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Intraspecific variation in prey quality affects the consumption rates of top predators

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Abstract

1. Prey quality, measured as energy density and energy content, is a key functional trait in predator–prey relationships. While the effects of interspecific differences in prey quality on predators have been examined previously, the consequences of intraspecific variation remain less understood.
2. To examine how within-species variation in prey quality influences predator foraging, we modelled the effects of prey size, maturity and sampling season and region on the quality of *Engraulis mordax*, *Sardinops sagax* and *Doryteuthis opalescens*—three common prey species for top predators in the California Current Ecosystem (CCE). We contextualized our findings using documented energy budgets of the California sea lion (*Zalophus californianus*), a consumer of these species and an important ecosystem indicator in the CCE.
3. We found significant within-species variation in prey quality related to size, maturity, season and region, with stronger effects in fish than squid. These patterns likely reflect prey life history and regional and seasonal oceanographic conditions that influence energy storage. Under static prey availability and predator energy demands, daily biomass requirements driven by intraspecific variation in prey quality were comparable to previous estimates based on interspecific differences. By integrating predator bioenergetics with prey energy content models, we found that the number of prey required can vary by tens of thousands depending on prey size—rendering smaller individuals an impractical energy source for non-filter-feeding predators. Even accounting for size, predators may need to consume up to twice as many individuals when foraging on lower-quality prey from certain regions, seasons or maturity stages compared to higher-quality conspecifics.
4. Our findings highlight the critical importance of incorporating intraspecific variation in prey quality into bioenergetics frameworks that inform predator foraging predictions. As climate change and resource exploitation intensify, integrating functional traits and energetic trade-offs into predator–prey studies will be essential for anticipating predator responses and evaluating ecosystem resilience.

KEYWORDS
bioenergetics, consumption rates, energy density, intraspecific variation, predator foraging, prey quality, top predators, trophic dynamics

1 | INTRODUCTION

Food availability is a key driver of predator behaviour, physiology, life history, and demographics (Abrams, 2022). When prey are limited, predators may respond by increasing foraging effort or altering resource use (Abrams, 1992; Perry & Pianka, 1997; Stephens & Krebs, 1986). If alternative prey or foraging options are unavailable, such responses may be constrained, leading to declines in body condition and population growth (Bogstad et al., 2015; Dodson et al., 2016; Tremblay & Cherel, 2003). These functional responses can be especially pronounced in top-level predators, given their substantial energy requirements for growth, reproduction and survival (Williams et al., 2004).

The consequences of changing food availability for predators are traditionally assessed in terms of prey quantity (e.g. biomass) and taxonomic composition (Cohen et al., 2014; Goss-Custard et al., 2002; Shine & Madsen, 1997). However, more recent approaches emphasize the role of specific prey characteristics (functional traits) in shaping predator–prey dynamics, highlighting how trait variation can influence prey selection and consumption patterns (Keppeler et al., 2020; Schmitz, 2017; Spitz et al., 2014). For example, prey selection is often linked to prey quality (Hildebrand et al., 2022; Meynier et al., 2008; Schrimpf et al., 2012; Spitz et al., 2018), a functional trait characterized by energetic metrics such as energy density (kJ g^{-1}) or total energy content per prey item (kJ prey^{-1}).

Decreases in the availability of high-quality prey species have been hypothesized as drivers of predator abundance by reducing breeding success, lowering offspring condition and increasing mortality rates (Karlson et al., 2020; McClatchie et al., 2016; Trites & Donnelly, 2003; von Biela et al., 2019). For example, the diet composition of African penguins shifted from primarily lipid-rich pelagic prey to nutritionally inferior species in the mid-1900s, coinciding with marked declines in penguin breeding success and population growth (Ludynia et al., 2010). While the effects of prey quality on top predator populations are typically examined in the context of species-level shifts, from high- to low-quality prey (Haug et al., 2002; Österblom et al., 2008), variation in prey quality within a single species may also influence predator–prey interactions by affecting the quantity of prey required to meet energetic demands (Figure 1). Intraspecific differences in prey quality are widespread (Dessier et al., 2018; Van Pelt et al., 1997; Vollenweider et al., 2011) and shaped by extrinsic factors (e.g. spatial and temporal environmental variability) and intrinsic life history characteristics (e.g. reproductive cycles, ontogeny, sex). These patterns suggest that using average energy density or energy content values for a prey species may obscure important predator–prey relationships and that within-species differences in quality should not be overlooked.

Bioenergetics models offer a powerful framework for evaluating the ecological consequences of variation in prey quality (Pirotta, 2022). These models integrate predator energy requirements with information on predator diet composition and prey energy values to estimate the biomass of prey consumed (Pirotta, 2022). Bioenergetics approaches are also embedded within ecosystem-based models that assess ecological responses to environmental change and resource exploitation (Megrey et al., 2007; Rose et al., 2015), underscoring the importance of accurate model parameterization for conservation and management. However, most models rely on mean energy values for a given prey species to estimate predator consumption (Barnett et al., 2017; Goldbogen et al., 2011; Roby et al., 2003). Finer-scale

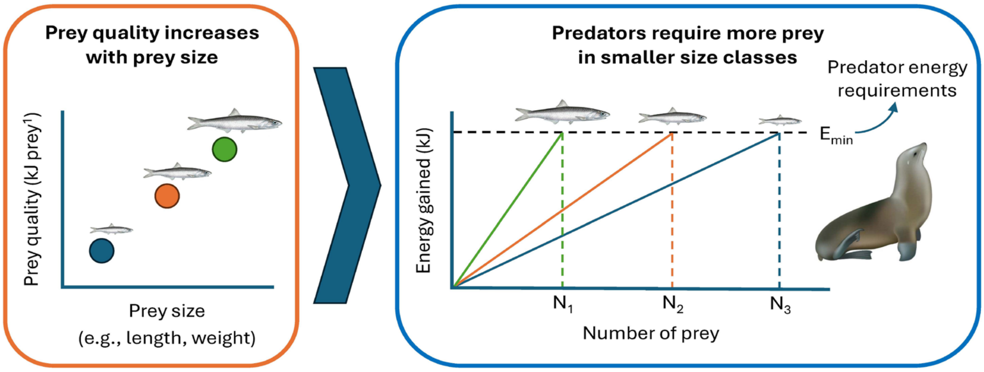


FIGURE 1 Intraspecific variation in prey quality affects the number of prey required for predators to meet energetic demands. In this scenario, energy content (kJ prey^1) is the metric of prey quality, and three size classes of a single prey species are presented: small (blue), medium (orange) and large (green). Prey energy content increases with size (e.g. length, weight), thus the number of individual prey required for consumption to meet the gross energetic needs of predators (E_{min}) is higher for smaller size classes ($N_3 > N_2 > N_1$). California sea lion (*Zalophus californianus*) illustration by Uko Gorter; northern anchovy (*Engraulis mordax*) image courtesy of NOAA Fisheries. Used with permission.

metrics, such as spatial and temporal variation in prey quality within a species, are rarely included, largely due to the challenges of quantifying intraspecific variation in energy density and content (McHuron et al., 2022).

To address this gap, we empirically evaluated how several factors influence intraspecific variation in prey quality and the consequences for predator consumption rates. Specifically, we quantified the effects of prey size, maturity, season and region on prey energy density and energy content and integrated these data with documented predator energy budgets to assess their influence on foraging demand. Our study focused on the California Current Ecosystem (CCE), a productive upwelling zone off the West Coast of North America where spatial and temporal environmental variability drive substantial shifts in food web structure and function (Kämpf & Chapman, 2016). We assessed the quality of three key prey species that support numerous top predators in the system: northern anchovy (*Engraulis mordax*), Pacific sardine (*Sardinops sagax*) and market squid (*Doryteuthis opalescens*).

We examined how within-species variation in prey quality affects predator foraging using the California sea lion (*Zalophus californianus*; hereafter sea lions), a frequent consumer of these prey species in the CCE. Sea lions represent an ideal case study because diet data reveal shifts in prey use across space and time (Lowry et al., 2022; Melin et al., 2012), with transitions from presumably high-quality prey (anchovy and sardine) to lower-quality alternatives (e.g. squid) linked to food limitation and elevated pup mortality (Laake et al., 2018; McClatchie et al., 2016; Nehasil & Lowry, 2015). As such, sea lions are sensitive indicators of prey quality and abundance in the CCE (Harvey et al., 2023; Thompson et al., 2019) and provide a valuable system for investigating how intraspecific variation in prey quality influences energy transfer through food webs.

To isolate the effects of prey quality on predator consumption rates, we assumed static prey availability and energetic requirements, allowing us to identify patterns in prey quality that may drive shifts in food intake. We expected sea lions to adjust their consumption rates based on the physiological condition of their prey, reflecting prey life history characteristics, ecosystem phenology and regional environmental conditions. Although such comprehensive predator–prey relationships are challenging to measure empirically, our study leveraged a detailed sea lion bioenergetics model, a robust diet dataset and extensive prey samples. While our findings provide region-specific insights into a highly productive upwelling ecosystem, this framework is generalizable to other systems characterized by strong spatial and temporal variability.

2 | MATERIALS AND METHODS

2.1 | Study system: California Current Ecosystem

Coastal upwelling zones are among the most productive marine environments worldwide (Pauly & Christensen, 1995), and the CCE offers an ideal context for examining variability in resource quality for predators. Strong seasonal upwelling during spring and summer (King et al., 2011) fuels high primary productivity (Deutsch et al., 2021; Eppley et al., 1985; Guo et al., 2014), leading to mesozooplankton biomass peaks (Guo et al., 2014) and supporting dense aggregations of forage species such as small schooling fish and invertebrates (Hutchings et al., 1995; Kämpf & Chapman, 2016). These forage species are key energetic links between lower and upper trophic levels (Benoit-Bird et al., 2019), and their density and demographics are shaped by seasonal and longer-term oceanographic variability, with cascading effects on predators that rely on them (Hutchings et al., 1995; Kaplan et al., 2019; Santora et al., 2017; Thompson et al., 2019; Wells et al., 2008; Zwolinski & Demer, 2012).

We examined the quality of three forage species that inhabit the CCE—northern anchovy, Pacific sardine and market squid, hereafter referred to as anchovy, sardine and squid, respectively. While the entire system can be divided into three regions (the Northern CCE, the Central CCE and the Southern CCE, see Figure 2 for map), our study focused on the central and southern regions of the system. In general, squid are considered lesser quality prey in the CCE because of their presumed low caloric and fat content, whereas sardine and anchovy are considered higher quality, lipid-rich prey (McClatchie et al., 2016). Sardine, anchovy and squid demonstrate predictable seasonal patterns in their spatial distributions, and the locations of large spawning aggregations vary seasonally. Adult anchovy and sardine aggregate along the West Coast of North America for spawning during winter, with peak spawning in late winter/early spring for anchovy and in spring for sardine (Dorval et al., 2014, 2018; Kuriyama et al., 2020). Anchovy and sardine may spawn throughout summer, but generally spend the summer feeding (Checkley & Barth, 2009; Schwartzkopf et al., 2022). Squid can spawn year-round, with

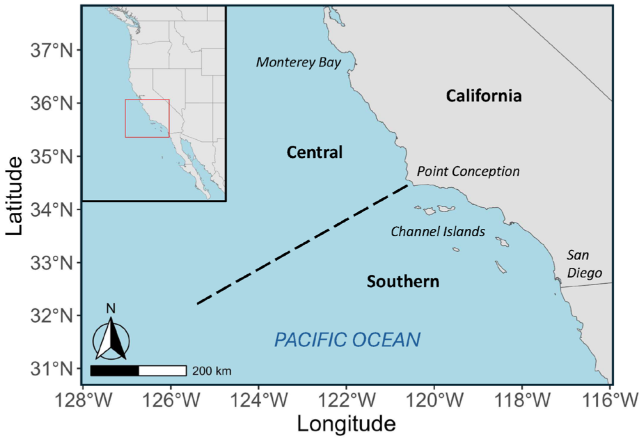


FIGURE 2 Sampling regions within the California Current Ecosystem (CCE) where fish and squid specimens were collected. The Central and Southern CCE are separated by a biogeographical barrier at Point Conception (black dashed line) and experience different oceanographic conditions. Central CCE samples were collected from Monterey Bay to Point Conception, and Southern CCE samples were collected from Point Conception to San Diego. Note that the map depicts only the sampled locations, not the full extent of each CCE region.

peak spawning from spring through fall in the Central CCE and from fall through spring in the Southern CCE (Dorval et al., 2024; Sweetnam, 2005).

To understand how shifts in prey quality affect the amount of prey needed to meet predator energetic demands, we used data on adult female California sea lions—abundant, year-round predators in the CCE whose bioenergetics have been previously detailed (McHuron et al., 2017). These adult females primarily breed and pup on the Channel Islands (Figure 2), which support the population's largest colonies (Laake et al., 2018). For clarity, all subsequent references to 'sea lions' refer specifically to adult females. Sardine, anchovy and squid comprise a large proportion of sea lion diets, with relative contributions varying by season, year and foraging location (Lowry et al., 2022). Diet differences among breeding colonies on the Channel Islands, particularly during the spring, suggest access to common prey species may vary across the population's foraging range (Lowry et al., 2022; Melin et al., 2012).

2.2 | Prey sample collection

We obtained frozen whole specimens of anchovy ($n=153$), sardine ($n=96$) and squid ($n=51$) collected during spring and summer seasons from 2015 to 2019 (Table S1). We obtained adult (sardine and anchovy) and juvenile (sardine, anchovy and squid) whole specimens from the NOAA Southwest Fisheries Science Center (SWFSC) spring and summer trawl surveys off the West Coast of the US (Dorval, 2022; Macewicz et al., 1996). We obtained young-of-the-year and additional adult sardine and anchovy from the Central and Southern CCE during SWFSC Rockfish Recruitment and Ecosystem Assessment Surveys (see Field et al., 2021). The California Department of Fish and Wildlife (CDFW) also provided adult sardine landed by commercial fisheries within the Southern CCE and the Everingham and Bros. Bait Company provided juvenile and adult sardine and anchovy from the Southern CCE off San Diego. Sea lions consume these prey across the range of sizes sampled, including fish and squid as small as larvae, though they tend to target larger individuals (Figure S1; Bizzarro et al., 2023). It is important to note that, while our prey samples for fish and squid included individuals within the lower and middle size quantiles typically consumed by sea lions, we were unable to sample the largest individuals (upper quantile) that are also commonly consumed (Figure S1; Table S1). We collected all prey samples between 2015 and 2019, a period that encompassed 2 years of an anomalous marine heatwave in the CCE followed by 3 years of post-heatwave conditions. This study did not require additional ethical approval, as we did not directly handle live animals. All specimens were collected by government and commercial collaborators under relevant federal and state research permits and licences. For details on sampling years, seasons and regions for each species, see Table S1.

To detect potential spatially-driven environmental differences in prey quality, we sampled from areas north and south of Point Conception, which correspond to the Central and Southern CCE, respectively (Figure 2), because they experience distinct oceanographic conditions (Deutsch et al., 2021; Newman, 1979). To account for the effect of fish maturation and reproduction, as well as seasonal patterns of ocean productivity (Eppley et al., 1985; Guo et al., 2014; Small & Menzies, 1981), we separated our collections into spring/spawning and summer/non-spawning periods. We did not collect mature, spawning squid, as squid spawn in nearshore locations not accessible to large NOAA fishery research vessels. We stored samples in freezers (−80°C to −20°C) until they were ready to be processed.

2.3 | Sample processing

We recorded measurements to the nearest mm of standard length (SL), fork length and total length, when possible, for sardine and anchovy and mantle length (ML) for squid. We recorded wet weights to the nearest 0.01 g from fresh samples if specimens were processed on-board survey vessels, or from thawed samples if specimens were frozen for processing later. We determined the sex and maturity of juvenile and adult fish through visual gonad inspections when possible and assigned them to maturity Stage 1 (immature) or Stage 2 (developing mature gonads [i.e. intermediate] or mature but not yet spawning; Macewicz et al., 1996). The midwater trawls used to collect squid do not target bottom depths <90 m where mature squid spawn. Therefore, all squid collected in this study were considered juveniles and assigned to maturity Stage 1 (immature). Henceforth, 'squid' will refer only to individuals in Stage 1. We returned specimens to a −20°C freezer until fully frozen (at least 24 h), then freeze dried them until dry weights stabilized (i.e. two successive weights differed by ≤0.01 g, typically within 4–14 days depending on prey size). We recorded dry weights to the nearest 0.01 g and used higher precision (0.001 g) for some juvenile fish when necessary.

Following von Biela et al. (2019) we determined prey caloric densities ($\text{kcal}\,\text{g}^{-1}$ dry wt) by homogenizing each freeze-dried specimen in a coffee grinder, then analysing three pellets of the resulting fish or squid meal using bomb calorimetry (Parr 6200 oxygen bomb calorimeter). We used benzoic acid standards and, when possible, triplicate tissue samples to evaluate precision. We converted the measurements of kcal g^{-1} dry wt to $\text{kJ}\,\text{g}^{-1}$ dry wt and calculated an average energy density for each sample. We also calculated the energy content of an individual fish or squid (i.e. whole-body energy in kJ per specimen; kJ prey^{-1}) by multiplying each specimen's dry weight (g) by its mean energy density ($\text{kJ}\,\text{g}^{-1}$ dry wt). Finally, we determined energy density on a wet weight basis ($\text{kJ}\,\text{g}^{-1}$ wet wt) for each specimen because model predictions based on wet weight measurements provide a more applicable interpretation of our results, reflecting the scale at which predation occurs in natural environments. To convert from $\text{kJ}\,\text{g}^{-1}$ dry wt to $\text{kJ}\,\text{g}^{-1}$ wet wt, we divided each specimen's energy content (in kJ) by its wet weight (g).

2.4 | Data analysis

We began by visualizing prey energy density and energy content across the full range of sampled body sizes and combinations of factor levels (season, region, maturity). We then modelled energy density ($\mathrm{kJ\,g^{-1}}$) and whole-body energy content ($\mathrm{kJ\ prey^{-1}}$) separately to evaluate the effects of prey size, season, region and maturity on intraspecific variation in prey quality. These two metrics offer complementary ecological insights: energy density is relevant for understanding biomass-based consumption (e.g. filter feeders or food web modelling; Mooij et al., 2010; Pethybridge et al., 2018), while energy content more directly reflects prey value per capture for predators that target individual prey (i.e. Figure 1; von Biela et al., 2019). Given the importance of body size in structuring predator–prey interactions (Petchey & Belgrano, 2010; Scharf et al., 2000) and its role in forage fish dynamics (Hughes & Connell, 1987), we included length (SL for fish and ML for squid) as a continuous covariate in all energy density and content models described below.

2.4.1 | Energy density modelling

To model energy density, we used linear models with prey length, maturity, season and region as predictors for anchovy and sardine. For squid, models included fewer predictors (size, season and region) since all squid in our study were classified as juveniles. Residuals from both simpler additive and more complex interaction models were approximately normally distributed. However, many exhibited increasing variance with fitted values, indicating potential heteroscedasticity, which we further evaluated during model selection. To address this, we explored generalized linear models (GLMs) with a gamma (γ) distribution and log link, which are well-suited for modelling positive, right-skewed responses where variance scales with the mean (McCullagh & Nelder, 1989) and are widely used for modelling energetic traits in animals (e.g. Bazzino Ferreri, 2014). While gamma GLMs modestly improved residual balance in some cases, they did not consistently resolve variance patterns or improve predictive performance based on model fit metrics or cross-validation (Table S2). Given the minimal performance differences and the improved interpretability of linear models, we retained them for energy density models across all species. We interpret any remaining model misfit as likely reflecting biological variability not fully captured by the predictors, rather than a failure of the linear modelling framework.

2.4.2 | Energy content modelling

We modelled energy content using GLMs with a gamma distribution and log link. This approach accounts for the allometric relationship between length and mass (Palance et al., 2019) and the increasing variance in energy content with body size (Froese, 2006; Fulton, 1902). All models included log-transformed length and tested season, region and maturity, where applicable. As with energy density models, maturity was included for anchovy and sardine but excluded for squid, since all individuals were juveniles. This GLM framework was applied consistently across all species.

2.4.3 | Model selection and evaluation

We began with simpler additive models including prey length and other biologically relevant predictors (season, region and maturity), then incrementally increased model complexity to evaluate the contribution of additional terms and interactions. Initial model performance was assessed using R^2 for linear models and the proportion of deviance explained (D^2) for GLMs, where D^2 represents the reduction in deviance relative to a null model (Guisan & Zimmermann, 2000). Residuals were visually evaluated for independence and homoscedasticity.

To identify a set of candidate models, we used a dual approach that balanced explanatory power and predictive accuracy: (1) Akaike's Information Criterion corrected for small sample sizes (AICc) to evaluate model fit and parsimony (Burnham & Anderson, 2004) and (2) Leave-One-Out Cross-Validation (LOOCV) to assess out-of-sample predictive performance. We selected models that both met key assumptions (e.g. residual diagnostics, lack of overdispersion or misfit for GLMs; homoscedasticity and normality for LMs) and performed well under AICc and LOOCV criteria.

Final model selection prioritized simplicity and biological interpretability, with preference given to the highest-ranked AICc model unless LOOCV indicated a clear predictive advantage for an alternative. For all fish and squid energy density models, we found strong support for a single best model in each case (AICc weight of evidence [w] >0.90; Table S2; Burnham & Anderson, 2004). Accordingly, all further analyses and predictions (see below) were based on the parameters of these top-ranked models, which also performed well in LOOCV (Table S2). For energy content models, which were fit using GLMs to account for increasing variance with size, no single model achieved an AICc weight >0.90 (Table S3). We therefore averaged the top set of models with ΔAICc <4 and a cumulative AICc weight of at least 0.90 to account for model selection uncertainty using the MuMIn package (Bartoń, 2024). In some cases, a few lower-ranked models according to AICc performed marginally better in LOOCV (Table S3). These models are reported in Supporting Information S1 for transparency, but we based our main predictions on the AICc-averaged models, prioritizing parsimony and interpretability.

Following model selection, we compared model outputs from dry weight and wet weight energy density formulations to evaluate consistency. Although wet weight energy density is more relevant for ecological and management applications, it can be sensitive to specimen processing (Hislop et al., 1991; Montevecchi & Piatt, 1987). For fish, model results were consistent across both formulations, so we proceeded with wet weight-based interpretations. For squid, however, parameter estimates differed, likely due to processing error in high-water-content specimens. To address this, we predicted wet weight energy density from dry weight model outputs using a regression-based conversion ($R^2 = 0.99$, $p < 0.001$; Figure S2). For clarity, energy density refers to kJ g^{-1} wet wt in the remainder of this section.

We report standardized regression coefficients (β) for both linear models and GLMs. For linear models with Gaussian error, we additionally report partial R^2 values to quantify the unique variance explained by each predictor. For GLMs, where partial R^2 is less straightforward to interpret, we relied on standardized coefficients alone. For full model details and descriptions of our best-supported models by species, see Methods S1 and Results S1.

2.4.4 | Model predictions

We predicted energy density and content using the highest-ranked single model and the model-averaged estimates, respectively, for each species. To support visualization and interpretation of these multidimensional model outputs, we generated post hoc predictions across all combinations of the modelled categorical predictors (e.g. season, region, maturity) along the range of length values observed for each species. For clarity in presentation, we refer to these unique combinations of factor levels as 'prey groups' (see Methods S1 and Table S4); however, we emphasize that these combinations were not modelled as a separate covariate but were used post hoc to visualize predictions across the full range of observed conditions. For example, immature (Stage 1) sardine collected in the Southern CCE during summer were labelled as the prey group 'Stage 1 summer southern' sardine.

To understand how a predator must shift its foraging effort in response to intraspecific variability in prey quality, we accessed published data on the mean gross daily energetic requirements of sea lions. These range from ~48,000 kJ (reproductively inactive) to ~83,000 kJ (reproductively active) per day while at sea (McHuron et al., 2017). Gross energy requirements reflect not only net energetic demands—such as field metabolic rate, lactation and gestation—but also include losses to faeces, urine and the heat of digestion. These losses are accounted for by dividing the net requirement by *p_metabolized*, the proportion of ingested energy available for metabolism (assumed to be 0.87; Costa, 1986; McHuron et al., 2017). This parameter effectively incorporates assimilation efficiency and avoids the need to apply a separate correction to prey energy density. For our analysis, we assumed a constant gross energy requirement and used the lower, conservative estimate of 48,000 kJ/day, corresponding to a reproductively inactive female who spends ~71% of her time at sea. This value facilitates comparison with other marine predators, as sea lions are among the more energetically demanding pinniped species (McHuron et al., 2017). For each prey type, we then estimated the biomass of prey, B_{prey} and number of individuals, N_{prey}, needed to meet this daily requirement, using the following equations:

$$B_{\text{prey}} = {}^{E_{\text{pred}}}/_{\text{ED}_{\text{prey}}} \tag{1}$$

$$N_{\text{prey}} = {}^{E_{\text{pred}}}/_{\text{EC}_{\text{prey}}} \tag{2}$$

where E_{pred} is the average daily energy requirement of sea lions (kJ day^{-1}), ED_{prey} is the predicted energy density (kJ g^{-1} wet wt) of each prey species, and EC_{prey} is the predicted energy content per individual prey item (kJ prey^{-1}) for each species, based on the best-supported model. All statistical analyses were conducted in R v4.2.2. (R Core Team, 2024).

3 | RESULTS

3.1 | Variability in prey quality within species

Individuals from the three forage species we analysed exhibited over a threefold difference in energy density, ranging from 3.0 to 10.8 kJ g^{-1} wet wt (Figure 3a; Figure S3a–c). The mean kJ g^{-1} wet wt values of anchovy, sardine and squid were 5.81, 6.59 and 5.12, respectively (Table 1). Squid showed minimal intraspecific variability in kJ g^{-1} wet wt (CV = 4.00%), while anchovy and sardine exhibited considerably more variability with CVs of 31.95% and 18.08%, respectively (Table 1). Energy density measurements by dry weight followed similar trends

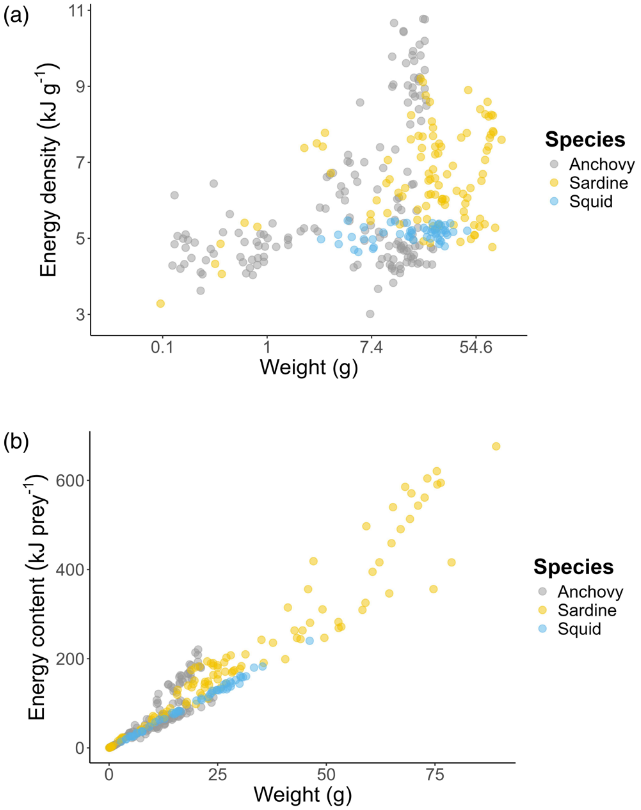


FIGURE 3 Variations in prey quality with size (weight [g]) within three key prey species for predators in the California Current Ecosystem. Mean and variance of (a) energy density (kJ g^{-1} wet wt) and (b) energy content (kJ prey^{-1}) increased with size for fishes, but not squid. As there is a positive relationship between weight and length, we can infer similar patterns of energy density and content hold for length. Each point is an individual prey specimen: anchovy ($n = 153$), sardine ($n = 96$) and squid ($n = 51$). Note that in (a) the x-axis is on a logarithmic scale.

TABLE 1 Mean and coefficient of variation (CV) of energy density ($\mathrm{kJ\,g^{-1}}$) by wet weight ($\mathrm{ED_{wet}}$) and dry weight ($\mathrm{ED_{dry}}$), and energy content per individual (EC; kJ $\mathrm{prey^{-1}}$) across season, region and maturity stage (i.e. prey group, see Table S4) for the three prey species collected in the California Current Ecosystem (CCE).

				$\mathrm{ED_{wet}}$		$\mathrm{ED_{dry}}$		EC	
Species	**Season**	**Region**	**Maturity**	**Mean**	**CV**	**Mean**	**CV**	**Mean**	**CV**
Anchovy	Spring	Central	1	4.79	12.33	20.18	4.14	5.39	93.64
			2	4.78	12.58	20.01	6.11	50.35	27.81
		Southern	1	4.92	12.70	20.18	4.79	9.50	146.33
			2	4.58	10.62	20.04	5.15	68.44	32.81
	Summer	Central	1	7.79	18.91	23.77	9.08	92.11	72.68
			2	9.46	8.43	24.76	6.70	173.28	16.87
		Southern	1	7.76	35.87	23.75	14.09	74.13	81.13
			2	5.63	19.41	20.24	7.05	68.83	29.42
	All anchovy			5.81	31.95	21.27	10.91	56.44	97.83
Sardine	Spring	Central	1	—	—	—	—	—	—
			2	5.99	7.95	21.73	3.47	219.89	24.78
		Southern	1	5.13	14.59	20.44	4.55	52.08	162.14
			2	5.27	5.55	20.01	3.78	276.05	26.05
	Summer	Central	1	7.75	9.52	23.61	6.38	100.33	68.36
			2	9.11	—	25.57	—	180.22	—
		Southern	1	6.40	12.45	21.55	5.08	152.67	61.38
			2	7.68	9.78	23.30	4.40	439.00	41.67
	All sardine			6.59	18.08	21.95	7.62	216.86	76.28
Squid	Spring	Central	1	5.10	4.98	21.60	1.63	83.25	63.77
		Southern	1	5.20	3.10	21.37	2.17	104.81	40.60
	Summer	Central	1	5.20	2.71	21.96	1.09	110.81	57.89
		Southern	1	4.95	3.91	21.48	2.10	91.68	50.23
	All squid			5.12	4.00	21.65	2.01	100.15	53.56

Note: Maturity is classified as Stage 1 (immature) and Stage 2 (intermediate or mature but not yet spawning). Seasons refer to the time of collection (spring/summer), and regions denote sampling locations in the Central and Southern CCE. No Stage 1 sardine were collected in the Central CCE during spring, and only one Stage 2 sardine was collected in the Central CCE during summer. All squid specimens were classified as Stage 1 (immature). Mean values reflect all sizes sampled within each prey group (season × region × maturity combination).

across species as those by wet weight, with forage fishes exhibiting more variability in $\mathrm{kJ\,g^{-1}}$ dry wt relative to squid (Table 1).

The energy content of individual prey items ranged from 0.7 to 676.5 kJ across the three species (Figure 3b). All species demonstrated substantial intraspecific variability in energy content, largely attributable to differences in body size. For example, sardine energy content ranged from 1.6 to 676 kJ per individual (~38 to 190 mm SL), with the largest individuals providing over 400 times more energy than the smallest conspecifics. In addition, variability in both energy density and energy content increased substantially with length for anchovy and sardine, but not for squid (Figure 3; Figures S3a–c and S4a–c).

3.2 | Energy density and content model predictions

From here on, energy density refers to $\mathrm{kJ\,g^{-1}}$ wet wt, and all modelling results discussed are based on wet weight data. For energy density linear models, we report both standardized effect sizes (partial R^2) and standardized coefficients (β) to facilitate comparison with energy content GLMs. All final energy density models performed relatively well under LOOCV, with predictive R^2 values ranging from 0.51 (squid) to 0.73 (anchovy). Model selection results, including AICc rankings and LOOCV metrics, are summarized in Table S2. Final model coefficients and effect sizes are presented in Table 2 and described in Results S1. The final model for anchovy energy density ($R^2=0.75$, $p<0.001$; Equation S1) included interactions between length and season ($\beta = 0.64 \pm 0.11$, $p<0.001$, partial $R^2=0.20$) and length and region ($\beta = 0.31 \pm 0.09$, $p<0.001$, partial $R^2=0.08$), as well as a main effect of maturity state ($\beta = -0.67 \pm 0.12$, $p<0.001$, partial $R^2=0.17$). Among all prey groups, the highest predicted energy density values—exceeding 10 $\mathrm{kJ\,g^{-1}}$—were observed in large (>80 mm), Stage 1 anchovy from the Central CCE during summer (Figure S5a). In contrast, energy density was generally lower among larger size classes in the Southern CCE during summer, where regional comparisons were possible, and was consistently lower across both regions in spring (Figure S5a).

TABLE 2 Factors contributing to energy density (kJ g^{-1} wet wt) in anchovy, sardine and squid were assessed using linear regression models.

Species	Parameter	Estimate	SE	Standardized β	t	p	Partial R^2	F (df)
Anchovy ($n = 153$)	(Intercept)	4.37	0.34	—	13.02	**<0.001**	—	76.17 (6, 146)
	Length	0.01	0.005	1.17	2.70	**0.008**	0.05	
	Season	−2.36	0.68	0.65	−3.44	**<0.001**	0.08	
	Region	−1.24	0.47	0.24	−2.63	**0.009**	0.05	
	Maturity	−1.36	0.25	−0.67	−5.49	**<0.001**	0.17	
	Length:season	0.04	0.007	0.64	5.96	**<0.001**	0.20	
	Length:region	0.02	0.006	0.31	3.60	**<0.001**	0.08	
Sardine ($n = 96$)	(Intercept)	4.36	0.32	—	13.62	**<0.001**	—	43.94 (5, 90)
	Length	0.01	0.003	0.42	3.83	**<0.001**	0.14	
	Season	0.73	0.31	0.69	2.33	**0.02**	0.06	
	Region	1.47	0.19	0.61	7.91	**<0.001**	0.41	
	Maturity	−1.09	0.41	0.14	−2.65	**0.009**	0.07	
	Maturity:season	1.92	0.39	0.43	4.88	**<0.001**	0.21	
Squid ($n = 51$)	(Intercept)	4.60	0.08	—	55.34	**<0.001**	—	16.71 (4, 46)
	Length	0.005	0.001	0.06	5.44	**<0.001**	0.39	
	Season	0.06	0.02	0.03	2.78	**0.008**	0.14	
	Region	0.44	0.10	0.04	4.54	**<0.001**	0.31	
	Length:region	−0.004	0.001	−0.04	−3.67	**<0.001**	0.23	

Note: Predictor variables included sampling season (spring or summer), sampling region (Central or Southern California Current Ecosystem [CCE]), prey length (standard length [SL] for fish, mantle length [ML] for squid) and maturity stage (Stage 1 = immature, Stage 2 = intermediate or mature). Parameter estimates include standard errors (SE), standardized coefficients (β), t values, p values and partial R^2 values. Parameters listed together and separated by a colon indicate those with interaction effects. The F statistics and their degrees of freedom (df; numerator, denominator) are presented for the entire model. Indicator variables are: Summer (I_s), Central CCE (I_c) and Stage 2 maturity (I_m). For categorical predictors, standardized coefficients indicate relative strength within the model, while unstandardized estimates provide the direction of the effect. Maturity was excluded from squid models, as all squid were classified as juveniles (Stage 1). Significant predictors ($\alpha = 0.05$) are bolded.

The final sardine model ($R^2 = 0.69$, $p < 0.001$; Equation S2) included an interaction between maturity state and season ($\beta = 0.43 \pm 0.09$, $p < 0.001$, partial $R^2 = 0.21$) and main effects of length ($\beta = 0.42 \pm 0.11$, $p < 0.001$, partial $R^2 = 0.14$) and region ($\beta = 0.61 \pm 0.08$, $p < 0.001$, partial $R^2 = 0.41$). Model predictions indicated that, at comparable lengths and seasons, sardine from the Central CCE were generally more energy-rich than those from the Southern CCE, with Stage 1 individuals from the Central CCE collected in summer exhibiting the highest predicted energy densities (Figure S5b).

More broadly, energy density predictions among fish prey groups revealed that conspecifics could be up to 1.5–2× more energy-rich than others, depending on season and region, with the magnitude of this difference varying by maturity stage. In some cases, smaller individuals exhibited predicted energy densities equal to or exceeding those of larger individuals (Figure S5a,b). Maturity effects also differed between species: for anchovy, Stage 2 maturity was associated with a decline in energy density, whereas for sardine, the effect of maturity depended on season. (Figure S5a,b; Table 2).

The final model for squid energy density ($R^2 = 0.56$, $p < 0.001$; Equation S3; Table 2) included an interaction between length and region ($\beta = -0.04 \pm 0.01$, $p < 0.001$, partial $R^2 = 0.23$) and a main effect of season ($\beta = 0.03 \pm 0.01$, $p < 0.001$, partial $R^2 = 0.14$). Model predictions indicated a more distinct size-based trend in the Southern CCE, where larger size classes (>90 mm ML) were more energy-rich than smaller ones (<90 mm ML), and regional differences in energy density were more pronounced among smaller squid (Figure S5c). Predicted energy density was also higher in squid collected during summer than in spring ($p = 0.008$; Table 2), although the magnitude of this effect was relatively small (Figure S5c). Overall, model-estimated seasonal, regional and size effects on squid energy density were less pronounced than those observed in fish (Table 2).

Prey size alone explained most of the deviance in the initial energy content GLMs for anchovy ($D^2 = 0.93$), sardine ($D^2 = 0.92$) and squid ($D^2 = 0.97$), consistent with expectations given that energy content reflects both energy density and prey mass. However, when maturity, season and region were included in candidate model sets, each emerged as a significant predictor in species-specific models (Table S3). The underlying candidate models used for averaging explained 97%–98% of the deviance across species and performed well in cross-validation (Table S3). Final model-averaged energy content GLMs are presented in Tables 3 and Results S1. For anchovy and squid, the same covariates used in the energy density models were retained, while the sardine model included an additional interaction between region and season (Table 3). Not all model-averaged parameters were statistically significant, in contrast to the energy density

TABLE 3 Factors contributing to energy content (kJ prey^{-1}) in anchovy, sardine and squid were assessed using generalized linear models (GLMs).

Species	Parameter	Estimate	SE	Standardized β	z	p	Relative importance (w^{+})
Anchovy ($n=153$)	(Intercept)	−12.68	0.30	—	42.18	**<0.001**	—
	Log (length)	3.62	0.07	1.67	49.33	**<0.001**	1.00
	Season	−0.60	0.72	0.17	0.84	0.40	1.00
	Region	−2.10	0.38	0.03	5.46	**<0.001**	1.00
	Maturity	−0.25	0.05	−0.12	4.56	**<0.001**	1.00
	Log (length):season	0.22	0.16	0.04	1.35	0.18	0.78
	Log (length):region	0.49	0.09	0.10	5.51	**<0.001**	1.00
Sardine ($n=96$)	(Intercept)	−11.40	0.28	—	40.05	**<0.001**	—
	Log (length)	3.34	0.07	1.22	50.16	**<0.001**	1.00
	Season	0.37	0.07	0.20	5.47	**<0.001**	1.00
	Region	0.06	0.11	0.10	0.57	0.57	1.00
	Maturity	0.11	0.10	0.07	1.04	0.30	1.00
	Region:season	0.25	0.13	0.05	1.88	0.06	0.86
	Maturity:season	0.04	0.10	0.008	0.37	0.71	0.14
Squid ($n=51$)	(Intercept)	−8.51	0.64	—	13.22	**<0.001**	—
	Log (length)	2.91	0.14	0.72	20.29	**<0.001**	1.00
	Season	−0.08	0.03	−0.04	2.68	**0.007**	1.00
	Region	1.08	0.79	0.001	1.36	0.17	0.74
	Log (length):region	−0.24	0.18	−0.03	1.36	0.18	0.74

Note: Model-averaged estimates are presented from candidate models incorporating sampling season (spring or summer), region (Central or Southern California Current Ecosystem [CCE]), prey length (standard length [SL] for fish, mantle length [ML] for squid) and maturity stage (Stage 1 = immature, Stage 2 = intermediate or mature). Models were averaged based on AICc weights across the top candidate models. Parameter estimates include standard errors (SE), standardized coefficients (β), z values, p values and relative importance (w^{+}). Relative importance quantifies each predictor's contribution to the model's explanatory power, calculated as the sum of Akaike weights across all models in which the predictor appears. Parameters listed with a colon indicate interaction effects. Indicator variables are: Summer (I_s), Central CCE (I_c) and Stage 2 maturity (I_m). For categorical predictors, standardized coefficients indicate relative strength within the model, while unstandardized estimates provide the direction of the effect. Maturity was excluded from squid models, as all squid were classified as juveniles (Stage 1). Significant predictors ($\alpha = 0.05$) are bolded.

models (Table 3). While body size was the strongest predictor, model predictions showed that individuals of similar size could differ in energy content by up to 1.5–2× depending on other factors, such as region, season and maturity (Figure S6). These patterns closely parallel those observed for energy density and emphasize substantial within-species variation in prey quality, even after accounting for size.

3.3 | Predator consumption rates

The variability in energy density and content exhibited within forage species translated to differences in the amount of daily prey required to adequately support sea lions in the CCE (Figures 4 and 5). Using predicted values of prey energy density and whole-body energy content for anchovy, sardine and squid across sampled size spectra, our models revealed that the daily single-species biomass and counts of prey required to support a single sea lion ranged considerably, from 4.8 to 12.0 kg and from fewer than a 100 to over 70,000 individuals, respectively (Figures 4 and 5).

Specifically, the ranges of daily biomass requirements we found due to intraspecific variation in prey quality were 5–12 kg for anchovy, 6–11 kg for sardine and 9–10 kg for squid (Figure 4). For sardine, sea lions generally require more biomass in the Southern compared to the Central CCE and during spring relative to summer, with seasonal differences depending on maturity stage (Figure 4b). Since anchovy energy density models included interactions between size and season and size and region, trends in consumption rates among anchovy prey groups were more nuanced. For example, approximately twice the biomass of Stage 2 anchovy in the Southern CCE during spring is required compared to Stage 1 individuals in the Central CCE during summer when sea lions target the larger size class (Figure 4a). However, this pattern broke down within the smaller size class (<80 mm SL) where differences in quality, and therefore consumption rates, among prey groups were minimal (Figure 4a). In addition, maturation stage differentially influenced the biomass of fish required by sea lions. For example, within the Southern CCE, where maturity stages could be compared, sea lions require just over 10% more Stage 1 sardine than Stage 2 sardine of a given size during summer, a trend not observed for anchovy (Figure 4a,b).

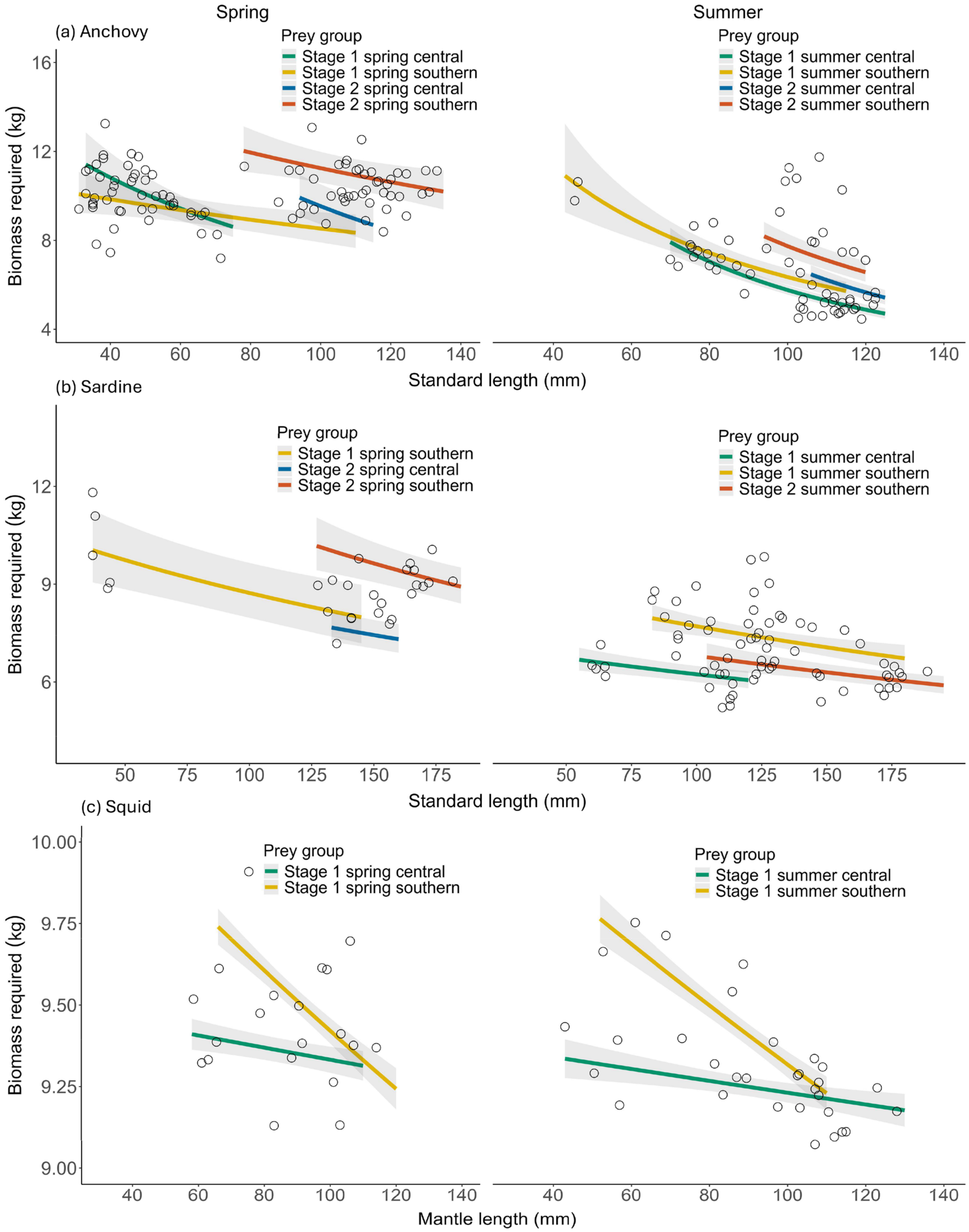
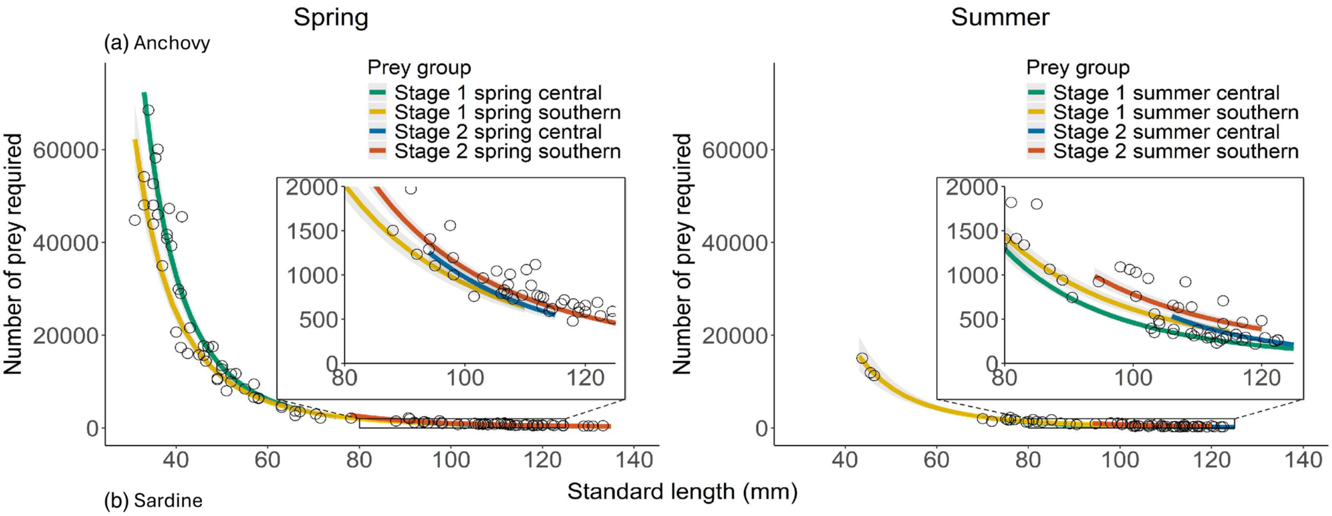


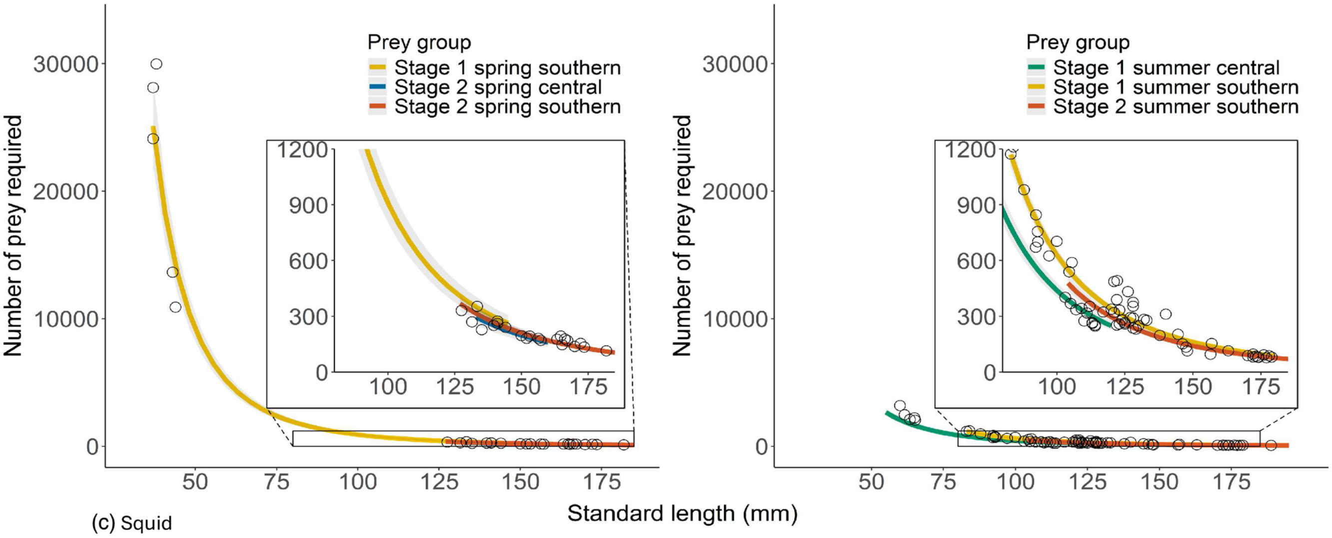
FIGURE 4 Daily prey biomass required to adequately support a non-reproductive adult female California sea lion for (a) anchovy, (b) sardine and (c) squid. Estimates are based on species-specific model predictions of energy density by wet weight (kJ g^{-1} wet wt) across the observed range of prey lengths. Colours represent model predictions for different prey groups defined by combinations of season, region and maturity stage. Maturity stages are classified as Stage 1 (immature) and Stage 2 (intermediate or mature but not yet spawning). Regions correspond to sampling locations in the Central (cool colours) and Southern (warm colours) California Current Ecosystem. Grey shaded areas represent the 95% confidence intervals for predicted daily biomass requirements.

Sea lion daily biomass requirements varied less among squid prey groups compared to fishes, reflecting the low variability in energy density across squid size classes (Figure 4c; Figure S5c). For example, sea lions require at most 5%–7% more squid biomass when foraging on the least energy-rich prey group (i.e. smallest individuals from the Southern CCE in any season) versus the most energy-rich prey groups (i.e. largest individuals from any region or season; Figure 4c).



(a) Anchovy

(b) Sardine



(c) Squid

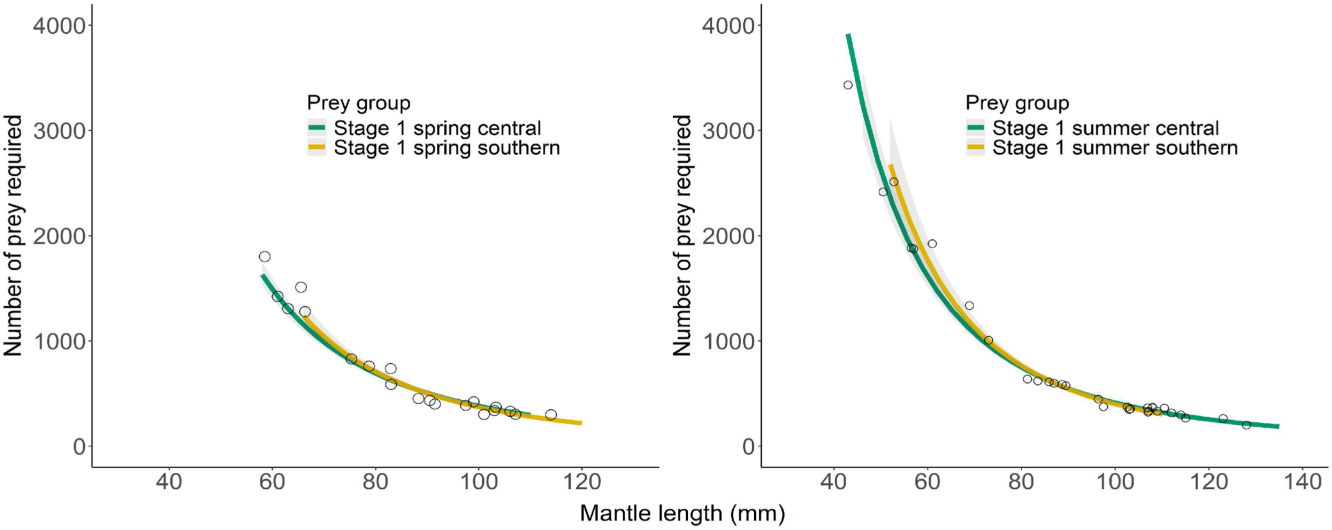


FIGURE 5 Daily number of individual prey required to support a non-reproductive adult female California sea lion for (a) anchovy, (b) sardine and (c) squid. Estimates are based on species-specific model-averaged estimates of energy content across the observed range of prey lengths. Colours represent predictions for different prey groups defined by combinations of season, region and maturity. Maturity is classified as Stage 1 (immature) and Stage 2 (intermediate or mature but not yet spawning). Regions correspond to sampling locations within the Central (cool colours) and Southern (warm colours) California Current Ecosystem. Insets highlight finer-scale differences among prey groups within species at larger prey sizes. Grey shaded areas represent the 95% confidence intervals around model-averaged predictions.

When applying predicted prey energy content values across the sampled size ranges of anchovy, sardine and squid, we found that sea lion consumption rates varied substantially depending on prey size and species. In general, more individuals were required to meet energetic demands when sea lions consumed smaller prey. Anchovy and sardine exhibited the steepest differences in prey requirements across size classes, reflecting their broad predicted energy content ranges (anchovy: 0.7–288.9 kJ; sardine: 1.9–816.7 kJ; Figure 5a,b; Figure S6a,b), while squid showed a narrower pattern within the range of anchovy and sardine requirements (12.3–258.5 kJ; Figure 5c; Figure S6c). Even within narrow size classes, the number of prey required varied due to intraspecific differences in predicted energy content based on categorical factors. For example, up to twice as many anchovy are required daily by sea lions in the spring than in the summer for large size classes, depending on fish maturity stage and sample collection region (Figure 5a). The largest differences we estimated in the number of squid required by sea lions for a given size class were among small individuals: sea lions foraging on squid at 60 mm ML in the Central CCE during the spring require ~1500 individuals, whereas those foraging on squid of the same length in the Southern CCE during the summer require ~1800 individuals (Figure 5c).

4 | DISCUSSION

Prey quality is a key functional trait shaping predator foraging strategies and the maintenance of healthy predator populations (Haug et al., 2002; Ludynia et al., 2010; Spitz et al., 2014; Trites & Donnelly, 2003). We examined factors driving intraspecific variation in the quality of three ecologically important forage species within one of the world's most productive marine ecosystems (Kudela et al., 2008). By integrating high-resolution prey energy data with predator bioenergetics, our study illustrates how fine-scale differences in quality within species can influence predator foraging requirements. In line with previous work (Dessier et al., 2018; Price et al., 2024; Spitz & Jouma'a, 2013), we show that prey quality is not uniform within species, and our study further demonstrates that these differences have measurable implications for predator foraging dynamics.

Prey quality varied markedly among species, with anchovy and sardine exhibiting substantial intraspecific variability driven by size, maturity, season and region. Forage fish sampled in summer within the Central CCE had energy densities up to twice those of individuals collected in spring in the Southern CCE, even at similar sizes. Notably, some smaller fish occasionally displayed energy densities equal to or exceeding those of larger individuals, underscoring the complex interplay between environmental conditions and energy allocation to growth and reproduction. In contrast, squid showed relatively consistent energy density across size classes and environmental gradients. Although all sampled squid were presumed juveniles, forage fish at similar developmental stages displayed pronounced regional and seasonal variation, suggesting that low variability in squid is not merely an artefact of developmental stage. Comparable energy values have also been reported for mature squid elsewhere in the CCE, with variation generally lower than that observed for forage fishes (Price et al., 2024). This pattern points to the potential for broader consistency in squid energetic traits across the CCE. Given their widespread consumption by marine predators in the region, including mammals, seabirds and fishes (Becker et al., 2007; Bizzarro et al., 2017, 2023; Lowry et al., 2022), squid may play a more significant and underrecognized role in supporting predator energy budgets, particularly when high-energy forage fish are seasonally scarce or variable. These results emphasize the importance of evaluating prey quality both across and within species, with attention to ecological scales and conditions.

Across species, body size emerged as the dominant driver of energy content, reflecting the allometric relationship between length and mass in forage fishes (Froese, 2006; Palance et al., 2019) and cephalopods (e.g. Bazzino Ferreri, 2014; Önsoy & Salman, 2022). Larger individuals generally offered greater energetic returns, consistent with mass-dependent patterns reported in other marine prey taxa (Booth, 2020). In sardine and anchovy energy content models, this size dominance substantially reduced the apparent regional, seasonal and maturity-related extremes that were evident in energy density models. Model averaging yielded more conservative estimates and better captured uncertainty, often further dampening the influence of these covariates. Nevertheless, even at similar sizes, prey from the Central CCE in summer contained up to twice the energy content of individuals from the Southern CCE in spring—paralleling spatial and seasonal differences observed in energy density. These findings indicate that while allometric scaling explains broad patterns of energy content, it may obscure biologically important variation driven by environmental conditions and life history. Although body size frequently predicts prey selection (Petchey & Belgrano, 2010; Scharf et al., 2000) and energetic return (Carbone et al., 1999; Ortiz et al., 2023), our results underscore the limitations of size-based assumptions and the need to incorporate additional species-specific traits and ecological context when evaluating prey quality.

Prey quality varied with maturity stage and season in forage fishes, but distinct patterns emerged between species. In anchovy, Stage 2 individuals exhibited reduced energy density across seasons—a pattern that persisted in energy content models. Sardine, by contrast, showed a season-dependent maturity effect in energy density: Stage 2 individuals had lower energy density than Stage 1 in spring, but higher in summer, potentially reflecting reproductive dynamics and subpopulation structure (Hayashi, 1988; Lo et al., 2011; Zwolinski & Demer, 2024). These maturity effects were not statistically significant in the sardine energy content model, suggesting weaker or more uncertain influences after accounting for size. Despite these contrasts, both species showed sensitivity to seasonal and reproductive drivers. Such trends likely reflect differences in reproductive investment (Henderson et al., 2000; Kitts et al., 2004; Smith et al., 1988) and environmental factors such as seasonal upwelling (King et al., 2011), which enhances primary productivity (Deutsch et al., 2021; Eppley et al., 1985; Guo et al., 2014) and drives mesozooplankton peaks (Guo et al., 2014). Notably, prey quality increased for individuals collected in summer, sometimes nearly doubling spring values at a given size, indicating that environmental drivers can amplify energy accumulation beyond reproductive effects.

In aquatic ecosystems, consumer responses to bottom-up forces are often assessed through abundance-based metrics (Bustamante et al., 1995; Conti & Scardi, 2010; Froneman, 2001; Ware & Thomson, 2005). Our results suggest that seasonal productivity may also shape the energetic value of prey species, in addition to their abundance, revealing a potentially overlooked scaling of prey energy density with productivity. In the CCE, the summer upwelling season coincides with predator aggregations, including seabirds and marine mammals (Ainley et al., 2009; Szesciorka et al., 2020; Webb & Harvey, 2015), which are often attributed to increased prey availability. However, our findings indicate that prey quality, particularly energy density, may also be a key driver, with implications for predator energy budgets and ecosystem functioning. Across ecosystems and taxa, synchrony between consumers and their resources is a well-documented phenomenon (Crick et al., 1997; Moore et al., 2022; van Asch & Visser, 2007). Disruptions in this synchrony, whether due to shifts in prey abundance or declines in prey quality, can negatively impact predator populations by altering foraging success and reproductive output (Hipfner, 2008; Hunt Jr et al., 2011; Peñuelas & Filella, 2001). The potential for such mismatches is intensifying with climate change (Edwards & Richardson, 2004; Johansson et al., 2015), making seasonal baselines in prey quality increasingly important for forecasting predator responses.

While seasonal upwelling and fish reproductive cycles likely help explain some of our observed trends, regional differences in prey quality reflect divergent oceanographic conditions north and south of Point Conception, a major biogeographic boundary (Deutsch et al., 2021; Newman, 1979). Stronger upwelling and seasonal productivity in the Central CCE may produce higher-quality prey than the more stable but less productive Southern CCE (Kämpf & Chapman, 2016; King et al., 2011). These regional disparities in forage energetics have important implications for predator–prey dynamics. Oceanic predators, including sea lions, can traverse biogeographic boundaries and access prey from multiple regions (Bizzarro et al., 2023). For example, sea lions from northern breeding colonies routinely forage beyond Point Conception (Antonelis et al., 1990; Melin et al., 2008), potentially obtaining prey of higher quality—particularly in summer, when regional contrasts in anchovy and sardine quality are most pronounced. In contrast, southern colonies typically remain within the Southern CCE (Kuhn & Costa, 2014), where prey quality may be lower during the same period. Such spatial variation, shaped by regional environmental gradients and seasonal dynamics, could influence predator foraging strategies and energetic outcomes, with consequences for both mobile individuals that exploit multiple regions and populations constrained to less productive habitats.

Our results show that under constant prey availability and energetic demands, sea lions targeting a single forage species must adjust the amount of prey consumed according to prey location, season, size and maturity. Even when controlling for prey size, sea lions may need to consume up to twice the biomass or number of individuals within a species to meet daily energetic requirements, reflecting the intraspecific trends in energy density and content described above. Estimated daily biomass needs ranged from 5 to 12 kg for anchovy, 6–11 kg for sardine and 9–10 kg for squid—values comparable to those previously attributed to interspecific prey differences (McHuron et al., 2017), yet here observed within a single species. These findings indicate that variation in prey quality within species can have bioenergetic consequences equivalent to those caused by differences among prey species.

Our results show that the number of prey required by sea lions can differ dramatically, by several orders of magnitude, depending on variation in prey quality within species. For example, sea lions feeding on the smallest, low-energy fish may require tens of thousands of prey per day—a rate likely infeasible for non-filter feeders. By contrast, targeting the largest, high-energy conspecifics substantially reduced required consumption rates. Squid exhibited similar, though less pronounced, size-related trends. Even so, sea lions pursuing higher-quality prey may still need to consume hundreds to thousands of moderately sized individuals daily (Figure 5), a level of demand consistent with marine mammal dive rates and feeding studies (Adachi et al., 2021; Bejarano et al., 2017; McHuron et al., 2020; Rojano-Doñate et al., 2024). Although prey in those studies were generally smaller than those considered here, their findings nonetheless support the feasibility of capture at these daily rates.

Such variability in prey quality can drive compensatory foraging responses by predators, including increased consumption of lower-quality prey or shifts toward more energy-rich alternatives. These shifts may occur across species (e.g. sardine to squid) or within species (e.g. juvenile to adult sardine), depending on the relative availability and energetic value of prey types. While generalist predators such as sea lions may exhibit some dietary flexibility, those with specialized or constrained foraging strategies are particularly vulnerable when prey quality declines (Haug et al., 2002; McMahon et al., 2019). Even generalists face physiological and ecological limits, and energetic mismatches can result in substantial biological consequences. During the 2013–2016 sea lion mortality event (NOAA Fisheries, 2022), a collapse in adult anchovy (MacCall et al., 2016) was reflected in a dietary shift toward more abundant but lower-quality juveniles (Bizzarro et al., 2023; Curtis et al., 2024), which failed to meet the energetic demands of lactating females and growing pups. This case highlights how changes in prey size structure and energy density—in the absence of viable alternatives—can precipitate population-level impacts. When both prey quality and availability decline, even flexible predators may approach critical energetic thresholds, increasing the risk of food web disruption and ecosystem instability.

Our findings highlight how intraspecific variation in prey quality can shape predator responses, yet these effects operate within a broader energetic landscape. The feasibility of any response depends on predator traits, such as dietary breadth and foraging flexibility, as well as ecological and physiological constraints that influence net energy gain—including prey availability, foraging and digestive costs and temporal shifts in metabolic needs (Booth et al., 2023; McHuron et al., 2017). For instance, we assumed prey-specific foraging costs were static and did not explicitly account for variation in predator effort across prey types. In reality, factors like prey size, behaviour and antipredator defences (e.g. schooling, mobbing, evasive manoeuvres; Caro et al., 2004; Magurran, 1990; Palmer & Packer, 2021) elicit variable energetic demands. Larger prey may require longer handling times (Bindoo & Aravindan, 1992; Bowen et al., 2002; Cansse et al., 2020; Hoyle & Keast, 1987), whereas sustained pursuit of smaller prey can increase overall energy expenditures (Adachi et al., 2021). We also used a commonly cited digestive efficiency value for sea lions (Costa, 1986; McHuron et al., 2017), though assimilation rates can vary across prey types and nutrient profiles (Costa & Williams, 1999; Rosen & Trites, 2000). For example, fish generally yield higher digestive efficiency than invertebrates (Booth et al., 2023). Prey quality itself could be more fully described by macronutrient profiles, including lipids, proteins and carbohydrates (Van Pelt et al., 1997), but this was outside the scope of our study.

Additionally, we assumed static prey availability and a single-species diet, whereas sea lions often consume multiple species within a single foraging trip and adapt to seasonal and spatial prey shifts (Lowry et al., 2022; McHuron et al., 2017). Such variation influences dietary choices and associated foraging costs. Our estimate of energy requirements also did not account for individual variation linked to predator life stage, season or reproductive status (Hellgren et al., 1989; McHuron et al., 2017; Robbins et al., 2004), which may drive shifts in macronutrient targets or energy intake. Finally, while we measured seasonal variation in prey quality, we did not incorporate year effects. Samples spanned 2 years of extreme marine heatwave conditions in the CCE, followed by 3 post-heatwave years. Marine heatwaves can alter prey quality (von Biela et al., 2019), and some unexplained variation may reflect differences in environmental conditions among years. Capturing such effects will require expanded temporal and spatial sampling, including a range of size classes, maturity states and collection regions across multiple seasons. Given the boom-and-bust cycles of forage species (Chavez et al., 2003), this remains a challenge, but increasing sample size per season and diversifying collection locations could improve resolution in future research.

5 | CONCLUSION

Understanding intraspecific variation in prey quality is critical for evaluating energy transfer to top predators. Because many predators access a range of prey sizes or specialize in particular size classes, accounting for variation along size gradients is essential for interpreting foraging ecology and calibrating ecosystem models. Although our study focused on a coastal upwelling system, the approach is broadly applicable, particularly in ecosystems characterized by strong seasonal cycles, dynamic life histories or environmental variability. Energy is a universal currency linking biological and ecological processes; thus, incorporating intraspecific fluctuations in prey quality will enhance predictions of energy flow through food webs. As climate change and resource exploitation intensify, examining predator–prey dynamics through the lens of functional traits and energetic trade-offs will remain essential for predicting predator responses and assessing ecosystem resilience.

AUTHOR CONTRIBUTIONS

Stephanie E. Nehasil conceived the study, designed the methodology, collected and analysed the data and led the writing of the manuscript. Carolyn M. Kurle contributed to methodology development, interpretation of results, supervision, funding acquisition and writing and editing. Emmanis Dorval and Juan P. Zwolinski contributed to methodology, data analysis and interpretation of results. All authors contributed critically to manuscript drafts, approved the final version for publication and agree to be accountable for all aspects of the work they contributed, ensuring that any questions related to accuracy or integrity are appropriately investigated and resolved.

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CONFLICT OF INTEREST STATEMENT

The authors of this manuscript have no conflict of interest.

DATA AVAILABILITY STATEMENT

Data available from UC San Diego Library Digital Collections: https://doi.org/10.6075/J0P84C3T (Nehasil et al., 2025).

STATEMENT OF INCLUSION

Our data were collected in waters off the coast of California, USA, in collaboration with local fishers, scientists from the California Department of Fish and Wildlife, and federal scientists from the National Oceanic and Atmospheric Administration. This study also included an outreach component in collaboration with Ocean Discovery Institute, a local non-profit that engages youth from an underserved community in San Diego, CA.

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SUPPORTING INFORMATION

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

Table S1. Summary of prey samples and length ranges by season, region and maturity stage for anchovy, sardine and squid collected in the Central and Southern CCE.

Table S2. Candidate linear and generalized linear models predicting energy density for anchovy, sardine and squid as a function of prey length, season, region and maturity stage.

Table S3. Candidate generalized linear models predicting energy content for anchovy, sardine and squid as a function of prey length, season, region and maturity stage.

Table S4. Prey groups used for model predictions based on combinations of categorical factor levels tested in energy density and energy content models for anchovy, sardine and squid.

Figure S1. Length-frequency distributions of anchovy, sardine and squid consumed by California sea lions in the CCE, estimated from hard part measurements derived from scat samples using species-specific regressions.

Figure S2. Dry-to-wet weight regression for squid specimens used to estimate energy density and biomass consumption by California sea lions.

Figure S3. Factors contributing to intraspecific variation in energy density for anchovy, sardine and squid in the CCE.

Figure S4. Factors contributing to intraspecific variation in energy content for anchovy, sardine and squid in the CCE.

Figure S5. Model-predicted energy density for anchovy, sardine and squid by season, region and maturity stage across observed prey lengths.

Figure S6. Model-averaged energy content for anchovy, sardine and squid by season, region and maturity stage across observed prey lengths.

Methods S1. Additional model diagnostics, selection criteria and prediction procedures for energy density and energy content models, including species-specific prey group construction.

Results S1. Equations and parameter structures for the best-supported energy density and energy content models by species, including predictor variables used to estimate model parameters.

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