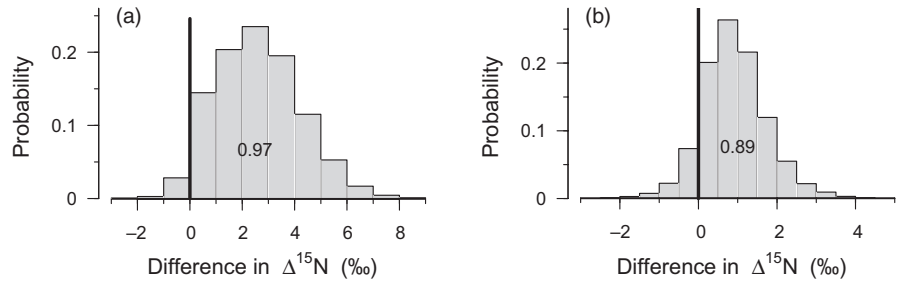

FIGURE 7 Histograms of posterior samples of the difference in the trophic index Δ^{15}N estimated by the nonlinear model (Equation 6) for the 28 dolphins >160 cm in body length and (a) the weaning calf of 145 cm and (b) the juvenile of 156 cm. The fractional numbers in the histograms are the proportions of samples that indicate that the trophic index is higher for the larger dolphins

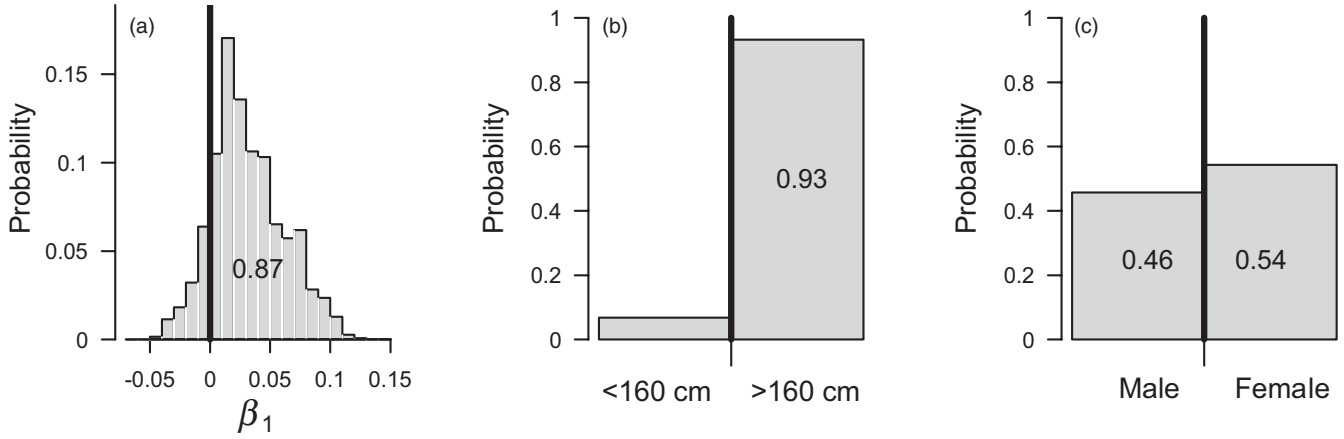

FIGURE 8 Histograms of posterior samples of the linear model (Equation 5) for (a) the coefficient β_1 of body length, (b) the binary indicator for dolphins less than or greater than 160 cm in body length and (c) the binary indicator of sex. The fractional numbers in the histograms are the proportions of samples in the indicated ranges

based on more data were more precise. The differences between estimates of trophic indices using all seven trophic and four source AAs ($\Delta^{15}N^{Tro\text{-}Src}$, Equation 3a) and those using the canonical trophic AA Glx and source AA Phe ($\Delta^{15}N^{Glx\text{-}Phe}$, Equation 3b) were highly variable among dolphins (Appendix 3A). For most dolphins, $\Delta^{15}N^{Tro\text{-}Src}$ was higher than $\Delta^{15}N^{Glx\text{-}Phe}$ (Figure 5a), because the mean of δ^{15}N Glx was lower, and the mean of δ^{15}N Phe higher, than the overall trophic and source means (Figure 3). More importantly, estimates of Δ^{15}N based on all AAs were more stable and more precise (Figure 5). Other studies have also found that weighted means of trophic and source AAs were more informative than single AAs from each group (e.g. Bradley et al., 2015). In our study, weighting of different AAs was carried out implicitly within the HBM. The means of the posterior distributions were not exactly equal to the observed means in Figure 5b because the latent means $\mu_{i,tro}$ and $\mu_{i,tro}$ and their difference $\Delta^{15}N^{Tro\text{-}Src}$ were weighted by the uncertainty of their components through partial pooling at the replicate and AA levels (λ_{rep}, λ_{tro}, λ_{src} in Appendix 2A).

The precision of Δ^{15}N and TP estimates was further increased when information was shared among dolphins. Partial pooling at the individual dolphin level (λ_{dol} in Appendix 2B) allowed the estimates of Δ^{15}N for each individual to be informed by the isotope data from other dolphins according to the structure specified in the model. The random effects model assumed that Δ^{15}N differences among individuals were normally distributed. The increase in precision in estimates of $\Delta^{15}N^{RE}$ (Equation 4) over $\Delta^{15}N^{Tro\text{-}Src}$ (Equation 3a) was due to this assumption, not to any additional data. The linear (Equation 5) and nonlinear (Equation 6) models brought in additional data, namely the length of each dolphin. These models assumed that Δ^{15}N differences among dolphins could be at least partly explained by body length. Without sharing information among dolphins, the precision of $\Delta^{15}N^{Tro\text{-}Src}$, as measured by average *SD* of the posteriors, was 1.9‰ (Appendix 3A). When information was shared among dolphins, average *SD* was reduced to about one-third of that, 0.6–0.7‰ (Appendix 4A). There was a similar increase in precision measured by reduction in lengths of 95% highest density intervals: Mean HDI was reduced from 7.4 to 2.4‰ (Table 1, Appendix 4A).

Partial pooling also resulted in the shrinkage of individual estimates towards the mean value of the model. The means of the 30 posterior distributions of $\Delta^{15}N^{RE}$, $\Delta^{15}N^{L}$ and $\Delta^{15}N^{NL}$ were close to the model predicted value, and sometimes rather different than the observed means (Figure 6). Such shrinkage is a known strength of hierarchical models. For these data, the degree of pooling was high (Appendix 2B), evidently because individual estimates of Δ^{15}N were quite uncertain due to the substantial stochasticity of AA δ^{15}N data.

The increased precision and stability of estimates in a hierarchical model are not necessarily captured by model comparison scores which assess out-of-sample predictive accuracy. In this case, WAIC for the best model without pooling (1990.7, Appendix 2A) was slightly lower than the best model with pooling (1990.9, Appendix 2B).

The HBM explicitly modelled three different sources of variability. Some of the observed AA δ^{15}N heterogeneity was due to laboratory error, some to variation in metabolic pathways of each AA and some to biological differences among individual dolphins. The Bayesian machinery propagated uncertainty from the different sources through the marginal posterior distributions of Δ^{15}N, TP and TDF. Furthermore, analysing all data within a single likelihood framework avoided the loss of information that occurs when data are summarized by means and variances at intermediate steps (Gerrodette, 2011). In this analysis, each AA was treated as an equivalent trophic or source indicator, but one could consider alternative models in which some AAs count more than others, based on their intrinsic metabolic characteristics.

4.2 | Trophic position

The mean TP estimate for the 30 common dolphins was 2.6 using all trophic and source AAs and 2.2 using Glx and Phe (Table 1), much lower than the value of 4.2 based on stomach content analysis (Pauly et al., 1998). TP values from 2 to 3 would correspond to primary and secondary consumers; TP between 2.2 and 2.6 would be considered unrealistic for common dolphins and would disagree with stomach content studies for this species (Evans, 1975; Osnes-Erie, 1999; Preti, 2020). Underestimates of TP were documented in other cetaceans using δ^{15}N AA values and various published equations (Matthews et al., 2020). We conclude that the value of TDF = 6.6‰ in Equation 7 was too high, and inappropriate for estimating dolphin TP. Using a TP value of 4.2 and Equation 8, we obtained an average value of TDF = 3.1‰ using all AAs with all of the models (Appendix 4F). This value is approximately one half of the TDF value proposed by Chickaraishi et al. (2009) and Nielsen et al., (2015) using Glx and Phe. To date, it is recognized that TDFs vary among trophic levels and taxonomic groups (McMahon & McCarthy, 2016; Nielsen et al., 2015) and could be taxon specific (Nuche-Pascual et al., 2018). The results of our analysis suggest that cetaceans should have an AA δ^{15}N TDF ~ 3‰ to obtain reasonable TP estimates. Thus, a search of a universal TDF for all taxa, with values higher than 4‰, would underestimate cetaceans' TP as well as those of other top predators. We recommend identifying the main factors driving AA isotopic fractionation in cetaceans and integrating more AA data for each group to evaluate variability in source and trophic levels in relation to physiological and ecological factors.

4.3 | Ontogenetic variation of trophic proxies

The δ^{13}C and δ^{15}N standard ellipses indicated that males and females and the three older life stage classes largely shared their isotopic niches (Figure 2). Dependent calves, however, had a larger isotopic niche with higher δ^{15}N values that gradually decreased until ~140 cm (Figures 1 and 2a). This pattern of variation is consistent with previous findings on mammals that show milk-dependent calves have higher δ^{15}N values because lactating mothers catabolize their own tissues to produce milk. Hence, δ^{15}N values decrease as calves reduce milk dependence and incorporate nutrients from prey (Mendes et al., 2007; Newsome et al., 2009). On average, Chivers et al. (2016) reported that common dolphin calves transition to swimming separately from their mothers, and presumably foraging more independently, at 140.1 cm (~1.3 years old). Our results support this finding with the sharpest shift in δ^{15}N values occurring in weaning calves at 139 cm, suggesting that prey consumption dominates the diet of dolphins after that.

The AA Δ^{15}N patterns of trophic indices in relation to body size (Figure 6b,c) partially agreed with results from bulk tissue that suggested equal isotopic niches among weaning calves, juveniles and adults (Figure 2). The nonlinear model based on AAs showed that weaning calves and smaller juveniles had lower Δ^{15}N than adults (Figure 6c). Stomach content analysis of 259 common dolphins, collected across the same years and area as this study, showed that the main prey item differed by dolphin size (Preti, 2020). Bigger dolphins are usually older and more experienced and possibly capture prey of larger size and of higher TP, as observed in other small dolphin species (Robertson & Chivers, 1997). Thus, adults may select larger prey than juveniles, or adults may hunt in groups composed by dolphins of similar age and size classes. However, our $\delta^{13}C_{bulk}$ data suggest that all size classes use the same foraging area (Figure 2). Beak size could explain the observed Δ^{15}N difference; smaller beak size (and perhaps limited diving ability) may constrain weaning calves and juveniles to catching smaller prey resulting in a lower TP than adults even when feeding together.

A recent study on cetaceans' δ^{15}N-AAs showed that marine mammal-eating (MME) killer whales (*Orcinus orca*; this ecotype consumes cetacean calves) were ~5‰ lower in $\Delta^{15}N^{Glx\text{-}Phe}$ than fish-eater killer whales, and just ~1‰ higher than bowhead whale tissues (Matthews et al., 2020). The $\Delta^{15}N^{Tro\text{-}Src}$ values of the MME killer whales were 2.75‰ higher than our common dolphin weaning calves (a potential prey), and agree with our estimates of $TDF^{Tro\text{-}Src}$ = 3.1‰ using Equation 8. It remains unknown why MME killer whales and weaning dolphin calves would have lower Δ^{15}N than other cetaceans that feed on fish and cephalopods. AA imbalances due to limiting dietary supplements and protein level in the diet are proposed to explain differences in trophic AA isotopic fractionation in fish tissues (McMahon et al., 2015; Nuche-Pascual et al., 2018), which could occur during the weaning stage in dolphins, but unlikely to explain adult MME killer whales' AA δ^{15}N values.

4.4 | Feeding strategy as suggested by bulk isotopes and AAs

Comparable isotopic niches among males, females and the three larger size classes suggest that dolphins have similar diet composition and

feed in the same areas. These results agree with Chivers et al. (2016), who suggested limited segregation by sex and life-stage classes for common dolphins, but disagree with Danil et al. (2010) who suggest spatial segregation. As with other small odontocetes, females likely feed throughout pregnancy and lactation periods, since they are not required to fast, migrate or sexually segregate like some large cetaceans (Oftedal, 1997). For odontocetes like sperm whales with strong sexual dimorphism and segregation, stable isotope ratios from resident females and juveniles are distinctive from the highly migratory adult males, reflecting the dietary differences associated with feeding in different geographic areas with unique isotopic values (Ruiz-Cooley et al., 2004). In common dolphins, if school members frequently cooperate during feeding, each member would have access to similar prey items, which would explain the observed homogeneity in bulk isotope values among dolphins, as opposed to species composed of individual specialist feeders that result in wide isotope ellipses (Newsome, Tinker, et al., 2009). It remains unknown if the observed overlap in isotope ratios is mainly driven by diet, habitat or both, since SIA from bulk tissue cannot separate these effects.

Together and in agreement with our $\delta^{15}N_{bulk}$ results, AA $\Delta^{15}N$ analysis did not show differences between males and females, supporting lack of sexual segregation during feeding. The isotope values from skin samples of dolphins integrate diet from approximately 3 months prior to tissue collection (Hicks et al., 1985). If males and females coexist during feeding, individuals would tend to find solutions to reduce intraspecific competition and the energetic cost of searching and catching prey (e.g. through sex-based niche partitioning by using habitat differently or feed at different times in the same habitat). Sex-based trophic partitioning would favour isotopic differentiation between sexes, which was not observed in our results. An alternative strategy to reduce sexual competition would be to cooperate, increasing the likelihood of catching prey in the same place and time. Strong social cohesion and highly coordinated behaviour among group members for aggregating dispersed prey have been documented in other common dolphin populations (Reynoso, 1991) and other dolphin species (*T. truncatus*; Rossbach & Herzing, 1999; *S. longirostris*; Benoit-Bird & Au, 2009). Thus, cooperation during feeding is a plausible behaviour that may explain the lack of isotopic differences between sexes in common dolphins. Furthermore, it can provide advantages like increasing chances of prey capture, and perhaps reduce energy cost for catching prey. Such behaviour may represent the main feeding strategy that shapes common dolphins' life history.

Our SIA study combined bulk tissue and AA-specific stable isotope data to understand the effect of life-stage-specific traits on dolphin feeding habits using Bayesian analysis. This combination is a powerful approach to improve our understanding of trophic niches, since $\delta^{15}N$ AAs are strongly linked to animal metabolism and can distinguish diet from habitat effect. Combining SIA and life-history data in a HBM can provide insights of ecological adaptations within marine species like cetaceans that are inherently difficult to study.

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AUTHORS' CONTRIBUTIONS

R.I.R.-C. and T.G. conceived the ideas and designed methodology; R.I.R.-C., S.J.C. and K.D. collected the data; R.I.R.-C. and T.G. analysed the data; R.I.R.-C. and T.G. led the writing of the manuscript. All authors contributed to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

All data are deposited at https://cicese.repositorioinstitucional.mx/jspui/handle/1007/3374.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the Supporting Information section.

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