Assessing the influence of traits and environment on the nutritional value of small pelagic species in the California Current

by

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Abstract

Marine food webs are increasingly disrupted by climate change, with implications for fisheries management. Understanding how changing ocean conditions are likely to affect the nutritional quality of prey species that predators depend on could assist with predicting population responses. Here we examine the extent to which environmental conditions and life history traits (body size, maturity status, and sex) are linked to variation in the nutritional traits of five small pelagic species varying in habitat use, feeding behaviour, size, and degree of importance as prey for top predators in the California Current Large Marine Ecosystem (CCLME). Boreal clubhook squid (*Onychoteuthis borealijaponica*), northern anchovy (*Engraulis mordax*), bigfin lanternfish (*Symbolophorus californiensis*), market squid (*Doryteuthis opalescens*), and pyrosomes (*Pyrosoma atlanticum)* were collected during two summer trawl surveys conducted by the National Oceanic and Atmospheric Administration in 2021. Specimens were processed for energy density (ED) via bomb calorimetry and for % lipid, % protein, and ED via proximate composition analysis, providing moisture values as well. Collection sites in the north and south regions of the CCLME varied in upwelling, sea surface temperature, and chlorophyll-a, allowing us to compare the nutritional values of specimens from two different environments. We used Bayesian multiple linear regression analysis with MCMC estimation to analyse the relationships among nutritional metrics, regions, and traits. Region of collection had little effect on the nutritional value of specimens—a result that was consistent across the species we sampled. Overall, pyrosomes had significantly lower ED and % lipid than the squid and fishes. Both ED and % lipid increased significantly with mass across the five species. However, species identity modulated this relationship; both ED and % lipid increased more slowly with increasing mass in boreal clubhook squid, market squid, and northern anchovy than in bigfin lanternfish. There was no overall effect of specimen mass on % protein, except in boreal clubhook squid, for which % protein increased with larger size. Pyrosomes and boreal clubhook squid had significantly lower % protein than all other species. As expected, there were significant, positive relationships between specimen body size and total energy (i.e., energy density multiplied by specimen mass), total lipid, and total protein. However, the strength of the relationships between size and total energy and total lipid increased with mass at a greater rate for the fishes than for the squids. We found that ED estimated from proximate composition was generally lower (especially for squids), but tightly correlated with ED from bomb calorimetry for all species (and our results provide conversion values that can be used for cross-study comparisons). The relationships we found between species, size, and nutritional metrics may provide generalizable insights useful for predicting foraging behaviour of top predators and for fisheries management as food webs adjust to climate change.

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Chapter 1

1. Introduction

Optimal foraging theory (OFT) provides a framework for understanding predator-prey relationships and food web interactions within dynamic environmental systems (Charnov 1976; Townsend & Winfield, 1985). OFT assumes that predators will seek the most efficient way to obtain energy and nutrients, selecting prey based on relative profitability or maximal net gain. Profitability can be measured by quantifying costs (i.e. foraging-related risks, competition, and energy expenditures) and benefits (i.e. energetic and nutritional gains) relative to particular species, their prey, and the abiotic and biotic environment (Raubenheimer et al., 2009; Townsend & Winfield, 1985). Thus, monitoring the value and circulation of energy and nutrition can aid in explaining and predicting shifts in species distributions and abundance—supporting fisheries management as environmental conditions change (Friedman et al., 2018; Petrik et al., 2020; Schmidt et al., 2012).

An organism's nutritional status results from its ability to acquire energy and nutrients (such as lipids and proteins) within a complex milieu of physical environments and associated biotic interaction (McGill et al., 2006; Raubenheimer, 2009). In ocean environments, the nutritional content of organisms' tissues can vary both within and among species as a function of life history traits and the environmental conditions experienced by individuals (Anthony et al., 2000; Fisher et al., 2020; Litz et al., 2010; Wilder et al., 2010). In pelagic (i.e., open ocean) environments, variability in nutritional quality within species has been associated with ontogeny and feeding modes in squid, and with trophic level dietary changes in northern anchovy (Brodeur et al., 2019; Burning et al., 2022; Gong, 2020; Suntsov & Brodeur, 2008). Lipid content in pelagic invertebrates and fishes has been found to vary inter-annually, by season, with sea surface temperature, with upwelling, and by location (Deng et al., 1976; Fisher et al., 2020; Hellessey et al., 2018; Litz et al., 2010; McKinstry et al., 2013; Miller et al., 2017). The energy density (ED) of pelagic vertebrates and invertebrates can vary annually among species **(**Beaubier & Hipfner, 2013; McKinstry et al., 2013) and within species by month, size, reproductive status, and location (Anthony et al., 2000; Price et al., 2024). Given the range of traits and environmental factors that can affect the nutritional value of marine species, fine-scale information from individuals is needed to understand inter- and intra-species variation in nutritional content in open ocean systems.

Understanding drivers of variability in the nutritional content of pelagic species is especially important, given links between nutritional composition of prey and the body condition, abundance, and distribution of predators foraging in open ocean systems. Nutrient acquisition for both prey and predators is affected by complex food web dynamics between forage fish and other commercially and ecologically important predator fish species (Engelhard et al., 2014). For example, high diet electivity (i.e. consuming prey at greater ratios than would be expected based on abundance) has been linked in albacore tuna to high ED and protein, suggesting that nutritional quality may influence top predators' foraging choices and locations (Gleiber et al., 2024a). Forage fish body condition (measured as ED in sardines) has been linked to environmental conditions affecting recruitment, and researchers concluded that measuring biochemical indicators (i.e., nutritional value) is important to predicting predator consumption (Rosa et al, 2010). In turn, the quality (measured as ED) of mesozooplankton has been associated with recruitment of small pelagic fish and impacts on population dynamics amongst fishes at higher trophic levels (Dessier et al., 2018). Despite these examples, much more is known about how prey availability and abundance affect ocean food web dynamics than about how prey quality influences food web dynamics (Free & Jensen, 2021; Otero & Hidalgo, 2023). This imbalance can be rectified through research that fills gaps in nutritional values for marine species (Gleiber et al., 2024b) and identifies the mechanisms that influence how nutritional quality affects foraging and food web relationships (Rosa et al., 2010).

The California Current Large Marine Ecosystem (CCLME) is a diverse and productive marine ecoregion well-suited to examining the connection between environment and nutritional characteristics of small pelagic species (SPS) that are crucial forage for top predators in the system. The CCLME extends along the Northeast Pacific Ocean from southern British Columbia, Canada to Baja California, Mexico. The northern portion of the region shows relatively high productivity compared to the south (Hickey & Banas, 2008). Greater nutritional density (i.e., higher lipid content) is associated with lower sea surface temperatures (Litz et al., 2010) and greater upwelling in the north, which increases the transport of nutrients to surface waters from lower in the water column (Jacox et al., 2019). If regional differences in environment drive variation in nutritional content for SPS, then there may be energetic consequences for predators that forage on SPS in particular regions and/or under certain environmental conditions.

Here, we quantified and compared the energy, lipid, and protein content (collectively 'nutritional value') of five pelagic species that are abundant throughout the CCLME and that provide forage for several top predators (Friedman et al., 2018; Szoboszlai et al., 2015). We also compared ED values derived from direct bomb calorimetry measurement to those calculated through proximate composition analysis using % lipid and % protein values. Our goal was to characterise potential drivers of inter- and intra-specific variability in nutritional value for these taxa, focussing on two questions: 1) How does nutritional value vary between the northern and southern regions of the CCLME? 2) How do prey life history traits (e.g., body size, maturity status, and sex) affect the degree of variability in nutritional value within and among species? We predicted that SPS in the northern region of the CCLME would have higher ED, % lipid, and % protein than those in the southern region because low sea surface temperature and strong upwelling are more pronounced in the northern region—facilitating more nutritious zooplankton and generally higher nutrient availability to SPS (Gómez-Ocampo et al., 2018; Jacox et al., 2019). We also predicted that larger overall body size (length and mass) would be positively correlated with higher ED and % lipid, as seen in directly-related literature (Ball et al., 2007; Payne et al., 1999). Furthermore, organisms with larger gapes—often a function of body size—can consume larger and more nutritionally dense organisms (Barnes et al., 2021; Gong et al., 2018; Scharf et al., 2000) and research has shown food size can affect energy acquisition independent of nutritional content (Queiros et al., 2019). However, because protein has been negatively correlated with ED in some small pelagic species (Van Pelt et al., 1997), we predicted that % protein may not increase even if % lipid and ED were to increase. Finally, we predicted that mature females may have higher ED and % lipid than mature males because female gonads have been associated with especially high lipid content in fish (Dhurmeea et al., 2018). Clarifying the relative impact of environmental factors and traits on nutritional content of SPS will enhance understanding of food web dynamics and help predict how top predators may forage in response to environmental conditions.

2.0 Materials and Methods

2.1 Sample and environmental data collection

Samples of small-bodied coastal pelagic species were collected in the CCLME during annual scientific surveys conducted by the National Oceanic and Atmospheric Administration (NOAA; Figure 1). One set of samples came from the Southwest Fisheries Science Center Fisheries Resources Division (SWFSC FRD) annual summer survey from July 6 to October 15, 2021, where surface trawls (max depth ~30 m) were conducted at night with a Nordic 264 rope trawl targeting schools of pelagic species identified by scientific echosounders (Southwest Fisheries Science Center, 2021; Zwolinski et al., 2019). A second set of samples came from the Northwest Fisheries Science Center Juvenile Salmon Ocean and Ecosystem Survey (JSOES), which sampled coastal pelagic species in late May and June of 2021 using a Nordic 264 pelagic rope trawl with a fine mesh liner during daytime surface trawls (Daly et al., 2017; Daly et al., 2021). Specimens from both surveys were frozen in zip-closure clear plastic bags, separated by haul and roughly by species, and stored at -20°C or colder until analysed.

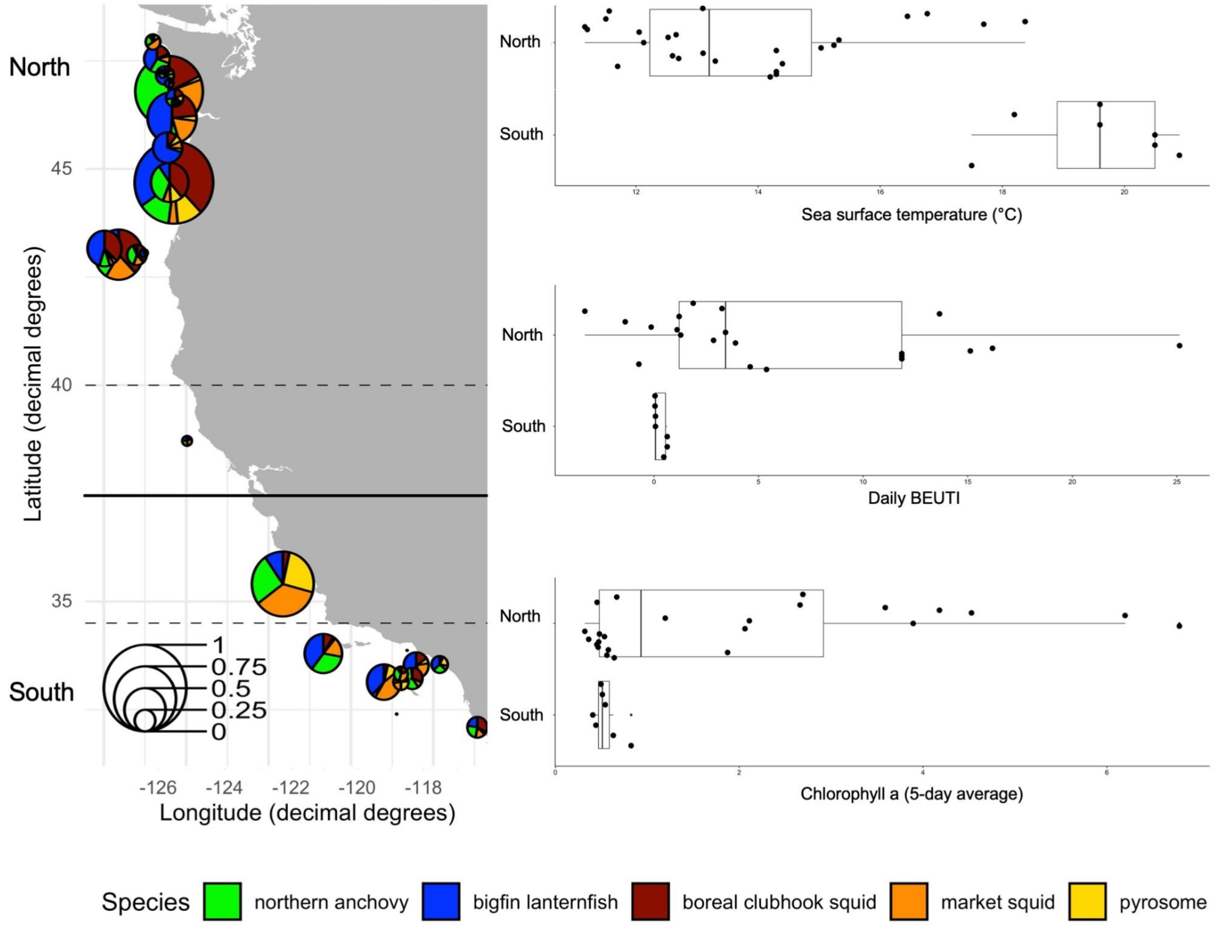

Figure 1. GPS locations of Northwest Fisheries Science Center Juvenile Salmon Ocean and Ecosystem Survey (JSOES) and Southwest Fisheries Science Center Fisheries Resources Division (SWFSC FRD) trawls from which specimens analysed in this study were collected and the sea surface temperature, biologically effective upwelling transport index (BEUTI; Jacox et al., 2018) and chlorophyll-a conditions at time of collection displayed by region. Size of pies is proportional to the number of individuals analysed from the respective haul. Largest haul n = 22 and smallest haul n = 1. Colour indicates species. Black dashed lines represent the commonly used boundaries between south-and-central (latitude 34.5000°N) and central-and-north (latitude 40.0000°N). Hauls shown at the edges of the central region were combined with the region (north or south) closest to them, so the regional boundaries in our study extended south to

38.7123°N for the north region and north to 35.4043°N for the south region. The solid black line highlights the division between our north and south regions.

Five SPS were selected for nutritional analysis: boreal clubhook squid (*Onychoteuthis borealijaponica,* n = 23), northern anchovy (*Engraulis mordax,* n = 31), bigfin lanternfish (*Symbolophorus californiensis,* n = 32), market squid (*Doryteuthis opalescens,* n = 35), and pyrosomes (*Pyrosoma atlanticum,* n = 5*)* (Table 1). In addition to being abundant throughout the CCLME, these species were selected to: i) include diverse life histories related to habitat use and feeding behaviour, ii) cover a range of SPS sizes, and iii) encompass differing degrees of importance as prey for albacore and other top predators in the CCLME (Friedman et al., 2018; Gleiber et al., 2024a; Szoboszlai et al., 2015). Species represented a range of IUCN statuses, and both commercial and no commercial importance.

Table 1. Key traits for study species. Five trait categories were considered: phylogenetic classification, habitat position, behaviour (Gleiber et al., 2022; 2024b), and example prey selectivity (over-representation in diet relative to availability) by a pelagic top predator (Gleiber et al. 2024a). Species represented a range of IUCN statuses, and both commercial and no commercial importance.

Broad Grouping	**Scientific Name**	**Common Name**	**Vertical Habitat**	**Horizontal Habitat**	**Aggregation Behaviour**	**Trophic Level**	**IUCN Status**	**Fishery**	**Selection by albacore**
Fishes	*Engraulis mordax*	Northern anchovy	epipelagic	coastal	schooling	3.1	Least Concern	commercial	high, variable
Fishes	*Symbolophorus californiensis*	Bigfin lanternfish	mesopelagic, epipelagic, & bathypelagic	oceanic	schooling	3.1	Least Concern	none	low
Squids	*Onychoteuthis borealijaponica*	Boreal clubhook squid	mesopelagic, epipelagic	oceanic	schooling	4.5	Data Deficient	commercial	high
Squids	*Doryteuthis opalescens*	Market squid	epipelagic	continental shelf	schooling	3.74	Least Concern	commercial	low, absent
Tunicates	*Pyrosoma atlanticum*	Pyrosome	epipelagic	oceanic	schooling or solitary	1.5 (Schram et al., 2020)	Not Evaluated	none	not consumed

Specimens were divided between north and south regions using latitudinal boundaries between oceanographic regions proposed by Sakuma et al. (2016). A small number of northern anchovy and pyrosomes specimens collected at the edges of the central region proposed by Sakuma et al. 2016, were combined with samples from whichever region (N or S) was closest to them, thereby increasing sample sizes while preserving characteristics of the defined regions. Thus, “north” was defined as 38.7123–47.9031°N and “south” was defined as 31.8359–35.4043°N.

We used three metrics to compare the environmental conditions in the north and south regions of the CCLME at the time of specimen collection. On the SWFSC FRD, SST was recorded during each haul using conductivity-temperature-depth probes. On the JSOES, the Daily SST was extracted from Multi-scale Ultra-high Resolution (MUR) for the high-resolution (0.01 x 0.01 degrees) grid cell associated with the day and location of the hauls. Biological Effective Upwelling Transport Index (BEUTI) was extracted from the Upwelling Indices website (Jacox et al., 2018), selecting the nearest degree latitude to each haul for all specimen collection days relevant to our study. European Space Agency (ESA) surface chlorophyll-a concentrations were extracted as five-day mean data (centred around the closest available day to the haul) from ERDDAP using the nearest possible GPS location for each haul. Extraction from ERDDAP was done in R, using the rerddapXtracto (v1.1.4; Mendelssohn, 2022) and rerddap (v1.0.3; Chamberlain, 2023) packages. All three environmental metrics were compared between regions using Student's t-tests in R with the rstatix (v0.7.2; Kassambara, 2023) package. Given our limited sample sizes (Table 2), these metrics were not used to explore environmental drivers directly, but to show the range in each environmental metric for specimens that comprise our northern and southern regional groupings.

Table 2. Mean and range of size (length and weight) for specimens of each species by region of collection in the CCLME. All lengths were measured to the nearest mm. Standard length measurements are provided for fish species and mantle length for squids. For pyrosomes, standard length is equivalent to total length. Standard deviations are in parentheses following the mean.

			Standard length/mantle length (mm)		**Whole body wet weight mass (g)**	
Species	**Region**	**n**	**Range**	**Mean**	**Range**	**Mean**
bigfin lanternfish	North	17	68.5–106	91.3 (11.3)	3.4–14.7	8.9 (3.3)
	South	15	47–93	68.7 (13.8)	1.1–9.0	4 (2.18)
boreal clubhook squid	North	7	87–200	121.1 (39.1)	17.9–148.6	51.5 (46.4)
	South	16	41.5–155	112.4 (26.8)	3.2–84.0	38.8 (22.4)
market squid	North	14	41–114	81.9 (21.7)	3.4–36.1	16.6 (9.0)
	South	21	46–134	98.5 (30.5)	6.4–46.0	27.5 (15.6)
northern anchovy	North	21	80–155	128.6 (18.4)	4.6–42	22.2 (8.8)
	South	10	92–113	105.4 (6.6)	7.1–11.2	10.4 (1.8)
pyrosome	North	2	37–39	37.9 (1.0)	1.0–1.5	1.3 (0.4)
	South	3	99.9–143	116 (23.8)	4.7–8.5	6 (2.2)

2.2 Sample processing and analysis

2.2.1 Morphometrics

Specimens of each species were semi-thawed to permit manipulation of their anatomy, then measured (standard length, total length, body height (i.e., excluding fins, etc.), total height; mantle length for cephalopods; to the nearest mm) while remaining cold on ice blocks. For market squid, boreal clubhook squid, and northern anchovy, we assigned sex and maturity status by visually inspecting reproductive organs. These categorizations were not possible for the two remaining species.

2.2.2 Drying and homogenisation

To prepare samples for nutritional analysis, whole individuals were either oven dried (at JSOES) or freeze dried (at SWFSC FRD), depending on the facility's equipment. Individuals were weighed (nearest 0.0001 g), refrozen at -80°C, and placed on a freeze-dryer (FreeZone 2.5L, Labconco, USA) in Whirl-Pak sampling bags or placed in a desiccating oven directly. Specimens >~9 g wet weight were dried individually. Specimens <~9 g wet weight were grouped with 2–6 similarly-sized individuals from the same haul to ensure enough dry tissue for all analyses (so one 'sample' for these small specimens consisted of all the combined individuals). Freeze drying continued for 3–7 days, until a consistent dry weight was achieved. Samples were dried at 60°C in a desiccating oven for 2–3 days, until reaching a consistent dry weight. Dry weights were recorded and % moisture calculated through comparison to the original wet weight. We then milled whole dried specimens using an IKA Tube-mill 100 (with 40 mL and 100 mL milling chambers) at 25000 rpm for 30 second intervals until powder-like consistency was reached. The mill chamber was wiped with Kimwipes and 95% ethanol between samples to avoid cross-contamination.

2.2.3 Bomb calorimetry for ED

Homogenised and dry tissue was pelleted for bomb calorimetry with a Parr pellet press using a 10 mm die. We examined the press for expressed oils and cleaned the press with 95% ethanol between specimens. If any residual oil was observed on the press after pelleting, the pellet was discarded, and subsequent material was pelleted at a lighter pressure to avoid extracting oils. Because bigfin lanternfish tissue had very high oil content, we hand-rolled (with gloves) these pellets rather than using the pellet press. Pellet sizes varied among species to target a consistent change in temperature during combustion (Delta K = 0.1ºC, 0.25–0.35 g for bigfin lanternfish, 0.35–0.45 g for market squid and boreal clubhook squid, and 0.35–0.40 g for northern anchovy).

We calculated energy density by combusting pellets either in: i) a semi-micro calorimeter with a water trap (6725, Parr Instruments, United States; Hatfield Marine Science Center, Oregon State University), or ii) in an isoperibol calorimeter without a water trap (C6000, IKA, Germany; Scripps Institution of Oceanography, University of California San Diego). Depending on ambient room temperature, combustion reactions in the IKA calorimeter were run at either 22ºC or 25ºC. Both types of calorimeters used two decomposition vessels that were separately calibrated at each reaction temperature. We checked calibrations at the beginning of each day by running 2–4 combustions of benzoic acid standard. Two replicates of each specimen were run, then averaged together to calculate the energy density value for the sample. If the first two replicates differed by >8%, a third replicate was run. To ensure the accuracy of energy density measurements collected throughout the day, we ran a benzoic acid standard every 10 sample runs.

2.2.4 Proximate composition for lipid and protein

Proximate composition analysis was conducted on specimens examined for energy density using the remaining dried, homogenised sample. We used Association of Official Analytical Chemists (AOAC, 2002) standard methods to determine percent protein, lipid, and dry matter. We did not calculate carbohydrate percentage because carbohydrate is negligible in our focal species. We measured lipid, dry matter, and ash gravimetrically in borosilicate glass test tubes using the same tissue for the entire process. We determined the total lipid content of each specimen gravimetrically, starting with ~0.50 g dry weight of prepared materials. For lipid extraction we used a solvent of 1 mL hexane per sample. A Leco C/N Analyzer was used to determine protein content from C/N ratios. We used 0.005–0.007 g of dry homogenised tissue for most specimens; however, to get a more homogeneous sample for bigfin lanternfish, which has very high oil content, we subset tissue for protein analysis following lipid extraction rather than using the initial tissue sample. A conversion factor of 6.25 was used to calculate crude protein from nitrogen. We measured residual moisture content after extracting lipids by heating lipid-free tissue overnight in an oven set to 40°C. We then placed the dry tissue in a 110°C furnace overnight to determine the ash content.

2.2.5 ED calculated from proximate composition

Although bomb calorimetry is commonly used for calculating ED, it can also be estimated for animal tissue by converting lipid and protein to their energy equivalents (Weil et al., 2019). We compared estimates of ED from bomb calorimetry and proximate analysis in order to generate conversion equations that would facilitate cross-study comparison when different methods had been used for determining ED. ED values were calculated from our proximate composition values for % wet weight lipid and % wet weight protein using nutrient-to-energy conversion factors of 39.75 kJ/g for lipid and 23.64 kJ/g for protein. Because Sinclair et al., (2015) focussed on similar small pelagic species, their conversion factors were used (but modified to change cal/100g to kJ/g). The values are at the upper range of the conversion factors suggested for fish by Brett (1995) (cited in Weil et al., 2019). Since our bomb calorimetry was done in two locations, with different machines and under different ambient conditions, running proximate composition on all samples in a single lab provided a common currency for ED. We therefore used ED derived from proximate composition in the statistical analyses outlined below.

2.2.6 Statistical analysis

We first used linear regressions to explore the strength and direction of relationships between the three nutritional metrics (ED, % protein, % lipid) for each species, between the three nutritional metrics (ED, % protein, % lipid) and % moisture for each species, between each nutritional metric and organism length and mass, and to compare the bomb calorimetry and proximate composition results by species.

We then used a Bayesian framework to evaluate a linear model with MCMC estimation to examine the effect of region (categorical; two groups), species (categorical; five groups), and wet weight mass (continuous) on log transformed ED, % lipid, and % protein (three models; one per response variable). The nutritional metrics were log transformed because the residuals were not normally distributed. Each model was fit using the R package 'rstan' (v2.21.8; Stan Development Team, 2023) to interface with Stan72 in R, and model outputs were summarised using the 'bayesplot' package (v1.10.0; Gabry & Mahr, 2022). An interaction term of mass*species was included to test our hypothesis that there could be species-specific mass-to-nutritional-metric relationships based on the differing life history and morphology. An interaction term of region*species was included because we predicted that species with specific traits would have different ED, % lipid, and % protein. All statistical analyses were done in R Studio (version 4.3.0) with general data manipulation and processing done with the 'tidyverse' family of R packages (v2.0.0; Wickham et al., 2019). This framework is suitable for data sets such as ours that have multiple covariates but a limited sample size (each of our nutritional metric models used 15 predictors on a sample size of 126).

MCMC sampling for each model was done over four chains using 1000 iterations each. From the posterior distribution generated for each coefficient in the model, we calculated: probability of direction (pd), median, the 95% CI (credible interval), high HDI (highest density interval) and the low HDI, and ROPE (region of practical equivalence). ROPE limits were set separately by each nutritional metric model. The pd is the probability of a negative or positive effect for each predictor (Makowski et al., 2019). The median represents the median effect size of each parameter over the posterior distribution. The high HDI and the low HDI bound the range around the median for each predictor, where 95% of the posterior distribution values are located (the 95% CI). The ROPE is a small range around zero, where greater than 1% of the estimated values of a predictor would have to fall for the effect to be considered non-significant; Thus, if the % in ROPE (ROPE%) is less than 1%, the effect is considered significant. So, to follow a parametric example, if ROPE is equivalent to the alpha-value in parametric statistics, then %ROPE is equivalent to p-value (except in this case a significant %ROPE would be <1%, while a significant p-value would be ≤0.05).

3.0 Results

3.1 Comparison of energy density estimation methods

We found that ED calculated from proximate composition values were tightly correlated with ED from bomb calorimetry for northern anchovy, bigfin lanternfish, boreal clubhook squid, and market squid (Figure 2; northern anchovy p = < 2.2e-16, bigfin lanternfish p = < 2.2e-16, boreal clubhook squid p = 7.776e-08, market squid p = 3.37e-08). The fishes (northern anchovy R^2 = 0.97, bigfin lanternfish R^2 = 0.98) showed greater correlation than did the squids (boreal clubhook squid R^2 = 0.75, market squid R^2 = 0.64), and except for bigfin lanternfish, ED values tended be lower for proximate estimation than for bomb calorimetry determination. We did not include pyrosomes here because they were too low in ED and too high in inorganic matter to accurately conduct bomb calorimetry following the methods used for our other species and because the sample size (n = 5) was too low for meaningful comparison.

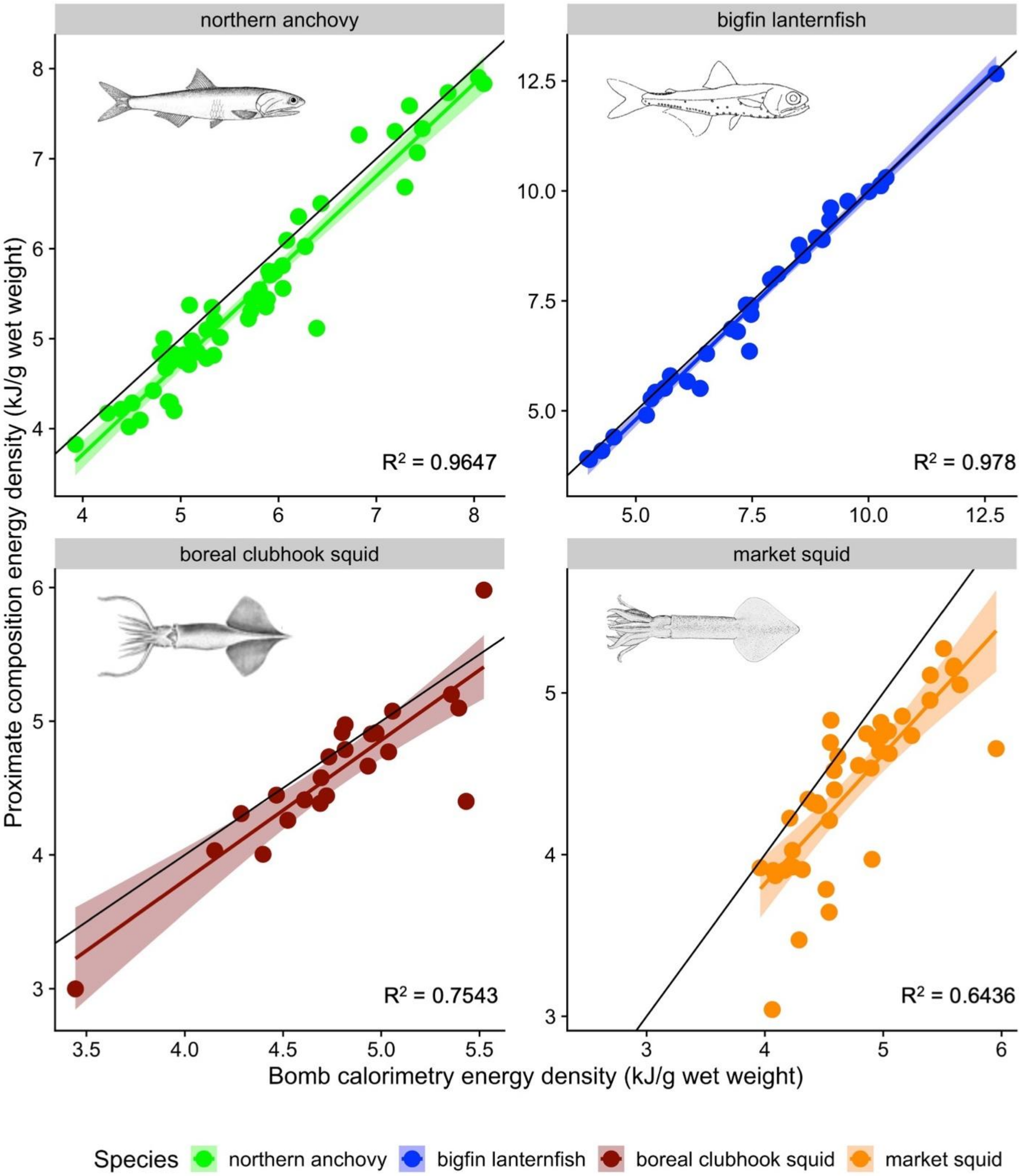

Figure 2. Relationship between energy density (ED) estimated from proximate composition analysis and ED derived from bomb calorimetry for four Pacific marine species. The black line represents a 1:1 ratio for each species. Regression equations, p-values, and sample sizes are as follows: northern anchovy $y = -0.41 + x$, $p = < 2.2e\text{-}16$, $n = 31$; bigfin lanternfish $y = -0.36 + x$,

$p = < 2.2e\text{-}16$, $n = 32$; boreal clubhook squid $y = - 0.39 + x$, $p = 7.776e\text{-}08$, $n = 23$; market squid $y = 0.62 + 0.8\,x$, $p = 3.37e\text{-}08$, $n = 35$.

3.2 Environmental conditions in each CCLME region

We identified differences in the environmental conditions associated with our specimen collections in the northern and southern parts of the CCLME system, supporting our focus on inter-region ocean conditions as a potential driver of nutritional value. In particular, SST was more variable and significantly ($t(15.1) = 9.34$, $p<0.001$) lower in the north (average: 13.8°C, range: 11.2°C to 18.4°C) than in the south (average: 19.5°C, range: 17.5°C to 20.9°C). Daily BEUTI was higher and more variable in the north (average: 7.25, range: -3.31 to 25.13), than in the south (average: 0.28, range: 0.05 to 0.64) ($t(23.8) = 3.60$, $p<0.002$). The chlorophyll-a five day average was higher and more variable in the north (average: 1.99, range: 0.32 to 6.79) than in the south (average of 0.55, range: 0.41 to 0.82) ($t(20.2) = 3.69$, $p<0.002$).

3.3 Predictors of ED, % lipid, and % protein

Despite environmental differences between our northern and southern sampling areas in the CCLME, region of collection had little effect on the nutritional value of specimens, an effect that was consistent across the species we sampled (Table 3). Overall, pyrosomes had significantly lower ED than the squid and fishes we examined (pd = 100%; Median = -2.15, 95% CI [-2.47, -1.83]; 0% in ROPE). ED increased significantly with mass across the five species we examined (pd = 100%; Median = 0.39, 95% CI [0.29, 0.49]; 0% in ROPE). However, species identity modulated this relationship, with ED increasing more slowly with increasing mass for boreal clubhook squid (pd = 100%; Median = -0.26, 95% CI [-0.40, -0.14]; 0% in ROPE), market squid (pd = 100%; Median = -0.32, 95% CI [-0.43, -0.20]; 0% in ROPE), and northern anchovy (pd = 100%; Median = -0.25, 95% CI [-0.41, -0.09]; 0% in ROPE) compared to the baseline species, bigfin lanternfish.

The same predictor variables had an effect on lipid as on ED in the above model. Percent lipid was significantly lower in pyrosomes than in all other species (probability pd = 100%; Median = -1.91, 95% CI [-2.83, -1.01]; 0% in ROPE). Across all species % lipid increased significantly along with mass (pd = 100%; Median = 0.94, 95% CI [0.66, 1.22]; 0% in ROPE). For the same three species as in the ED model, species identity modulated the % lipid to mass relationship. In boreal clubhook squid (pd = 100%; Median = -0.84, 95% CI [-1.20, -0.47]; 0% in ROPE), market squid (pd = 100%; Median = -0.95, 95% CI [-1.28, -0.61]; 0% in ROPE), and northern anchovy (pd = 98.92%; Median = -0.56, 95% CI [-1.02, -0.07]; 0.74% in ROPE) % lipid increased at a slower rate with increasing mass compared to the baseline relationship of % lipid to mass in bigfin lanternfish.

There was no overall effect of mass on % protein across all species. However, one species modulated the effect of mass: In boreal clubhook squid % protein increased with mass at a significantly higher rate compared to the other species (pd = 99.88%; Median = 0.12, 95% CI [0.05, 0.19]; 0% in ROPE). Compared to all other species, pyrosomes (pd = 100%; Median = -2.31, 95% CI [-2.49, -2.12]; 0% in ROPE) and boreal clubhook squid had lower % protein that could be considered significant (pd = 99.55%; Median = -0.29, 95% CI [-0.50, -0.07]; 0% in ROPE).

Table 3. Outputs for three Bayesian linear models predicting ED, % lipid, and % protein (response variables) as a function of region + mass + species + mass*species + mass*region. The baseline parameters levels are bigfin lanternfish and north region. Median = median effect size of each parameter, probability of direction (pd) is the probability of a negative or positive effect, the 95% CI (credible interval) is 95% of the data is located between the high HDI (highest density interval; HDI_{high}) and the low HDI (HDI_{low}), ROPE (region of practical equivalence) is a small range around zero where the size of the effect would be considered non-significant—ROPE limits are set separately for each nutritional metric model. If the % in ROPE (ROPE%) is less than 1% the effect is considered significant (bold font in table). ED model intercept: median = 1.29, 95% CI [1.06, 1.52]); pd = 100%; 0% in ROPE. Lipid model intercept: median = 0.46, 95% CI [-0.19, 1.08]); pd = 92.38%; 9.95% in ROPE. Protein model intercept: median = 2.66, 95% CI [2.53, 2.78]); pd = 100%; 0% in ROPE.

	ED					**Lipid**					**Protein**				
Parameters	**Median**	**95% CI**		**pd (%)**	**ROPE % [-0.05, 0.05]**	**Median**	**95% CI**		**pd (%)**	**ROPE % [-0.10, 0.10]**	**Median**	**95% CI**		**pd (%)**	**ROPE % [-0.04, 0.04]**
		$\mathrm{HDI}_{\mathrm{low}}$	**$\mathrm{HDI}_{\mathrm{high}}$**				**$\mathrm{HDI}_{\mathrm{low}}$**	**$\mathrm{HDI}_{\mathrm{high}}$**				**$\mathrm{HDI}_{\mathrm{low}}$**	**$\mathrm{HDI}_{\mathrm{high}}$**		
South	0.01	-0.13	0.16	57.10	56.71	0.13	-0.27	0.54	73.40	33.50	-0.02	-0.09	0.06	66.50	72.76
Mass	0.39	0.29	0.49	**100**	**0**	0.94	0.66	1.22	**100**	**0**	0.01	-0.04	0.07	66.55	89.71
Boreal clubhook squid	-0.16	-0.55	0.24	78.75	15.76	-0.06	-1.17	0.99	54.35	16.37	-0.29	-0.50	-0.08	**99.55**	**0**
Market squid	0.01	-0.29	0.28	53.02	29.68	-0.06	-0.91	0.71	55.57	20.21	-0.08	-0.23	0.09	83.85	27.63
Northern anchovy	0.06	-0.40	0.50	59.95	18.26	-0.23	-1.48	1.12	63.75	12.68	0.03	-0.22	0.30	58.70	25.79
Pyrosome	-2.15	-2.47	-1.83	**100**	**0**	-1.91	-2.83	-1.01	**99.98**	**0**	-2.31	-2.50	-2.14	**100**	**0**
Mass*boreal clubhook squid	-0.26	-0.40	-0.14	**100**	**0**	-0.84	-1.20	-0.47	**100**	**0**	0.12	0.05	0.19	**99.88**	**0**
Mass*market squid	-0.32	-0.43	-0.20	**100**	**0**	-0.95	-1.28	-0.61	**100**	**0**	0.07	0.01	0.14	98.25	18.82
Mass*northern anchovy	-0.25	-0.41	-0.09	**99.88**	**0**	-0.56	-1.02	-0.07	**98.92**	**0.74**	0.03	-0.06	0.12	74.85	56.97
Mass*pyrosome	-0.32	-0.85	0.17	88.67	8.42	-1.39	-2.85	0.10	97.02	1.66	0.15	-0.14	0.45	84.82	15.05
South*boreal clubhook squid	-0.08	-0.28	0.11	78.70	33.79	-0.38	-0.91	0.20	90.72	12.87	-0.02	-0.13	0.09	60.77	59.00
South*market squid	-0.10	-0.28	0.08	87.28	26.39	-0.35	-0.84	0.17	92.05	13.87	-0.05	-0.14	0.05	84.17	44.92
South*northern anchovy	0.02	-0.17	0.23	58.07	42.18	0.05	-0.51	0.64	56.93	29.68	-5.79e-03	-0.12	0.11	54.33	60.29
South*pyrosome	0.18	-0.63	1.02	66.55	9.61	0.59	-1.68	3.11	67.83	6.55	0.10	-0.38	0.57	65.95	13.68

3.4 Relationships among relative nutritional metrics

Protein varied more in squids than in fishes, correlating strongly with ED, while lipid varied more in fishes than in squids, correlating strongly with ED (Supplementary Figure 2). We also found that the relationship between nutritional metrics and moisture content varied by species (Supplementary Figure 3).

3.5 Species-specific relationships between relative nutritional value and body size

Our Bayesian linear models revealed that specimen mass had significant, species-specific relationships with all three nutritional metrics. Subsequent linear regressions illustrate how specimen mass and length predicts each nutritional metric for each species.

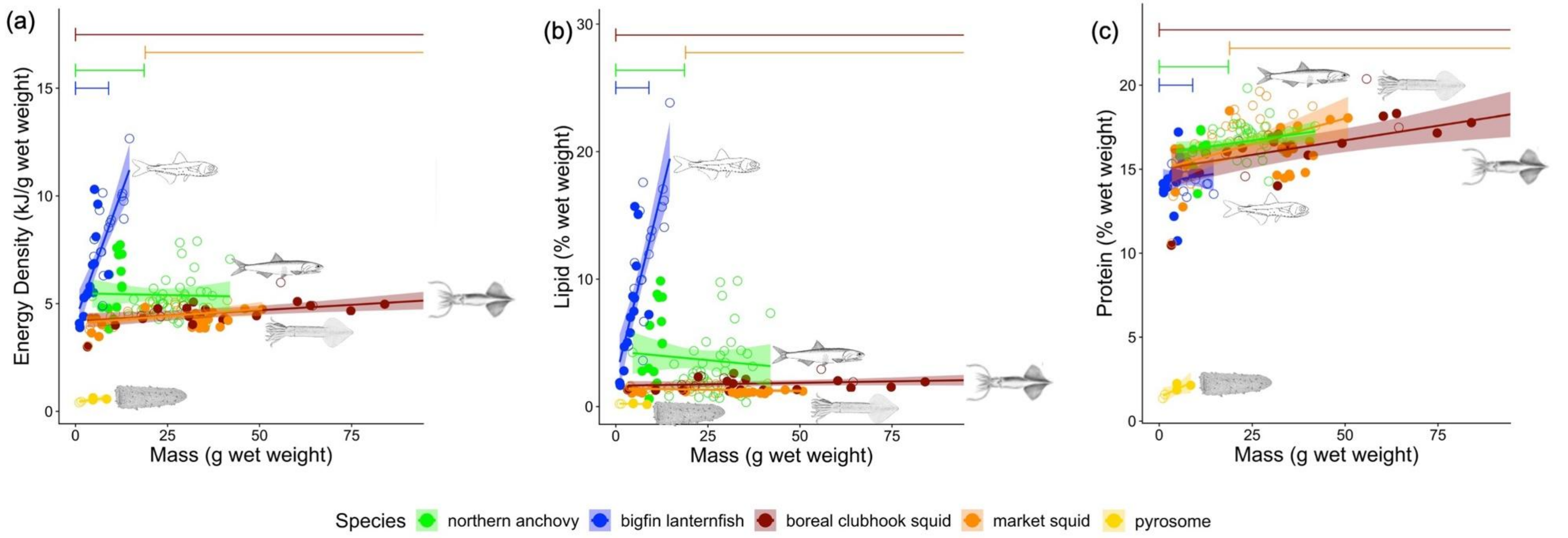

Figure 3. Relationship between mass (g wet weight) and ED (kJ/g wet weight), % lipid (wet weight), % protein (wet weight), for five Pacific small pelagic species: northern anchovy (n = 31), bigfin lanternfish (n = 32), boreal clubhook squid (n = 23), market squid (n = 35), and pyrosomes (n = 5). Lines indicate linear regression of each relative nutritional metric to standard length and mass, colour coded by species (for sample sizes and regression results, see Table 4). The x-axis has been cut to 90 g (excluding the largest boreal clubhook squid) to better show the relationships of the other species. Horizontal bars represent the size range of each organism found in albacore stomachs, pyrosomes are not consumed (Gleiber et al., 2024).

The strength and magnitude of relationships between size (mass in g) and relative nutritional value varied greatly among species and metrics (Table 4; Figure 3). Percent protein varied much less with mass than did ED and % lipid. In bigfin lanternfish, ED increased steeply with mass ($R^2 = 0.63$, $F(1, 30) = 51.05$, $p = 6.00E-08$) and % lipid increased steeply with mass ($R^2 = 0.64$, $F(1, 30) = 53.13$, $p = 4.08E-08$). In boreal clubhook squid, ED increased slightly with mass ($R^2 = 0.31$, $F(1, 21) = 9.449$, $p = 0.005759$) and % protein increased slightly with mass ($R^2 = 0.33$, $F(1, 21) = 10.37$, $p = 0.004109$). In market squid, % lipid slightly decreased with mass ($R^2 = 0.12$, $F(1, 33) = 4.296$, $p = 0.04608$) and % protein slightly increased with mass ($R^2 = 0.13$, $F(1, 33) = 5.138$, $p = 0.03009$). In northern anchovy, % protein increased slightly with mass ($R^2 = 0.23$, $F(1, 29) = 8.55$, $p = 0.006642$). In addition, as shown in the overlay, the size of the specimens we used to establish these relationships overlaps with the size of specimens found in albacore tuna stomachs (Glieber et al., 2024). We found that specimen length also had very similar relationships with each relative nutritional metric (Supplementary Figure 4 & Supplementary Table 1).

Table 4. Regression results and equations between mass (g wet weight) and ED (kJ/g wet weight), % lipid (wet weight), % protein (wet weight), for five Pacific small pelagic species.

Mass:Nutritional value

Regression	**Common name**	**n**	**Rˆ2**	***F***	***p***	**Nutri. metric (kJ/g wet weight or % wet weight) = m * mass (g wet weight) + b**
Mass (g wet weight):Energy density (kJ/g wet weight)	Northern anchovy	31	0.11	F(1, 29) = 3.728	0.06334	y = 0.044 x + 5
	Bigfin lanternfish	32	0.63	F(1,30) = 51.05	**6.00E-08**	y = 0.47 x + 4.3
	Boreal clubhook squid	23	0.31	F(1,21) = 9.449	**0.005759**	y = 0.01 x + 4.2
	Market squid	35	0.084	F(1,33) = 3.029	0.09113	y = 0.0095 x + 4.1
	Pyrosome	5	0.55	F(1,3) = 3.734	0.1488	y = 0.022 x + 0.43
Mass (g wet weight):Lipid (% wet weight)	Northern anchovy	31	0.066	F(1,29) = 2.06	0.1619	y = 0.082 x + 3.3
	Bigfin lanternfish	32	0.64	F(1, 30) = 53.13	**4.08E-08**	y = 1.2 x + 2.3
	Boreal clubhook squid	23	0.082	F(1, 21) = 1.876	0.1852	y = 0.0046 x + 1.6
	Market squid	35	0.12	F(1,33) = 4.296	**0.04608**	y = -0.0052 x + 1.4
	Pyrosome	5	0.13	F(1,3) = 0.4656	0.544	y = -0.0045 x + 0.23
Mass (g wet weight):Protein (% wet weight)	Northern anchovy	31	0.23	F(1,29) = 8.55	**0.006642**	y = 0.048 x + 16
	Bigfin lanternfish	32	0.012	F(1,30) = 0.3514	0.5578	y = 0.033 x + 14
	Boreal clubhook squid	23	0.33	F(1,21) = 10.37	**0.004109**	y = 0.035x + 15
	Market squid	35	0.13	F(1,33) = 5.138	**0.03009**	y = 0.049 x + 15
	Pyrosome	5	0.7	F(1,3) = 7.001	0.07726	y = 0.1 x + 1.4

As expected, we found significant, positive relationships between total energy, total lipid, and total protein content per specimen with body size, however the strength of the relationship continued to vary among species especially for total energy and lipid (Table 5). Total energy (energy density * specimen mass) increased with mass at a greater rate for the fishes than for the squids (Figure 4a). Bigfin lanternfish increased the most per unit of weight, followed by anchovy. The squids were similar, but boreal clubhook squid showed a higher ratio of total lipid to mass (Figure 4b). The relationship between total protein and mass was nearly identical among all species; however, pyrosomes showed a weaker relationship (Figure 4c).

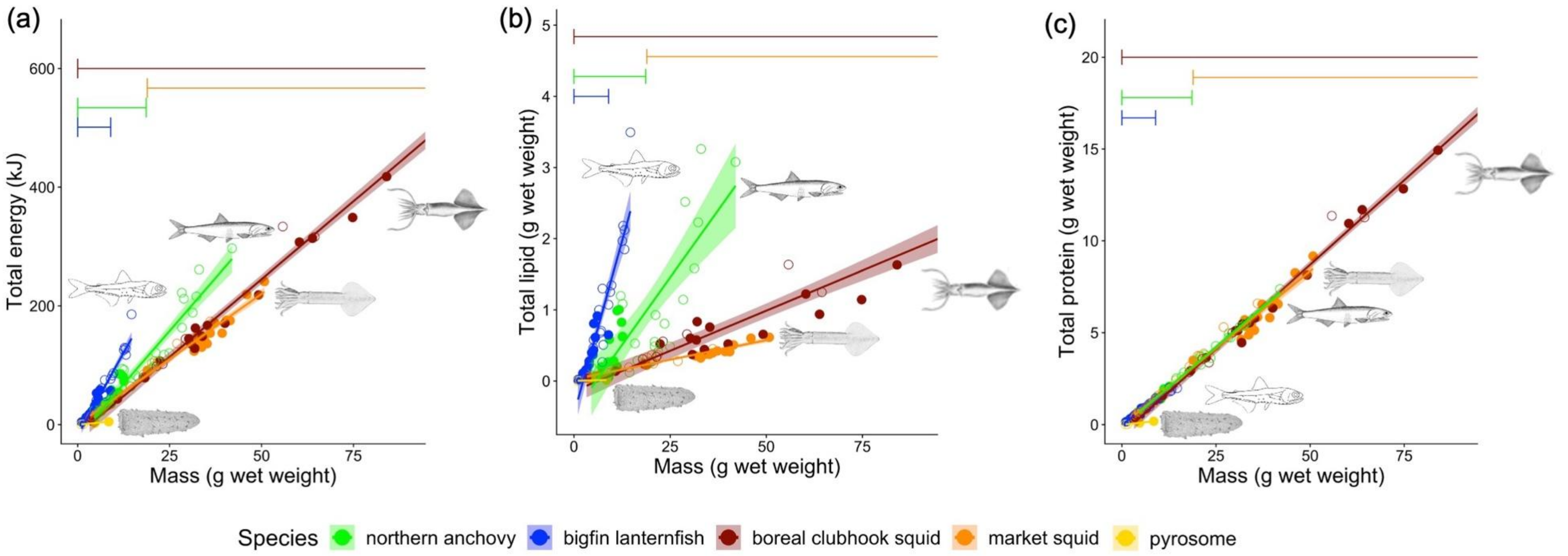

Figure 4. Relationship between total energy (ED*body mass), total lipid (% lipid*body mass) and total protein (% protein*body mass) to body mass for five Pacific small pelagic species: northern anchovy (n = 31), bigfin lanternfish (n = 32), boreal clubhook squid (n = 23), market squid (n = 35), and pyrosomes (n = 5). Lines indicate linear regression of each nutritional metric to standard length and mass, colour coded by species (for sample sizes and regression results, see Table 5). The x-axis has been cut to 90 g (excluding the largest boreal clubhook squid) to better show the relationships of the other species. Horizontal bars represent the size range of each organism found in albacore stomachs (Gleiber et al., 2024a).

Table 5. Regression results and equations for the relationship between mass (g wet weight) and total energy (kJ), total lipid (g wet weight), total protein (g wet weight), for five Pacific small pelagic species.

Mass:Total Nutritional value

Regression	**Common name**	**n**	**R^2**	***F***	***p***	**Nutri. metric (kJ or g wet weight) = m * mass (g wet weight) + b**
Mass (g wet weight):total energy (kJ)	Northern anchovy	31	0.8981	F(1,29) = 255.6	**6.41E-16**	y = 7.1 x – 21
	Bigfin lanternfish	32	0.9215	F(1,30) = 352.4	**< 2.2e-16**	y = 11 x – 18
	Boreal clubhook squid	23	0.9892	F(1, 21) = 1929	**< 2.2e-16**	y = 5.3 x – 18
	Market squid	35	0.9744	F(1,33) = 1258	**< 2.2e-16**	y = 4.4 x – 0.32
	Pyrosome	5	0.9881	F(1,3) = 249.2	**0.0005525**	y = 0.6 x – 0.16
Mass (g wet weight):total lipid (g wet weight)	Northern anchovy	31	0.6025	F(1,29) = 43.96	**2.87E-07**	y = 0.076 x – 0.44
	Bigfin lanternfish	32	0.8406	F(1,30) = 158.3	**1.70E-13**	y = 0.19 x – 0.46
	Boreal clubhook squid	23	0.9086	F(1,21) = 208.8	**2.20E-12**	y = 0.023 x – 0.14
	Market squid	35	0.9277	F(1,33) = 423.1	**< 2.2e-16**	y = 0.011 x + 0.025
	Pyrosome	5	0.8617	F(1,3) = 18.69	**0.02281**	y = 0.0017 x + 0.0016
Mass (g wet weight):total protein (g wet weight)	Northern anchovy	31	0.9932	F(1,29) = 4251	**< 2.2e-16**	y = 0.17 x – 0.14
	Bigfin lanternfish	32	0.9821	F(1,30) = 1647	**< 2.2e-16**	y = 0.14 x + 0.0058
	Boreal clubhook squid	23	0.9935	F(1,21) = 3231	**< 2.2e-16**	y = 0.18 x – 0.51
	Market squid	35	0.9733	F(1,33) = 1203	**< 2.2e-16**	y = 0.17 x – 0.055
	Pyrosome	5	0.991	F(1,3) = 329.7	**0.0003644**	y = 0.022 x – 0.0094

3.6 Within-species differences in nutritional quality by sex and maturity status

We had limited coverage of sex and maturity status data for several reasons. We only had the expertise to reliably assign maturity status to all of, and sex to some of, the northern anchovy, boreal clubhook squid, and market squid. Immaturity and small size of some specimens within these species made accurate classification by sex impossible. Pyrosomes' structure precludes these categorizations and there is limited knowledge of sexual dimorphic features for bigfin lanternfish (Martin & Smith, 2024). Values for ED, % lipid, and % protein were highly variable for males and females and for juveniles and adults (Supplementary Figure 5).

4.0 Discussion

4.1 Methodological considerations for determining energy density

As hypothesised, we found that ED estimated from proximate composition corresponded closely with ED measured via bomb calorimetry. This close relationship reinforces the viability of using proximate composition values for comparisons. In species where there is not perfect 1:1 correspondence between proximate composition-derived ED values and bomb calorimetry ED values, species-specific conversion equations can be used to adjust proximate composition derived ED to compare ED values across the two methods. Doing so could avoid more time-consuming and expensive bomb calorimetry determinations. Deriving ED from proximate composition information is also advantageous when the volume of tissues available is low (e.g., when analysing very small-bodied organisms or when a small subset of tissue is available; Cummins & Wuycheck, 1971; Weil et al., 2019), when bomb calorimetry-derived ED values are unavailable; or when large numbers of samples would make proximate composition analysis (capable of running large batches) faster than bomb calorimetry (requiring processing one replicate at a time).

Bomb calorimetry is considered the gold standard for determining ED (Weil et al., 2019), so it would normally be assumed that the less precise method of proximate composition led to the slightly lower ED values for some species in my analysis. However, bomb calorimetry may have introduced a degree of error because the success of the method depends on characteristics of the species' tissue. For example, we found bigfin lanternfish fully combusted in bomb calorimetry (i.e. left no uncombusted material) and that species showed a near perfect correspondence with proximate composition-estimated ED. In contrast, the other three species we compared were more prone to incomplete combustion and showed greater deviation from bomb calorimetry-derived ED values (through lower proximate composition-estimated ED values). This nuance raised the possibility that bomb calorimetry may lead to over-estimating ED in some species, rather than the proximate composition method underestimating ED or being the least accurate.

Even if bomb calorimetry is the most reliable method for quantifying ED, using less accurate alternatives can allow pre-existing data to fill gaps in knowledge of ED variation within and among species, thereby facilitating finer scale analysis. For example, Chen et al. (2022) increased their sample size and taxa diversity by using moisture content to estimate the ED of cephalopod taxa. Because moisture content and ED are inversely related, they used paired ED and moisture content values from published literature to fit an ordinary least squares regression between ED and moisture as a percentage of body mass. We found that the relationship between nutritional metrics and moisture content varied by species, suggesting that adjusting by species may be necessary when moisture is used as a proxy for ED. Beaubier & Hipfner (2013) also underscore the importance of monitoring water loss from partial thawing of samples during transport and processing when using this method, which we were unable to do. Other single metrics, including % lipid and % protein, are also sometimes used to calculate ED (Weil et al., 2019). Since our findings showed that protein varied more in squids than in fishes and correlated strongly with ED in our squids, protein may be more reliable than lipids to predict ED in that taxa. Alternately, since lipid varied more in fishes and correlated strongly with ED in our fish species, lipid may be more reliable in predicting ED in that taxa. We had % ash free dry weight values (dry tissue weight minus ash content weight) available from our proximate composition analysis, which can be reliably used to calculate ED. These values could also be used to test the correspondence between ED generated from this metric and the values generated through bomb calorimetry and proximate composition analysis.

4.2 Effect of environmental conditions on nutritional content

Sea surface temperature, chlorophyll-a, and BEUTI were all significantly different between the north and south regions of the CCLME. However, contrary to our prediction that ED and % lipid values would be higher in the north than in the south because environmental conditions foster higher productivity in the north, region of collection did not significantly affect any of the nutritional metrics we measured. While several studies have shown that indirect environment-related factors—including year, season, month, region and location—influence nutritional values of small pelagic species (Anthony et al., 2000; Deng et al., 1976; Dessier et al., 2018; Gatti et al., 2018; Hellessey et al., 2018; McKinstry et al., 2013; Miller et al., 2017; Price et al, 2024), only a few studies have tested for or found a direct connection between environmental conditions and the nutritional values of SPS. For example, Litz et al. (2010)

linked total lipid content in Pacific sardine to ocean conditions and Fisher et al. (2020) observed that lipid profiles in euphausiids (*Euphausia pacifica* and *Thysanoessa spinifera*) followed the upwelling cycle. While we did not test for effects of specific environmental parameters directly on individual specimen nutrient content, we saw a high amount of variability in nutritional values within regions (e.g., see Supplementary Figure 1 for spread of ED values across months and regions), including variability not explained by the factors we examined. Collectively, these findings suggest that there may be finer-scale, local environmental conditions that influence the nutritional preyscapes. The degree of environmental variability over the time period examined could also influence whether differences in environmental conditions translate to altered nutritional values in SPS. Litz et al. (2010) conducted their study over two spring periods—one in which upwelling was curtailed severely enough that it delayed biological productivity, and one that was relatively normal—which would have affected the degree of impact experienced up through the food chain. Links between environment and nutritional quality may also be easier to detect at lower trophic levels (Miller et al., 2017). For example, Fisher et al. (2020) examined euphausiids, which are at a lower trophic level than the SPS that we examined, so the impacts could be more visible because the plankton they feed on is more closely affected by upwelling variability. Given that the consistency we found in nutritional value between regions may not persist in periods of more rapid or extreme change, further studies should be done with a larger range of species and at broader temporal and regional scales.

4.3 Life history traits and nutritional value

4.3.1 Body size and nutritional value

We predicted that larger overall body size would be correlated with higher ED and % lipid because larger individuals have access to larger and more nutritionally-dense prey (Barnes et al., 2021; Gong et al., 2018; Queiros et al., 2019; Scharf et al., 2000). Relative nutritional value is important to organisms directly because it influences factors such as their body condition, resilience, and reproductive readiness (Saraux et al., 2019). These levels indicate whether individual organisms have been able to acquire sufficient protein, lipid, and energy for optimal functioning (Rombenso et al., 2021). In the all-species Bayesian models, mass showed a significant effect on ED and % lipid across all species, although both squids and northern anchovy had species-specific mass-to-ED and mass-to-lipid relationships that were weaker in magnitude than the ones for the baseline species, bigfin lanternfish. Using individual species-specific linear regressions, we found a significant relationship between size and ED for both bigfin lanternfish and boreal clubhook squid; however, the bigfin lanternfish relationship was much stronger than the boreal clubhook squid relationship. Bigfin lanternfish and market squid showed significant independent relationships between size and % lipid, and again, the bigfin lanternfish mass had a greater effect on % lipid. Contrary to our results, Price et al. (2024) found a positive relationship between ED and mass in anchovies, but not in market squid. Payne et al. (1999) found some evidence that, in capelin, significant differences in % lipid may be related to length. However, these findings conflict with studies that found no relationship between small pelagic fish size and proximate composition values (e.g., mackerel–Eder & Lewis, 2005; herring–Foy & Paul, 1999; eulachon and capelin–Payne et al., 1999; capelin–Van Pelt et al., 1997). Contradictions in the literature may reflect different methodological differences, such as whether species-specific comparisons considered all covariates together to control for species-based effects, regional effects, and species-region interactions.

Interestingly, we found that ED and lipid values for northern anchovies are highly variable, and that this variance is not associated with length—at least within the 110 mm and 150 mm length for the species. The nutritional value variability we observed in ED (<1-4kJ/g) of anchovy at this length is similar to the variability observed in other fish species (Atlantic cod and herring) at comparable sizes (Lawson et al., 1998; Paul et al., 1998). This observation could also be explained by a phenomenon noted in Love (1980), that when lipids are used, water can replace them to maintain body shape (cited in Rosa et al., 2010). Gatti et al., (2018) also observed that energy storage capacity varies with species, size, and age, so the variability we observed potentially reflects differences in individuals' abilities to fill their species and size storage capacities.

We also predicted that larger body size would not necessarily correlate with higher % protein, because protein has been negatively correlated with ED in some small pelagic species (Van Pelt et al., 1997). Contrary to our hypothesis, we found boreal clubhook squid, market squid, and northern anchovy showed a significant positive relationship between size and % protein. In the all-species model, boreal clubhook squid showed a strong mass-to-protein relationship relative to all the other species. However, in the same model, they also had a significantly lower protein value than market squid, bigfin lanternfish, and anchovy. This apparent incongruence may, in part, occur because our samples of boreal clubhook squid were generally larger than the samples for other species. Further exploration would be required to explain the relationships we found.

In the fishes we sampled, % lipid was most correlated with ED, whereas, in the invertebrates, % protein was most correlated with ED—a contrasting relationship we have not found in the literature. Van Pelt et al. (1997) also found a positive relationship between lipid and ED in schooling fish, as did Trudel et al. (2005). Gape size limitation may explain the more pronounced correlation between length and ED and length and % lipid in bigfin lanternfish. Larger bigfin lanternfish individuals with associated larger gape size would be able to consume larger zooplankton and obtain more high-quality prey than individuals with smaller gapes. Since squids have comparably flexible feeding apparatus and ability to hold their prey while consuming it, they are not gape-size-limited to the same extent as fishes, which is consistent with the weaker correlation between size and both ED and % lipid (Gong et al.; 2018, 2020). On the other hand, the positive correlation between size and % protein in both squid species may be explained by their lack of supporting skeletal structures and the consequent need for more muscle to support larger bodies (although the relationship between size and % protein is also seen in northern anchovy).

Overall, we concluded that mass and length may be useful in some taxa for predicting relative nutritional value; however, morphological and life history traits and phenology add complexity to nutritional profiles at the individual species scale. If mass or length are being used directly as a proxy for nutritional value, caution should be exercised because previous studies have shown that the relationship is not always reliable (Jonas et al., 1996; Sutton et al., 2000; Trudel et al., 2005).

4.3.2 Maturity status and sex and nutritional values

We predicted that adult females would be higher in ED and % lipid than juvenile females because female gonads have been associated with high lipid levels in fish (Dhurmeea et al., 2018). While this generally held true, we did not find large differences for any species, and unexpectedly, we found the reverse was true for anchovies only (which also was the species with the widest differences between juveniles and adults). Because many individuals could not be assigned a sex and maturity status, we had limited sample sizes for the various combinations of sex and maturity status for each species. Our unexpected finding that ED and % lipid in juvenile anchovy was higher than that in adult anchovy may be partially explained by the month of collection, since the juveniles were collected later in the season. Across anchovy species and regions, temperatures related to month and season have been associated with factors including recruitment, condition, gonadosomatic ratios and onset of gonad development in females (Bacha & Amara, 2012; Contreras-Reyes et al., 2016; Schismenou et al., 2013). In addition, in our study, male anchovy showed marginally higher ED and % lipid. Life cycle stage and timing could be a factor since reproductive stress can also reduce the nutritional quality of females (Brosset et al., 2016; Saraux et al., 2019). However, other studies have found that there is not always a relationship between age or sex and ED or % lipids (Eder & Lewis, 2005; Garrido et al., 2008; Foy & Paul, 1999; Payne et al., 1999; Van Pelt et al., 1997). Further investigation of the interactions among nutritional traits, sex, maturity, and environmental factors is required to understand the underlying principles.

4.3.3 Body size and total nutritional value

Total nutritional value, specifically the total organism value of each nutritional metric, is important to optimal foraging from the angle of predator choice—predators will choose the highest value prey to maximise profit from prey pursuit. The size of the specimens we tested overlap with the size of specimens found in albacore tuna stomachs (Gleiber et al., 2024), which consume similar prey types to a range of other top predator fishes (Scharf et al., 2000). We found that total energy and total lipid changed at different rates with mass across species (although protein did not), which means that the value of a prey item increases faster with body size in some species. Generally, we found that total energy and total lipid increased with mass at a greater rate for the fishes than for the squids, which parallels what we saw with ED and % lipid. However, the degree of increase of protein with increasing mass is consistent across all taxa. The positive relationships between mass and total energy, total lipid, and total protein for all five focal species reaffirm that size is associated with nutritional value at the whole organism level. Ball et al. (2007) found that total energy content was strongly influenced by body length in fishes, and we found the same for mass.

Larger prey in species with higher ratios of ED and lipid-to-mass would be most valuable nutritionally to predators seeking to maximise ED and lipid intake; however, all larger prey would be more valuable than smaller prey in terms of ED, lipid and protein content. Since the ratios of total energy-to-mass and total lipid-to-mass are higher for fish than for squid as mass increases, there will be more nutritional value in a larger fish than in a similarly large squid. Small increases in prey size may mean more relative nutritional value in some species than others, so predators could potentially benefit more by selecting for size in certain prey species and taxa. If small pelagic fish species have greater total nutritional value with smaller change in mass than small pelagic squids, they are potentially more nutritious for predators and that may influence predators' foraging habits and response to changes in food webs. Changes in ocean conditions that affect the availability of higher value prey—for example, fewer larger fish or fewer fish relative to squids—could affect predators' ability to store nutrients and reach reproductive readiness. Optimal foraging in changing marine environments could result in top predators selecting alternate prey with similar traits or moving to regions that better support higher preference prey, so understanding the nutritional variations could inform fisheries management.

Although predators would presumably favour high total energy prey, other factors complicate foraging decisions. For example, rapid climate change may thwart predators' easy access to energy. Lefort et al. (2015) found higher resilience to climate stress among small body-size organisms, which was attributed to their lower energy requirements and the reduced predation pressure from foragers with high energy needs. In addition, quality and not just quantity of nutrients and energy is relevant. For example, the lipids in most lanternfish species are more diverse and potentially less nutritionally available than those in other prey species (Neighbors & Nafpaktitis, 1982), which would reduce their nutritional value for some predators. Thus, nuanced nutritional analysis is key to understanding optimal foraging and how and why assemblages may change as climate instability intensifies.

4.4 Future implications for environment and traits

As climate change enhances ocean warming, optimal foraging suggests that predators will have two options: move to cooler waters (Childers et al., 2011) to search for currently preferred prey, or alternatively, switch to satisfactory prey that better tolerate warmer waters in their original habitat (Muhling et al., 2019; Wade, 2007). The range in nutritional quality of individuals in each of the five species we examined is similar under the different environmental conditions encapsulated by the northern and southern regions of the CCLME. This relative stability in nutritional patterns among regions differing in environmental conditions suggests that if predators shift their range northward to track environmental conditions they prefer, they may still encounter prey with similar nutritional profiles (Dudley et al., 2021). However, if climate conditions cause more extreme ocean warming, then these relatively stable nutritional relationships may break down, potentially requiring predators to select alternate prey (Dudley et al., 2021). Ecosystem modelling by Hernández-Padilla (2021) shows how high variability in SST can have more catastrophic ecosystem effects, affecting the structure and functioning of an ecosystem, decreasing its ecosystem resilience, and altering the trophic role of many species.

An example using albacore illustrates how climate change could lead a top predator to choose an alternate prey species. Market squid are relatively similar nutritionally to albacore's more preferred prey species, yet they inhabit warmer waters than albacore's current preferred prey (Gleiber et al., 2024a; Ottmann et al., 2024). Thus, market squid could potentially be consumed more frequently in the future by albacore if they acclimate to, rather than migrate from, warmer waters. Alternatively, if relatively stable food webs are disrupted more severely by climate warming, albacore may begin to forage more frequently for less preferred mesopelagic species, which also share higher ED and % lipid and inhabit the cooler waters that albacore currently use for foraging (Childers et al., 2011). Since even now tropical albacore consume more deep-water species than do temperate albacore, such a change in foraging behaviour is possible if Pacific waters warm (Williams et al., 2015). As the example with albacore shows, optimal foraging involves multiple environmental and trait-based factors alongside nutritional value, making conservation and fisheries management decisions complex.

5.0 Conclusion

Several methodological considerations arise from our research. The nutritional variability we found within species underscores the importance of using multiple nutritional values for each species, not just species averages (McKinstry et al., 2013). The close correspondence we found between bomb calorimetry-derived ED values and ED estimates based on proximate composition analysis demonstrates that both methods can be used for comparison if species-specific conversion values are available for the latter method. The gaps in knowledge about nutritional factors related to foraging and the importance of this information for predicting future foraging and food web changes justify using less precise methods for estimating ED. Further, taxa-related generalisations such as those we found related to % lipid and % protein, and species-specific adjustments to moisture, could improve these estimates.

This work filled gaps in nutritional metrics for several species, added replicates for all species, and identified multiple significant relationships between nutritional metrics and SPS traits that could be tested in future with more species, more samples, and broader temporal and regional sources. For instance, we found ED and % lipid were closely linked, and that ED and % lipid (but not % protein) increased significantly with mass across the five species, with species identity modulating this relationship. The finding that size is more important in certain species could be used to infer the nutritional quality of assemblages of species within specific regions in specific time frames, and thereby predict predator health or predator movement. The species-specific nutritional metric relationships we found could be used to estimate a range of nutritional values indirectly when species identity and size are available, but nutritional value cannot be measured directly—thus allowing for increased granularity in food web modelling. If they are generalisable, the relationships we identified will help predict marine predators' foraging behaviour and population responses that might alter food webs as ocean conditions change.

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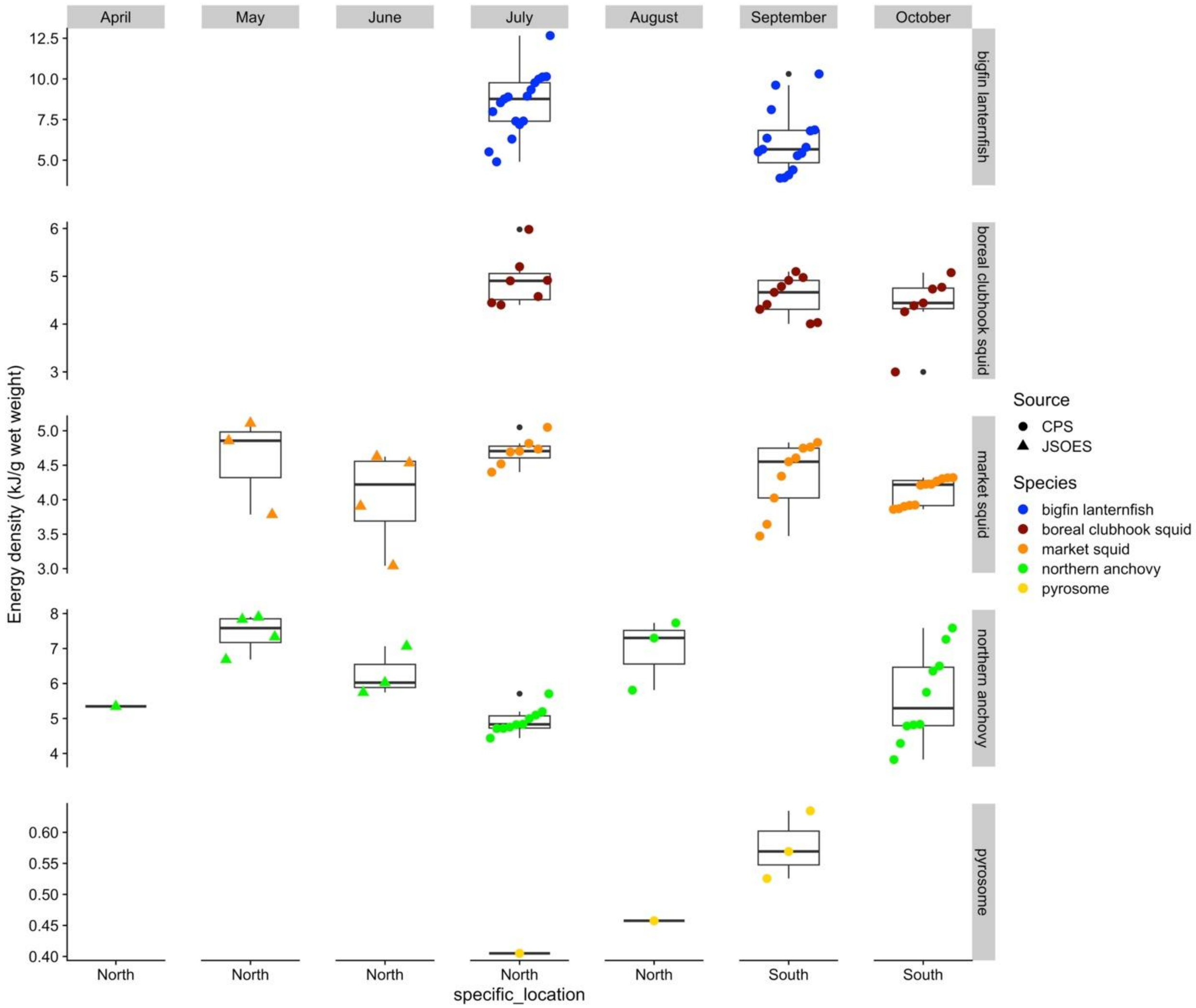
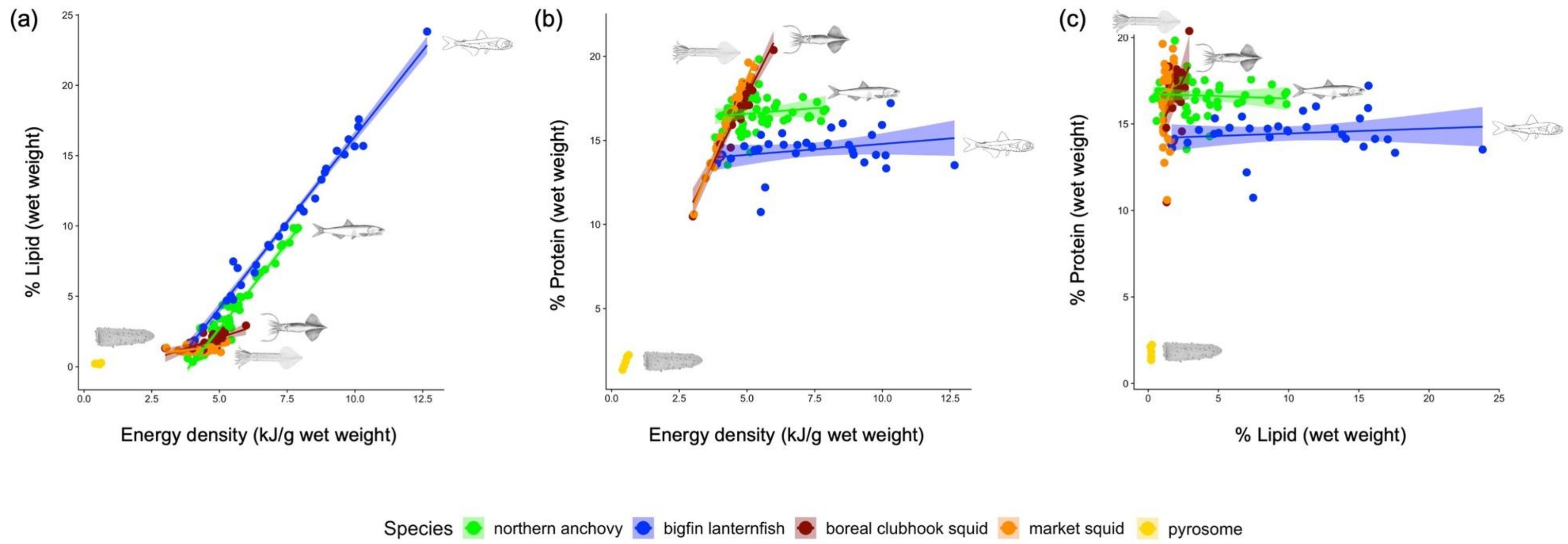
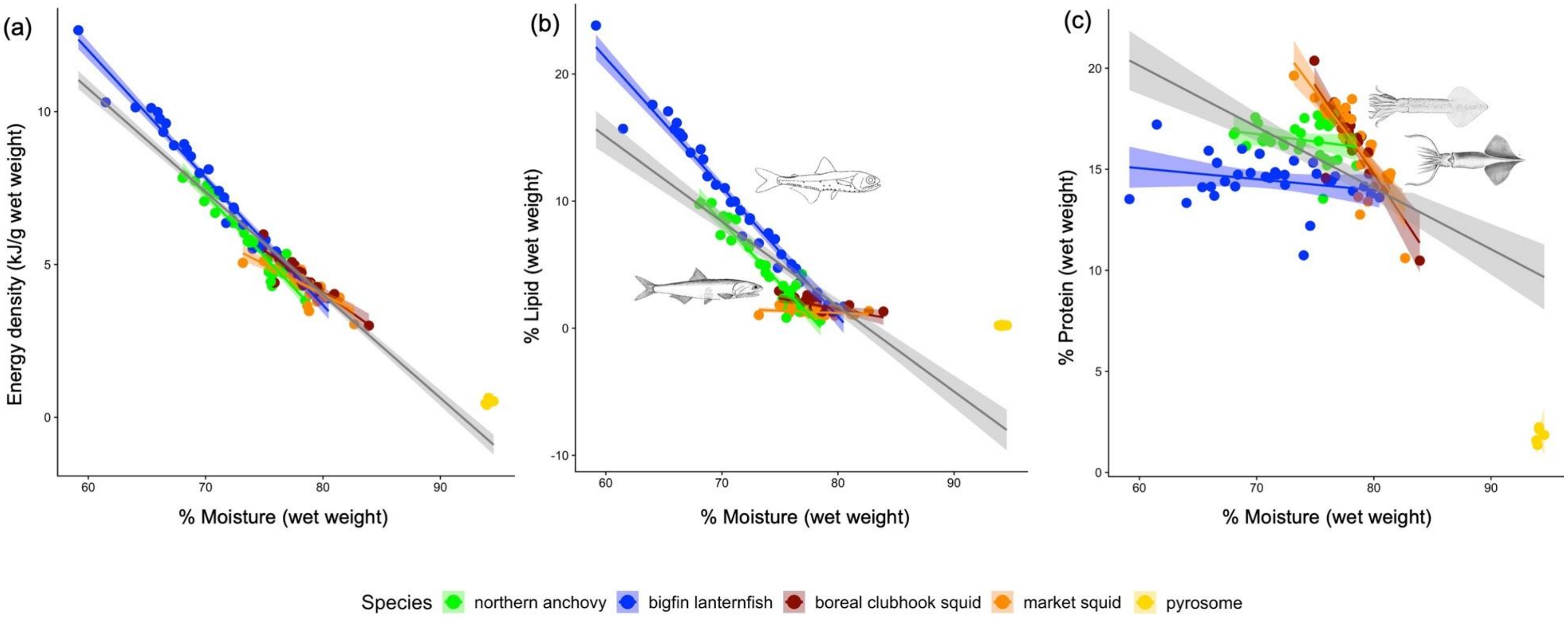
7.0 Appendices



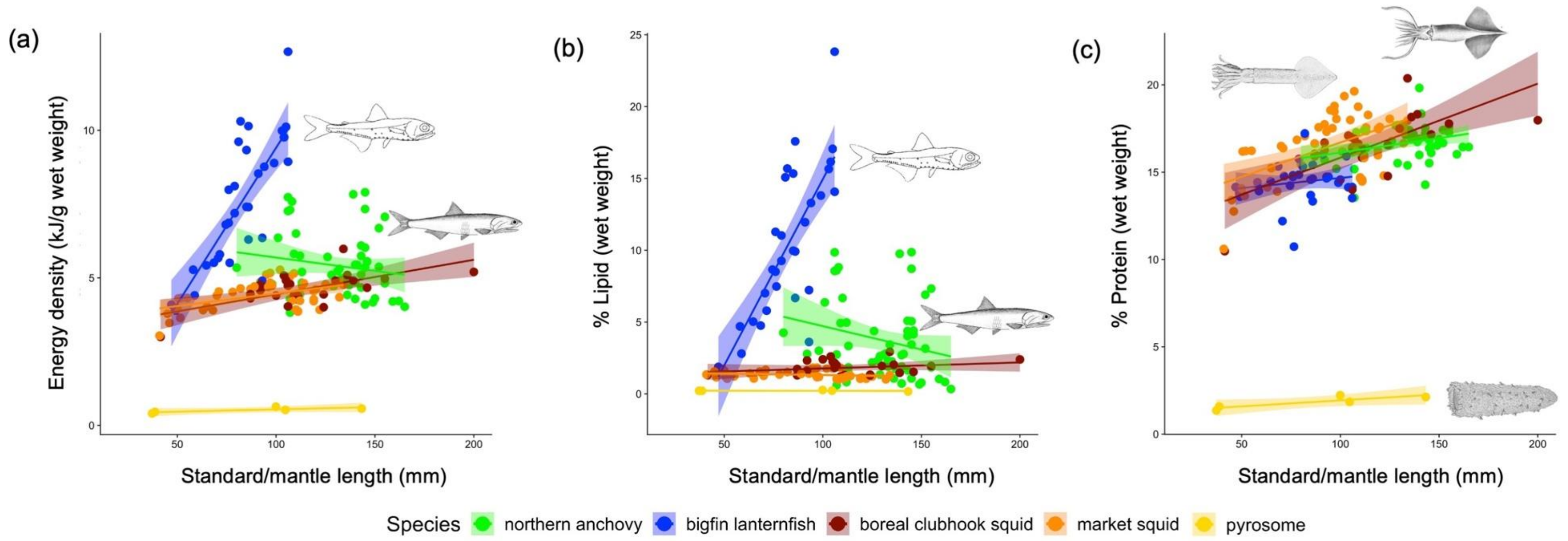
Supplementary Figure 1. Mean and range of energy density values from proximate composition analysis across months (April–October) of specimen collection. Coloured by northern anchovy (n = 31), bigfin lanternfish (n = 32), boreal clubhook squid (n = 23), market squid (n = 35), and pyrosomes (n = 5). Source cruise of specimens shown by shape.



Supplementary Figure 2. Linear relationships of nutritional metrics to each other (a) lipid to ED, (b) protein to ED, (c) protein to lipid for: northern anchovy (n = 31), bigfin lanternfish (n = 32), boreal clubhook squid (n = 23), market squid (n = 35), and pyrosomes (n = 5).



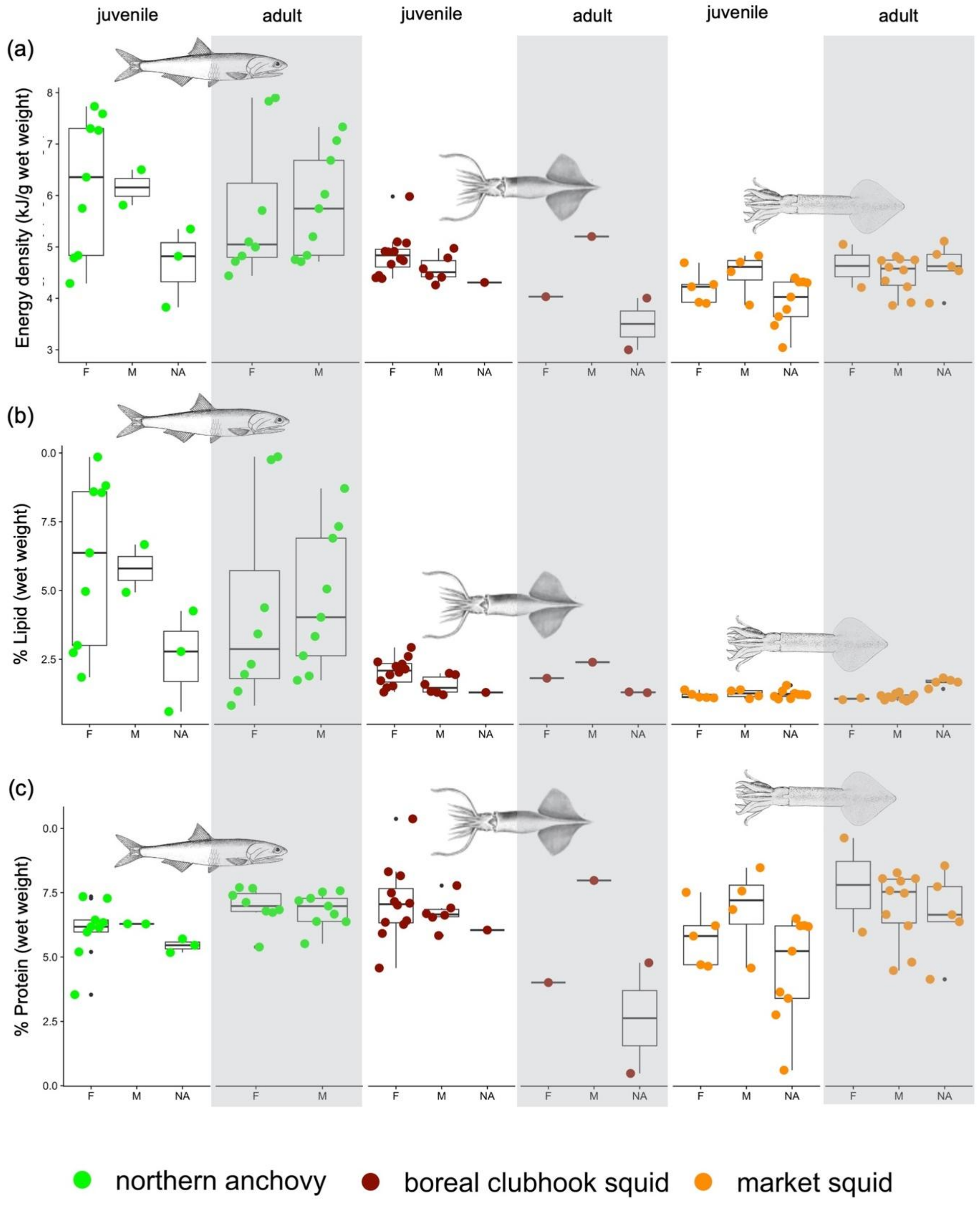
Supplementary Figure 3. Relationships of nutritional metrics to % moisture (of the total wet weight): (a) % moisture to energy density, (b) % moisture to % lipid, (c) % moisture to % protein for northern anchovy (n = 31), bigfin lanternfish (n = 32), boreal clubhook squid (n = 23), market squid (n = 35), and pyrosomes (n = 5). Grey lines indicate linear regression of each nutritional metric over all species.



Supplementary Figure 4. Relationship between length (mm; standard length used for fish species and mantle length for squids) and ED (kJ/g wet weight), % lipid (wet weight), % protein (wet weight), for five Pacific small pelagic species: northern anchovy (n = 31), bigfin lanternfish (n = 32), boreal clubhook squid (n = 23), market squid (n = 35), and pyrosomes (n = 5). Lines indicate linear regression of each nutritional metric to standard length and mass, colour coded by species (for sample sizes and regression results, see Supplementary Table 1).

Supplementary Table 1. Regression results and equations between length (mm, standard length used for fish species and mantle length for squids) and ED (kJ/g wet weight), % lipid (wet weight), % protein (wet weight) for five Pacific small pelagic species.

Length:Nutritional value						
Regression	**Common name**	**n**	**Rˆ2**	***F***	***p***	**Nutri. metric (kJ/g wet weight or % wet weight) = m * standard/mantle length (mm) + b**
Length (SL/ML):Energy density (kJ/g wet weight)	Northern anchovy	31	0.051	F(1,29) = 1.552	0.2228	y = 0.014 x + 4.1
	Bigfin lanternfish	32	0.63	F(1,30) = 51.97	**5.05E-08**	y = 0.11 x -1.2
	Boreal clubhook squid	23	0.4	F(1,21) = 14.19	**0.001131**	y = 0.012 x + 3.3
	Market squid	35	0.18	F(1,33) = 7.478	**0.009965**	y = 0.0071 x + 3.7
	Pyrosome	5	0.62	F(1,3) = 4.884	0.1141	y = 0.0016 x + 0.39
Length (SL/ML):Lipid (% wet weight)	Northern anchovy	31	0.019	F(1,29) = 0.5555	0.4621	y = 0.021 x + 2.2
	Bigfin lanternfish	32	0.63	F(1,30) = 51.27	**5.76E-08**	y = 0.26 x -11
	Boreal clubhook squid	23	0.066	F(1,21) = 1.475	0.2381	y = 0.0042 x + 1.4
	Market squid	35	0.095	F(1,33) = 3.465	0.07162	y = -0.0024 x + 1.5
	Pyrosome	5	0.061	F(1,3) = 0.1956	0.6882	y = -2E-04 x + 0.23
Length (SL/ML):Protein (% wet weight)	Northern anchovy	31	0.25	F(1,29) = 9.918	**0.003776**	y = 0.025 x + 13
	Bigfin lanternfish	32	0.029	F(1,30) = 0.9048	0.3491	y = 0.012 x + 14
	Boreal clubhook squid	23	0.47	F(1,21) = 18.74	**0.000296**	y = 0.042 x + 12
	Market squid	35	0.26	F(1,33) = 11.4	**0.001897**	y = 0.034 x + 13
	Pyrosome	5	0.74	F(1,3) = 8.57	0.06113	y = 0.0069 x + 1.2



Supplementary Figure 5. Boxplots of nutritional metrics (a) energy density, (b) % lipid, and (c) % protein by sex and maturity status for northern anchovy (n = 31), boreal clubhook squid (n = 23), market squid (n = 35).