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Energy densities of key prey species in the California Current Ecosystem

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The energetic content of primary and secondary consumers is central to understanding ecosystem functioning, community assembly, and trophodynamics. However, these foundational data are often limited, especially for marine ecosystems. Here we report the energy densities of important prey species in the California Current Ecosystem. We investigated variation in energy density within and between species and explored potential underlying causes of these differences. Northern anchovy (*Engraulis mordax*) is the most energy dense of the species analyzed with a median value nearly twice as high as was found in krill (*Euphausia pacifica* and *Thysanoessa spinifera*). Relationships with body size varied among species; krill energy density increased, with both length and wet weight. In addition, we find that anchovy, sardine (*Sardinops sagax*), and market squid (*Doryteuthis opalescens*) have higher energy content in the summer and fall as compared to the spring. This aligns with the ecosystem phenology of strong upwelling during spring (March – May) driving high primary productivity, followed by widespread predator presence through the summer and fall (June – October). Our results inform food web studies in the California Current and suggest new avenues for investigating differences in species and ecosystem energetics in an era of rapid global change.

KEYWORDS

bioenergetics, trophic ecology, calorimetry, California Current, forage fish, krill

Introduction

Understanding the flow of energy from prey to predators gives insight into ecosystem production and functioning in that the energy available at the lowest trophic levels limits potential production at higher trophic levels (Paine, 1972). The energetic content of prey species themselves is also likely to vary based on seasonality, sex, ontogeny, and other factors. Together with trophic efficiency, based on energy loss as it transfers up trophic

levels, these fundamental parameters mediate the proportion of that energy that ultimately supports predator populations and thus overall food web structure and productivity (Eddy et al., 2021). Despite the importance of these fundamental data, the energy content of prey species (primary and secondary consumers) remains poorly understood, particularly in marine ecosystems that are undergoing rapid environmental change. It is well established that energy density within food webs is influenced by environmental conditions. In the North Pacific, for example, the marine heatwave in 2015 and 2016 resulted in smaller krill (Robertson and Bjorkstedt, 2020), which may lead to lower energetic quality. Similarly, the 2015-2016 heatwave caused a decline in nutritional quality of Pacific sand lance (*Ammodytes personatus*), a forage fish species, in Prince William Sound, Alaska (Von Biela et al., 2019).

The California Current Large Marine Ecosystem (CCLME) is a highly productive ecosystem along the west coast of North America where wind-driven, coastal upwelling brings nutrient-rich deep waters to the surface. These physical forcings in the spring underlie strong primary production in the late spring and summer, which are the basis for a rich and biodiverse ecosystem (Checkley and Barth, 2009). The CCLME supports commercial fisheries and a robust ecotourism industry focused on resident and migratory predators, including fish, seabirds, and marine mammals, all of which rely on the prey from this ecosystem. Several studies have reported the energy densities of similar species in other ecosystems (Mr°rtensson et al., 1996; Davis et al., 1998; Abraham and Sydeman, 2006; Tirelli et al., 2006; Dubreuil and Petitgas, 2009; Färber-Lorda et al., 2009; Sánchez et al., 2013; Albo-Puigserver et al., 2017; Chenowith, 2018); however, there has been little published work on important prey species in the CCLME. Without these data it is challenging to develop bioenergetic models for this ecosystem (Dawson et al., 2020; Lawson et al., 2021).

Euphausiids (*Euphausia pacifica* and *Thysanoessa spinifera*; hereafter 'krill'), northern anchovy (*Engraulis mordax*; hereafter 'anchovy'), Pacific sardine (*Sardinops sagax*; hereafter 'sardine'), and market squid (*Doryteuthis opalescens*) are fundamental prey for predators including large fish, seabirds, and marine mammals throughout the CCLME (Szoboszlai et al., 2015). In addition, krill are key prey for anchovy, sardine, and market squid. Several predators in the CCLME specialize in krill including Cassin's auklet (*Ptychoramphus aleuticus*) and blue whale (*Balaenoptera musculus*); krill are also important prey for several species targeted by regional commercial and recreational fisheries, including Chinook salmon (*Oncorhynchus tshawytscha*) and anchovy (Miller et al., 2010). Forage fish, such as anchovy and sardine, are vital mid-trophic links between the base of the food web and top predators. Furthermore, the recent cultural history of some regions of the CCLME, like Monterey Bay, is inextricably linked to these forage fish and the canneries that operated in the 20th-century to harvest them (Palumbi and Sotka, 2011). Market squid comprise Monterey Bay's largest modern fishery by landings and are important mesopelagic prey for various predatory fish, toothed whales, and seabirds (Vojkovich, 1998; Szoboszlai et al., 2015; Wells et al., 2017; Thompson et al., 2019). Here, we measured the energetic content of krill, anchovy, sardine, and market squid from late spring through early fall in the CCLME. A better understanding of the energetics of these key prey species will provide useful data for fisheries, ecosystem ecology, and understanding responses of foodwebs in the CCLME to environmental change.

Methods

Sample collection

Krill samples were collected by the National Oceanic and Atmospheric Administration's (NOAA) Rockfish Recruitment and Ecosystem Assessment Survey (RREAS) in April and May of 2021, and separately in July of 2022 under State of California – Department of Fish and Wildlife SCIENTIFIC COLLECTING PERMIT S-210680001-21162-002 (Figure 1). Collected krill were grouped and frozen together, each group (i.e., individual net tow) were considered a separate "collection" as they will be referred to hereafter. A total of 3335 krill individuals weighing 194.34g total were tested in this study.

Samples of anchovy (n = 50), sardine (n = 59), and market squid (n = 115) were retrieved opportunistically from commercial fishing offload sites in Moss Landing and Monterey, CA USA. Market squid were collected in 2022, anchovy were collected in 2019, 2021, and 2022, sardine were collected in 2019 and 2022; these species were all collected between May and September. They were acquired from coastal waters of the southern Monterey Bay, and are distinct by species, general location, and date. These groups are hereafter referred to as "collections". Collections of all species were frozen and stored (approximately -20°C) until tested.

Protocol development

Energy density can be determined using various methods; calorimetry was chosen for this study as it is a common determination method in the literature, making the results easier to compare to reported values. In contrast, proximate consumption is another method commonly used in the literature which involves estimating the energy density of a biomass based on measured proportions of proteins, lipids, carbohydrates, and other energy-rich components. However, this is a more complex analytical procedure that was not required to answer our questions. Protocols for calorimetry were developed using published techniques (Paine, 1972; Davis et al., 1998; Tirelli et al., 2006; Dubreuil and Petitgas, 2009; Sánchez et al., 2013; Albo-Puigserver et al., 2017). Calorimetry requires thorough drying to ensure complete sample combustion. It is also important to minimize the volatilization of lipids and other energy-rich tissues during drying, which can occur even at low temperatures. Samples were dried in a lab oven at 60°C until near constant mass was achieved (Tirelli et al., 2006; Dubreuil and Petitgas, 2009; Sánchez et al., 2013; Albo-Puigserver et al., 2017). 60°C was chosen to minimize energy loss
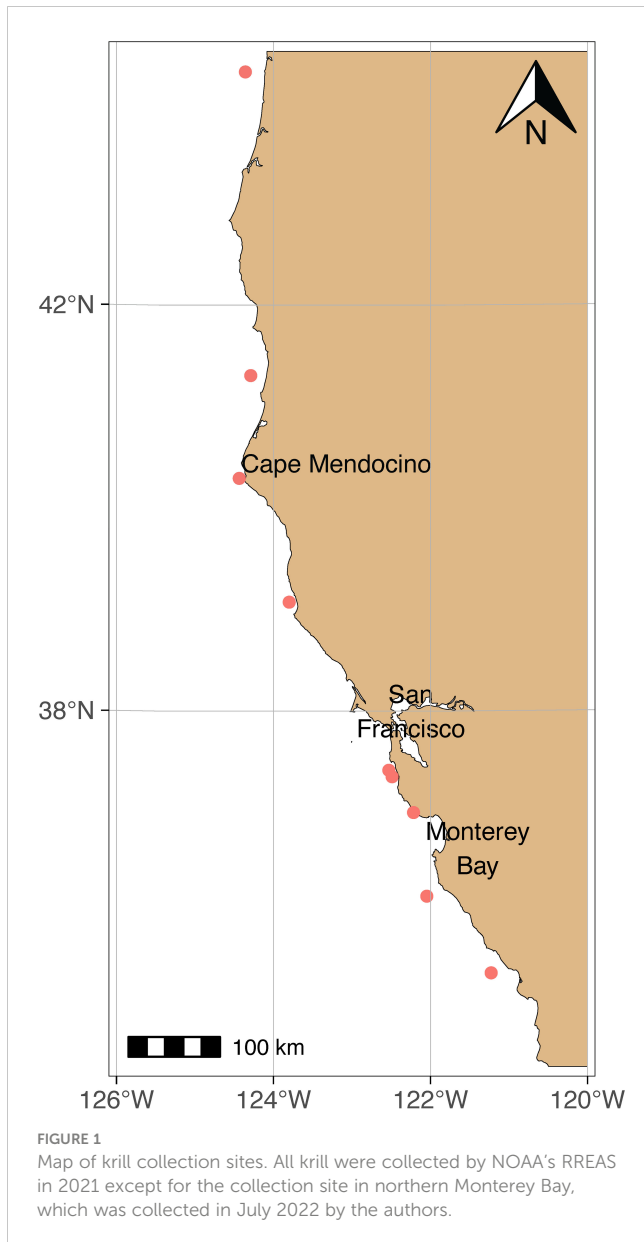
due to volatilization of energy-dense tissues. To determine appropriate drying times for each species, we used test samples of Antarctic krill (*E. superba*), Pacific sardine, and northern anchovy that were provided by the Monterey Bay Aquarium. A subset of test samples of market squid were taken from squid samples to be used for this study. Collections were removed from the freezer and allowed to thaw for one hour. At this point, it was possible to separate individuals from the larger mass of frozen samples which was returned to the freezer. After wet weight was recorded to the nearest 0.0001g using a microbalance, samples were placed in the drying oven and masses were subsequently measured every 24 hours. This process was repeated three times for krill, four times for squid, and five times for anchovy and sardine. Samples were determined to be sufficiently dry when the change in mass during a given drying period was less than 5% (Figure 2). Drying times determined by these methods were used for all subsequent experiments.

Calorimetry and ash-free dry weight

Collections were removed from the freezer and allowed to thaw for one hour. Individuals were separated from the larger mass of frozen samples which were then returned to the freezer. Samples were processed separately for either calorimetry or ash-free dry weight (AFDW), as both methods are destructive. Samples were blotted and their wet weights measured. All masses were recorded to the nearest 0.0001g using the same microbalance. Krill samples consisted of between 14 and 88 individuals grouped to a target weight of 2g wet weight and remained grouped for the entirety of the experiment. Krill samples were not sorted by species and were assumed to contain both *E. pacifica* and *T. spinifera*. Fish and squid samples were whole-body samples of single individuals. Length of each sample was recorded to the nearest 0.01mm. Fish total length was measured from the tip of the snout to the tip of the tail, ensuring that the tail was pinched together during measurement (Figure 3A). Squid mantle length was measured dorsally from the posterior tip to the anterior most point of the mantle (i.e., dorsal mantle length) (Kashiwada and Recksiek, 1979). Krill length was measured from the posterior of the eye to the end of the sixth body segment (Lawson et al., 2006). Samples were placed whole in a lab oven for varying times as previously determined (Figure 3B). After drying, the dry weight of each sample was recorded. Krill remained whole for both calorimetry and AFDW analysis while fish and squid were ground to a powder to ensure even combustion using a commercial coffee grinder, which was cleaned thoroughly between samples (Figure 3C). All samples were temporarily stored in Falcon tubes.

Due to small individual size and minimum mass requirements for proper combustion, krill samples were analyzed whole, and consisted of multiple dried individuals. For fish and squid, multiple ~1 g sub-samples of each dried and ground individual were compressed into pellets to ensure complete combustion. A minimum of three replicate pellets were combusted for each individual fish or squid. More pellets were combusted in cases when the reported gross heat values differed by more than 5%. Where possible, 10 samples of grouped krill, or 10 individual anchovy, sardine, and squid from each collection were analyzed. All samples were combusted in a Parr Instruments 6400 Automatic Isoperibol Calorimeter to determine gross heat. Energy densities are reported on a wet weight basis (Table 1).

When possible, five AFDW measurements were made for each collection. Dried samples were placed into a muffle furnace at 500° C; krill were combusted for 12 hours, anchovy and squid were combusted for 24 hours, and sardine were combusted for 36 hours (Figure 3D). The resulting ash was weighed using an analytical balance and subtracted from dry weight to give AFDW. Length, wet weight, water content, and ash content of AFDW samples are reported in Table 2. Wet weight energy density (E_W) was calculated using the following formula:

$$E_W = G * \frac{x_D}{x_W} * 10^{-6} \qquad (1)$$

where G is the gross heat of the dried sample in J kg^{-1}, x_D is dry weight of the sample in g, and x_W is wet weight of the sample in g Equation 1.
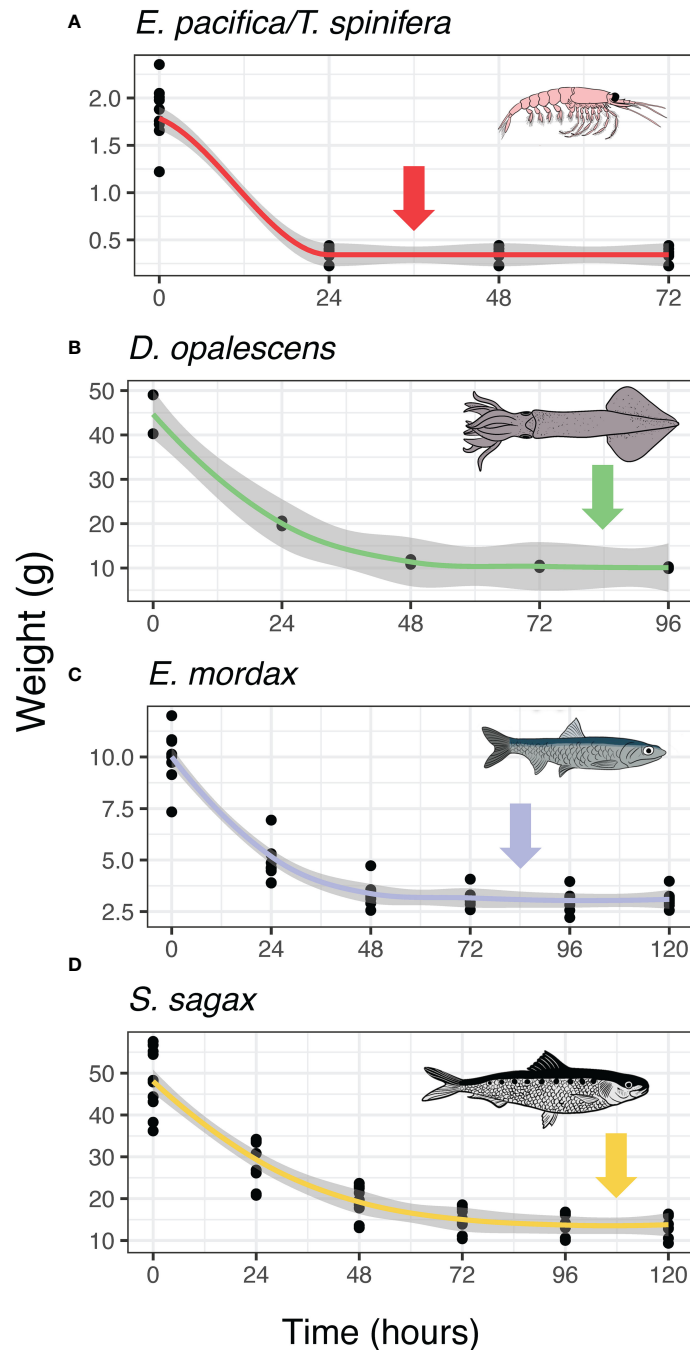
FIGURE 2
Drying curves for species in this study. Arrows indicate the drying period during which mass change was less than 5%. Drying time for krill **(A)** was 24 hours, drying time for squid **(B)**, and anchovy **(C)** was 72 hours, for sardine **(D)** drying time was 96 hours.

Statistical methods

To compare energetic differences within and between species, we used generalized linear mixed models using the package lme4 in R (Bates et al., 2014). The response variable for all models was energy density (either E_W or E_D), main effect predictors that were evaluated were either species, wet weight, or month. To control for pseudoreplication (Hurlbert, 1984), we used random effects of month (in models where month was not the main effect) and

year to control for inter-annual differences that were not the focus of this study. Year was not able to be used in models evaluating differences in squid energy density because squid were only collected in 2022. We used the package lmerTest (Kuznetsova et al., 2017) in R to test for statistical significance between levels of the interest within the main effect variable. For analysis within species by month, we used ordinary least squares regression as there were not ecologically relevant categories for random effects. For krill individual mass estimates, we divided the total mass of the
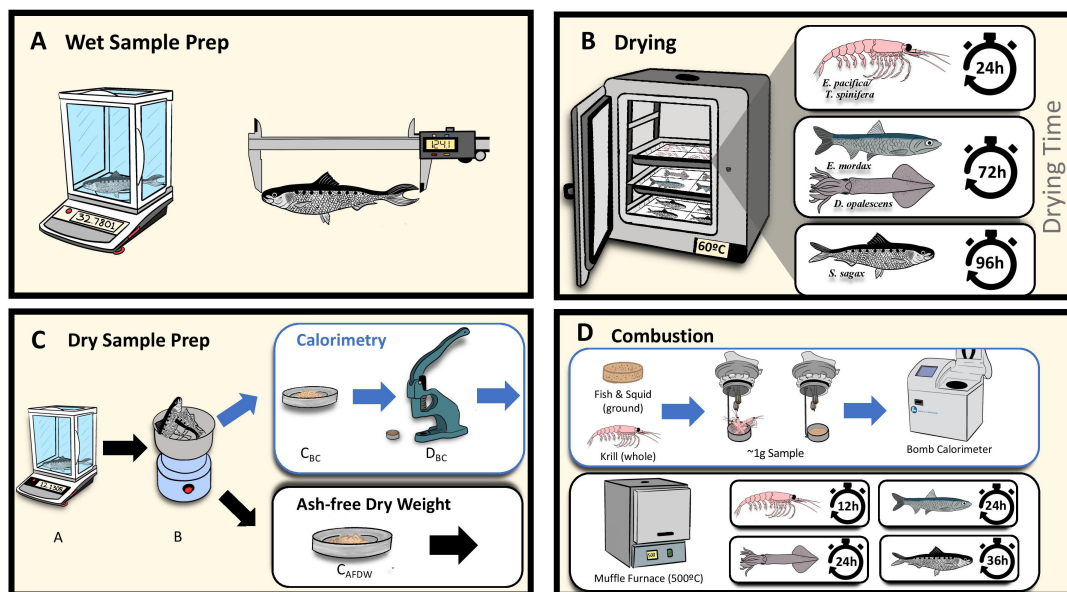
FIGURE 3
Experimental Workflow. **(A)** Wet Sample Prep: individual fish, squid, and grouped krill wet weight and lengths recorded. **(B)** Drying: samples dried in lab oven, time dependent on species. **(C)** Dry Sample Prep: sample dry weights recorded after drying. For calorimetry, fish and squid were homogenized with a grinder and compressed into ~1g sub-samples, krill remained whole. **(D)** Combustion: Samples combusted in calorimeter. AFDW samples placed in muffle furnace for varying time depending on species, remaining ash weighed. See methods for more details.

subsample prior to dying and combustion by the number of individuals in the subsample. Unless otherwise indicated, we report medians and interquartile range (IQR) as measures of central tendency.

Results

Overall, anchovy E_W was 7.85 (1.62) kJ g^{-1}, ahead of sardine 6.66 (1.75) kJ g^{-1}, squid 4.85 (0.83) kJ g^{-1}, and krill 4.22 (1.64) kJ g^{-1}

TABLE 1 Energy density, length, wet weight, and water content for each study species.

Species	Season	Year	n	Median energy density (kJ/g wet weight) $\pm$ IQR	Mean energy density (kJ/g wet weight) $\pm$ IQR	Mean length (mm) $\pm$ SD	Mean weight (g) $\pm$ SD	Mean Water Content (% Wet Weight) $\pm$ SD
E. pacifica/ T. spinifera	Spring	2021	2592	4.27 $\pm$ 0.74	4.41 $\pm$ 0.90	18.29 $\pm$ 1.45	0.08 $\pm$ 0.03	75.33 $\pm$ 5.02
E. pacifica/ T. spinifera	Summer	2022	743	3.21 $\pm$ 0.12	3.22 $\pm$ 0.12	16.91 $\pm$ 0.41	0.03 $\pm$ 0.003	78.07 $\pm$ 1.32
E. mordax	Summer	2019	10	8.52 $\pm$ 1.18	8.14 $\pm$ 0.63	116.06 $\pm$ 6.26	13.00 $\pm$ 2.48	66.85 $\pm$ 1.91
E. mordax	Summer	2021	10	7.75 $\pm$ 0.98	7.75 $\pm$ 0.53	122.43 $\pm$ 7.91	12.31 $\pm$ 2.95	68.06 $\pm$ 1.92
E. mordax	Spring	2022	10	6.80 $\pm$ 0.47	6.82 $\pm$ 0.34	129.06 $\pm$ 8.49	15.21 $\pm$ 1.45	70.02 $\pm$ 2.81
E. mordax	Summer	2022	20	8.01 $\pm$ 0.82	7.95 $\pm$ 0.49	130.28 $\pm$ 7.47	16.61 $\pm$ 2.63	64.75 $\pm$ 3.82
S. sagax	Summer	2019	10	6.18 $\pm$ 0.65	6.16 $\pm$ 0.34	164.47 $\pm$ 20.15	40.99 $\pm$ 12.59	67.33 $\pm$ 8.74
S. sagax	Spring	2022	10	4.39 $\pm$ 0.58	4.35 $\pm$ 0.49	199.95 $\pm$ 13.15	74.53 $\pm$ 11.72	72.87 $\pm$ 10.37
S. sagax	Summer	2022	39	7.15 $\pm$ 1.02	7.27 $\pm$ 0.80	182.16 $\pm$ 24.32	54.79 $\pm$ 20.71	65.88 $\pm$ 5.44
D. opalescens	Spring	2022	20	4.36 $\pm$ 0.50	4.36 $\pm$ 0.30	118.47 $\pm$ 10.20	39.54 $\pm$ 10.08	76.37 $\pm$ 3.09
D. opalescens	Summer	2022	95	4.90 $\pm$ 0.56	4.98 $\pm$ 0.40	119.01 $\pm$ 25.44	34.86 $\pm$ 8.96	75.33 $\pm$ 3.61

Spring refers to April and May, and summer refers to June, July, August, and September.

TABLE 2   Length, wet weight, water content, and ash content of AFDW samples.

Species	Season	Year	n	Mean length (mm) ± SD	Mean wet weight (g) ± SD	Mean Water Content (% wet weight) ± SD	Mean Ash Content (% dry weight) ± SD
E. pacifica/T. spinifera	Spring	2021	1315	18.42 ± 1.72	0.07 ± 0.03	76.59 ± 4.49	15.87 ± 3.70
E. pacifica/T. spinifera	Summer	2022	399	12.75 ± 0.53	0.03 ± 0.0008	80.53 ± 0.95	21.33 ± 2.36
E. mordax	Summer	2019	5	116.27 ± 2.02	12.43 ± 1.51	65.84 ± 4.75	9.82 ± 2.69
E. mordax	Summer	2021	5	121.26 ± 10.93	12.34 ± 3.36	68.83 ± 2.57	11.69 ± 1.51
E. mordax	Spring	2022	5	130.28 ± 11.28	16.40 ± 3.10	69.38 ± 7.11	9.48 ± 3.79
E. mordax	Summer	2022	6	132.78 ± 3.97	16.74 ± 2.81	66.93 ± 2.84	8.69 ± 1.38
S. sagax	Summer	2019	2	164.48 ± 13.19	41.58 ± 3.55	66.36 ± 4.11	8.77 ± 2.91
S. sagax	Spring	2022	3	188.19 ± 3.34	61.63 ± 4.81	71.57 ± 2.62	9.90 ± 1.05
S. sagax	Summer	2022	18	178.53 ± 30.45	51.91 ± 24.64	65.32 ± 5.83	9.40 ± 2.51
D. opalescens	Spring	2022	4	118.37 ± 12.26	34.14 ± 8.71	80.60 ± 4.73	5.64 ± 1.56
D. opalescens	Summer	2022	33	109.61 ± 11.90	30.54 ± 8.66	76.13 ± 3.22	5.97 ± 1.07

(Figure 4). Anchovy has a significantly greater energy density than sardine (E_W t-value = -9.76, $P < 0.001$; E_D t-value = -19.78, $P < 0.001$) and squid (E_W t-value = -27.18, $P < 0.001$; E_D t-value = -38.95, $P < 0.001$). Krill had the lowest energy density, less than squid, though the mean difference was < 0.5 kJ g^{-1} (E_W t-value = -14.76, $P < 0.001$; E_D t-value = -23.72, $P < 0.001$).

Market squid showed the lowest variation in energy density, whereas the greatest variation was found in sardine (Figure 4). Sardine and anchovy reported comparable amounts of water content which tended to be lower than either krill or squid. Ash content was highest in krill and lowest in squid with sardine and anchovy ash contents being comparable. There were no significant relationships for squid energy density (E_W) in relation to size (length: t-value = -1.69, P = 0.09; weight: t-value = -0.16, P = 0.87; Figure 5). The same was true of sardine (length: t-value = 0.41, P = 0.73; weight: t-value = 0.53, P = 0.60; Figure 5). Anchovy energy density showed a positive relationship with weight (t-value 5.12, $P < 0.001$), but no relationship with length (t-value = 1.75,
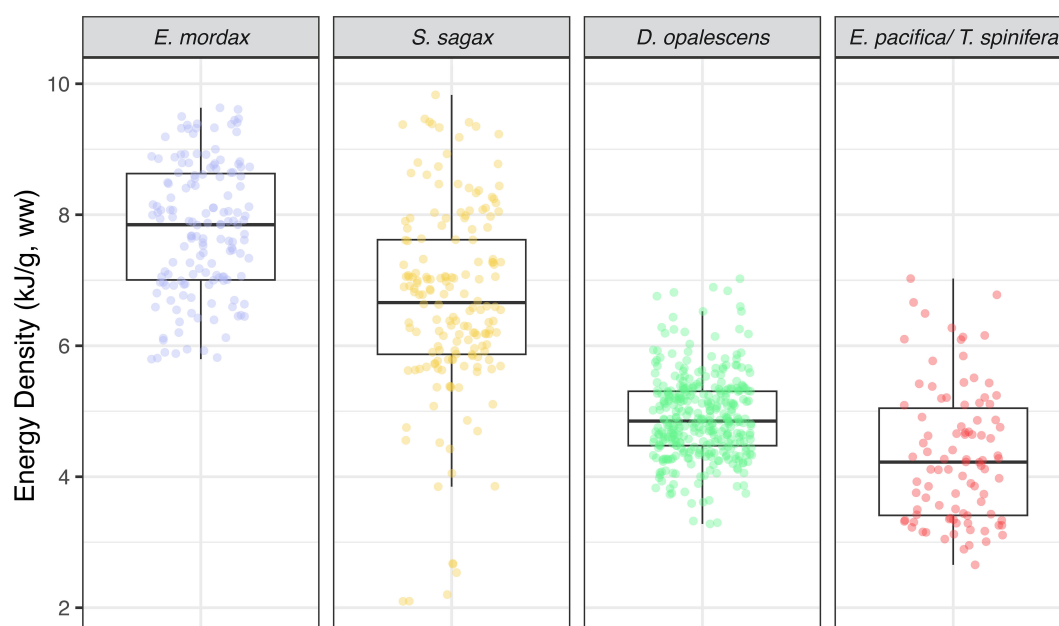

FIGURE 4
Energy densities (E_W) of study species. Boxplots for anchovy, sardine, market squid, and krill respectively. The E_W values of the forage fish are considerably higher than either market squid or krill.
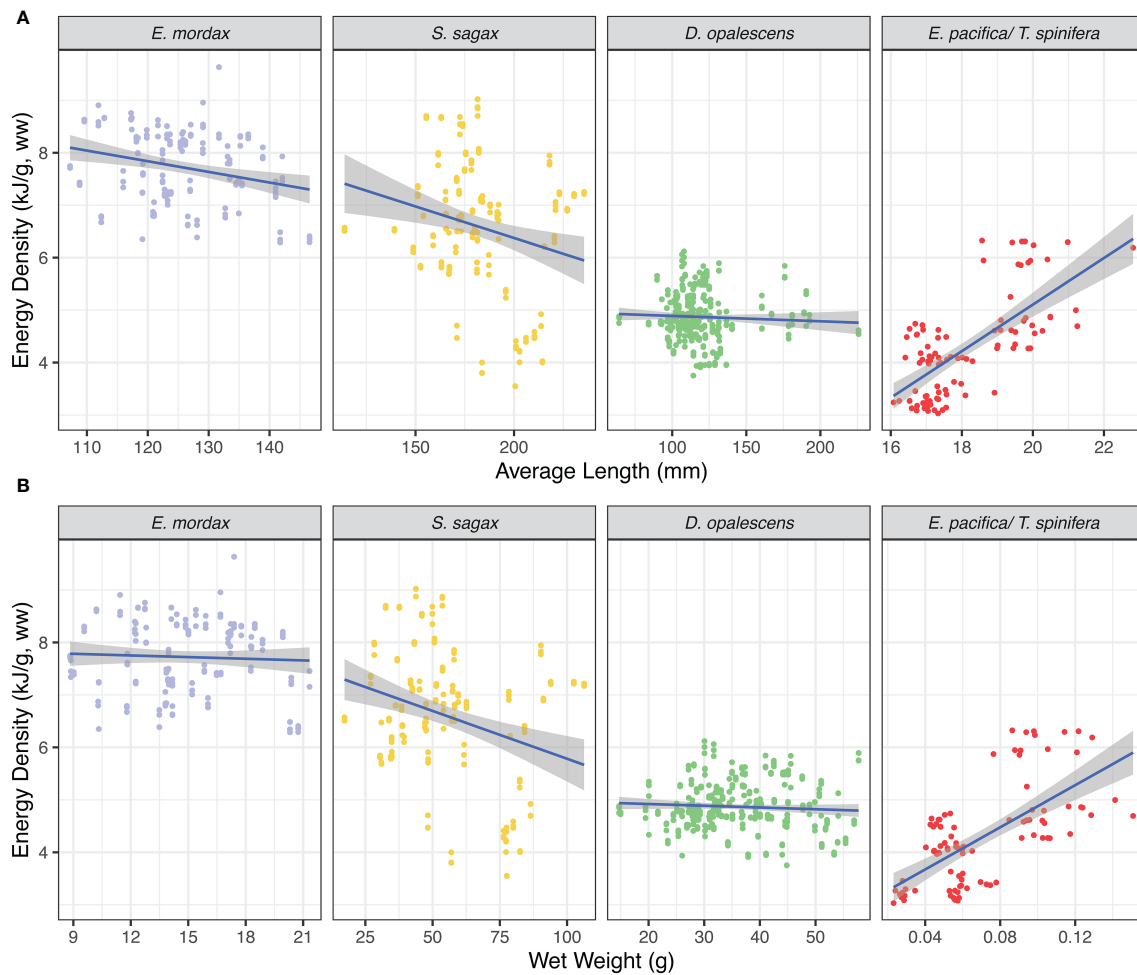
FIGURE 5
Relationships between energy density (E_W) and size. **(A)** E_W by length **(B)** E_W by weight; krill lengths and weights were a mean of the individuals in the sample.

P= 0.08; Figure 5). Energy density in krill showed a strong positive relationship for both length and weight (krill length: t-value = 5.88, *P*< 0.001; weight: t-value = -4.64, *P*< 0.001; Figure 5). Sufficient samples were available to test anchovy, sardine, and squid for energetic phenology from across seasons. For all three, energy densities increased significantly from late spring (May) to summer and early fall (June – September; anchovy: F-statistic = 14.65, *P*< 0.001; sardine: F-statistic = 26.86, *P*< 0.001; squid: F-statistic = 21.06, *P*< 0.001 Figure 6).

Discussion

Here, we report energy densities for four key prey groups in the CCLME collected from late spring to early fall. Overall, we find that forage fish are more energy dense than krill or squid (Figure 4). While these results are generally consistent with other studies for similar species, there are some notable discrepancies (Table 3). For example, our values for anchovy are higher than other values reported in the literature (Table 3). The overall lack of these fundamental data for these forage species in the primary literature is striking, especially considering their abundance and importance to the well-studied CCLME.

Within species, we found notable differences across seasons for certain groups. Specifically, we observed an increase in energy densities of forage fish and squid species from late spring (May) to the summer and early fall (June-September; Figure 6). This trend corresponds with the phenology of the ecosystem. During the early spring, upwelling winds drive high primary productivity, which persists throughout the spring and early summer months bolstering phytoplankton blooms that support primary consumers such as larval fish and krill, which subsequently support production at higher trophic levels (Cross et al., 2005; Checkley and Barth, 2009). As krill are a primary prey for other species in this study, increases in anchovy, sardine, and market squid energy densities from the spring to fall may reflect both increasing krill abundance (Cross et al., 2005) and lipid reserves, as has been found in the Oregon and Washington populations (Fisher et al., 2020). Other work has also uncovered seasonal variability in anchovy and sardine energy densities related to ecosystem phenology (Gatti et al., 2018; Albo-Puigserver et al., 2020), though the effects ontogeny and differences in reproductive energy allocation strategies were also significant.
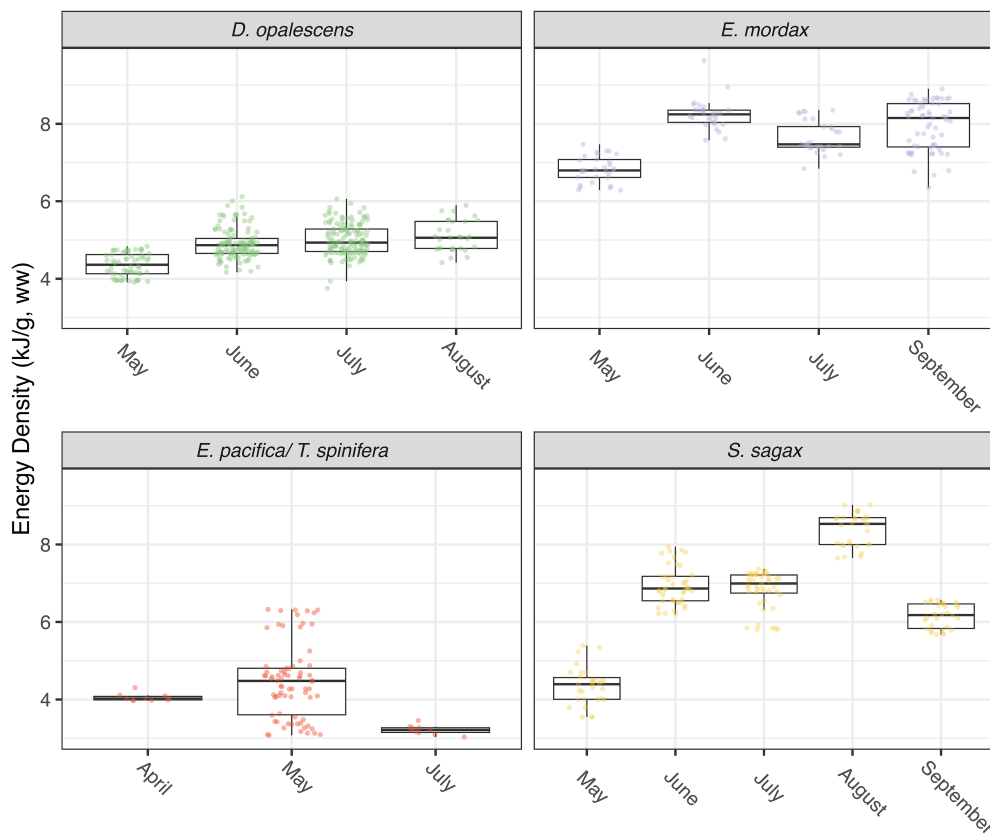
FIGURE 6
Boxplots showing energy density for each species by month of collection. Market squid were collected in 2022, anchovy were collected in 2019, 2021, and 2022, sardine were collected in 2019 and 2022, and krill were collected in 2021 and 2022.

TABLE 3 Comparison of energetic values found in this study to similar species in the literature.

Species	Location	Season	Year (s)	Mean Energy Density (kJ/g Wet Weight) ± SD	Mean Length (mm) ± SD or range	Source
E. pacifica/ T. spinifera	**California Current**	**Spring-Summer**	**2021-2022**	**4.33 ± 1.02**	**18.15 ± 1.44**	**This study**
Thysanoessa. sp.	NE Atlantic	Spring-Summer	1993	2.4		(Mårtensson et al., 1996)
Thyanoessa. sp.	NE Atlantic	Summer-Fall	1993	6.0 ± 1.3		(Mårtensson et al., 1996)
Thyanoessa. spp.	Bering Sea	–	1998	3.11		(Davis et al., 1998)
Krill	Northern Pacific (Sitka Sound)	–	2018	3.8		(Chenowith, 2018)
Krill	Northern Pacific (Seymour Canal)	–	2018	2.94		(Chenowith, 2018)
E. superba	South Georgia	Summer-Fall	1980	4.65 *		(Clarke, 1980)
E. mordax	**Monterey Bay**	**Spring-Summer**	**2019-2022**	**7.78 ± 1.00**	**125.65 ± 9.30**	**This study**

(Continued)

TABLE 3 Continued

Species	Location	Season	Year (s)	Mean Energy Density (kJ/g Wet Weight) ± SD	Mean Length (mm) ± SD or range	Source
E. encrasicolus	NE Atlantic (Bay of Biscay)	Fall	2009	5.2 ± 0.58	45-195	(Dubreuil and Petitgas, 2009)
E. encrasicolus	NE Atlantic (Bay of Biscay)	Spring	2009	6.01 ± 0.16	45-195	(Dubreuil and Petitgas, 2009)
E. encrasicolus	NW Mediterranean	Summer	2017	5.39 ± 0.57	121.9	(Albo-Puigserver et al., 2017)
E. encrasicolus	NW Mediterranean	Fall	2006	4.57	40-126.8	(Tirelli et al., 2006)
E. encrasicolus	NW Mediterranean	Spring	2006	4.35	70-132.5	(Tirelli et al., 2006)
S. sagax	**Monterey Bay**	**Spring-Summer**	**2019-2022**	**6.87 ± 1.69**	**182.18 ± 24.34**	**This study**
S. pilchardus	NW Mediterranean	Spring	2017	7.11 ± 1.03	134.2	(Albo-Puigserver et al., 2017)
S. pilchardus	NW Mediterranean	Summer	2017	6.56 ± 1.23	134.2	(Albo-Puigserver et al., 2017)
S. pilchardus	NW Mediterranean	Fall	2017	5.40 ± 0.55	134.2	(Albo-Puigserver et al., 2017)
S. pilchardus	NW Mediterranean	Winter	2017	5.21 ± 0.45	134.2	(Albo-Puigserver et al., 2017)
D. opalescens	**Monterey Bay**	**Spring-Summer**	**2022**	**4.91 ± 0.63**	**118.92 ± 23.52**	**This study**
Squid	North Pacific Ocean	–	1992-1995	3.06		(Davis et al., 1998)
Doryteuthis gahi	Patagonia	–	2007	4.95	60-90	(Croxall and Prince, 1982)

* Indicates that the value was calculated using proximate consumption. All other values were determined by bomb calorimetry.
Bolded values are values from this study.

These dynamics in the energy densities of fish, squid, and crustaceans have important ecological implications for higher trophic level predators. For example, the temporal patterns we find help explain why highly mobile predators, including seabirds, marine mammals, and predatory fish, aggregate in CCLME in the greatest numbers when their prey is abundant and most energy rich, during the summer and fall (Cross et al., 2005; Block et al., 2011), and spatial and temporal variability in their reproductive success (Warzybok et al., 2018).

For krill, our temporal sampling was too limited to test for differences in energy density related to season; however, changes in krill lipid reserves, likely reflecting energy density, related to phenology has been demonstrated in Oregon and Washington (Fisher et al., 2020). These dynamics many have important ecosystem implications. For example, recording krill energetic density before, during, and after blue whales arrive in Monterey Bay may shed light on how this species modulates the timing of their migration to and from the region (Abrahms et al., 2019; Oestreich et al., 2022). We demonstrated a strong positive relationship between size (both length and weight) and krill energy density (Figure 5). Similar findings have been reported for Antarctic krill (Färber-Lorda

et al., 2009), but not yet for krill in the eastern North Pacific. This result has important ecological implications, particularly given the emerging evidence that warm oceans, such as those in the CCLME during recent marine heatwaves, are associated with smaller sized krill for both krill species examined in our study (Robertson and Bjorkstedt, 2020; Killeen et al., 2022). The role of size, along with life stage, sex and species-specific (Färber-Lorda et al., 2009; Fisher et al., 2020), energy densities in mediating these shifts in krill structure is currently unknown and highlights the need to study the bioenergetics of krill, and other species such as forage fish and squid (Cross et al., 2005) that represent important links in marine food webs. Resolving how prey energy density varies in response to climate change and extreme climate events, such as marine heatwaves, could guide understanding and management of ecosystem health and resilience (Dawson et al., 2020). These results come at a critical time for the CCLME that is experiencing a rapid increase in cumulative anthropogenic stressors in recent decades (Calambokidis et al., 2019; Santora et al., 2020; Bograd et al., 2023).

While our study suggests that factors such as seasonality and size play an important role in explaining differences in energy densities, it is also important to consider other aspects that may

influence the observed variation within and among groups. For instance, in our study we were unable to account for known sex-specific differences in energy density in krill, anchovy and sardine, which vary with ontogeny (Färber-Lorda et al., 2009; Gatti et al., 2018; Albo-Puigserver et al., 2020) nor potential differences in seasonal energy density between *Euphausia pacifica* and *Thysanoessa spinifera* (Fisher et al., 2020). Reproductive cycles may play an important role in mediating energy density in mature individuals of both fish species independent of size, particularly anchovy which are known to exhibit a capital breeding strategy (McBride et al., 2015), accumulating fat in the spring through summer which is utilized for reproduction in the winter (Hunter and Leong, 1981). In addition, the observed variation in water content within sardine, which corresponded with variation in energy density, have been demonstrated elsewhere for sardine and other fish species (Wuenschel et al., 2006; Gatti et al., 2018) highlighting the importance of accounting for ontogeny or other physiological factors. Future studies should aim to account for these potential confounding factors to gain a more complete understanding of the drivers of energy density variation in marine prey species.

Nevertheless, our study outlines foundational understanding of the ecosystem energetics of the CCLME with potential implications for predicting how the environment will affect species and trophic dynamics in the region (Wells et al., 2017; Dawson et al., 2020; Lawson et al., 2021). By shedding light on the drivers of energy density variation among marine prey species, this work may ultimately inform our understanding of higher trophic level predator ecology, such as migration timing, foraging location, and reproductive success. Overall, our findings provide valuable insights into the energy content of CCLME prey species, which could prove instrumental in forecasting how this ecosystem will respond to future environmental change.

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: https://github.com/mssavoca/CCE_preyspp_energetics.

Ethics statement

Ethical approval was not required for the study involving animals in accordance with the local legislation and institutional requirements because samples were collected as part of commerical fishing operations or as part of NOAA cruises under State of California – Department of Fish and Wildlife SCIENTIFIC COLLECTING PERMIT S-210680001-21162-002.

Author contributions

SP: Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing. MS: Conceptualization, Data curation, Formal analysis, Methodology, Project administration, Software, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing. MK: Conceptualization, Data curation, Investigation, Methodology, Project administration, Supervision, Writing – review & editing. MC: Data curation, Software, Supervision, Validation, Writing – review & editing. DM: Data curation, Investigation, Resources, Writing – review & editing. SL: Methodology, Writing – review & editing. DC: Data curation, Project administration, Writing – review & editing. JG: Conceptualization, Funding acquisition, Project administration, Resources, Supervision, Writing – review & editing.

Conflict of interest

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

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