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*Review and Synthesis*

# Characterizing energy flow in kelp forest food webs: a geochemical review and call for additional research

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Kelp forests are highly productive coastal habitats that serve as biodiversity hotspots and provide valuable ecosystem services. Despite being one the largest marine biomes, kelp forests have been drastically understudied relative to other marine systems. Notably, while the role of kelp as habitat-forming, or 'foundation species', is well-documented, a comprehensive understanding of kelp forest food web structure is lacking, particularly regarding the importance of kelp-derived energy/nutrients to consumers. Here, we provide a biogeographic perspective on the energetic underpinning of kelp forests based on published literature. We targeted studies which used geochemical proxies – stable isotope analysis – to examine the transfer of carbon from kelp to local consumers. These studies (n = 94) were geographically skewed, with > 40% from Northern European Seas and Temperate Northeast Pacific. Quantitative estimates for the percentage of kelp energy (or kelp + macroalgae if sources were pooled) incorporated by local consumers came from 43 publications, which studied 141 species and 35 broader taxonomic groups. We examined these data for trends among functional groups and across upwelling regimes. No patterns are evident at present, perhaps due to the paucity or variability of available data. However, energetic subsides from kelps clearly support a wide range of diverse taxa around the globe. We also characterized biogeographic patterns in $\delta^{13}$C values of kelps and particulate organic matter (POM, a phytoplankton proxy), to evaluate potential limitations of stable isotope analysis in disentangling the relative contributions of pelagic versus benthic resources to coastal food webs. Globally, kelps and POM differed by > 4.5‰, but there was substantial variation among regions and kelp species. Accordingly, we discuss advances in stable isotope techniques which are facilitating more precise analysis of these complex energetic pathways. We end by proposing four main avenues of critical future research that will shed light on the resilience of these communities to global change.

Keywords: $^{13}$C, bulk tissue stable isotope analysis, compound-specific stable isotope analysis, energetic subsidies, macroalgae, nearshore consumers

## Introduction

Kelp forests are iconic nearshore ecosystems characterized by expansive swathes of fast-growing brown algae in the order Laminariales. These habitats are found along

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the coastline of every continent except for Antarctica and are widely distributed in temperate and northern polar latitudes (Dayton 1985, Steneck et al. 2002, Graham et al. 2007, Bolton 2010, Jayathilake and Costello 2021). The prolific production by kelp rivals that of tropical rainforests (Mann 1973) and provides a suite of important ecosystem services to local human communities (Mouritsen et al. 2021), including economic subsidies from direct harvesting (Vásquez et al. 2014), and the long-term sequestration of atmospheric $CO_2$ (Wilmers et al. 2012, Bennett et al. 2015, Queirós et al. 2019, Filbee-Dexter and Wernberg 2020). In addition, the complex three-dimensional 'forest' structure provided by kelps serves as home to a wide range of invertebrate and vertebrate consumers (Graham 2004, Fariña et al. 2008, Graham et al. 2008), many of which are also important natural resources (Vásquez et al. 2014). As with other marine habitats, kelp forests are currently facing a suite of direct and indirect threats from climate change and local human impacts (Steneck et al. 2002, Krumhansl et al. 2016, Rogers-Bennett and Catton 2019, Smale 2020). A clear picture of the structure of these ecosystems is thus a high priority to better understand and predict potential responses of kelp forest communities to ongoing global change.

Despite the conspicuous socioeconomic and ecological value of kelp forests, they have been drastically understudied relative to other productive coastal ecosystems such as coral reefs, mangroves and seagrass ecosystems (Fig. 1). While global declines in these latter habitats have driven a sharp increase in the number of studies since the 1990s, this has not been mirrored in kelp forests (Fig. 1). Indeed, despite recent evidence showing kelp forest cover in some regions is rapidly declining (Krumhansl et al. 2016), the state of our knowledge on kelp forest ecosystem functioning remains incomplete. Perhaps the largest knowledge gap relates to the dynamics of energy flow within kelp forest food webs. In stark contrast to the many works documenting kelp as a habitat-forming foundation species (Dayton 1985, Graham 2004, Miller et al. 2018), we have limited quantitative information regarding the use of kelp-derived energy and nutrients by consumers within these habitats. Early works on the topic (Mann 1988) suggested kelp may be an important resource for consumers due to 1) the tremendous amounts of biomass they produce (Mann 1973), which can greatly exceed that of associated phytoplankton (Fredriksen 2003, Kang et al. 2008, Paar et al. 2019), and 2) the fact that in some regions they can contribute year-round to the dissolved, and particulate organic matter pools (DOM and POM; Dyer et al. 2019a). Indeed, the assumed trophic associations of kelp forest consumers suggest an inherent linkage between kelp production and local food web structure (Graham 2004). However, the degree to which consumers rely on kelp-derived energy is poorly understood, and highly debated (Duggins and Eckman 1997, Miller and Page 2012, Docmac et al. 2017).

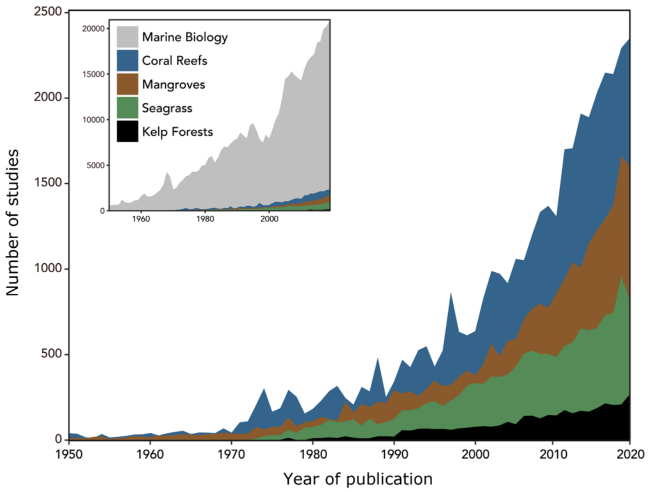

Figure 1. Studies of kelp forests lag behind other coastal ecosystems. Shown are the years of publication and number of studies for kelp forests (black), seagrass systems (green), mangrove habitats (brown) and coral reefs (blue). Data were compiled through the Web of Science search engine using separate searches for the following topics: 'kelp forest OR kelp OR kelp bed', 'coral reef', 'seagrass' and 'mangrove'. For each ecosystem, we counted papers from only the following research areas: 'environmental sciences ecology', 'zoology', 'marine freshwater biology', 'biodiversity conservation' and 'life sciences biomedicine other topics'. The complete list of citations for each ecosystem was then downloaded and plotted as a function of publication year. In addition, we compared these ecosystem-level trends to studies found using the topic 'marine biology'; this is depicted in the inset graph (marine biology shown in grey).

The main energetic pathways supporting kelp forest consumers can be broadly divided into two categories: benthic macroalgae production (presumably dominated by kelps), and pelagic phytoplankton production. The relative importance of each of these primary producer groups to consumers likely depends on several factors. For example, in the North Pacific, phytoplankton blooms are highly seasonal, occurring in late spring and early summer (Westberry et al. 2016), whereas several local kelp species (e.g. *Laminaria* spp., *Macrocystis pyrifera*, *Pterygophora californica*) are perennials (Duggins et al. 1989, Ramshaw et al. 2017). This makes kelp a potentially valuable source of energy to consumer communities in this region during periods of low phytoplankton production (Duggins et al. 1989, Elliott Smith et al. 2018). In contrast, in nearshore regions with high amounts of pelagic production year-round, such as in the Humboldt current of northern and central Chile, the phytoplankton-based energy channel provides a more consistent basal resource for consumers, and kelp-derived energy may be of minimal importance (Vargas et al. 2007, Docmac et al. 2017). In addition, the specific taxonomic groups present in the local ecosystem likely also matter, as kelp vary substantially in their concentrations of anti-herbivory compounds (Steinberg 1989). For example, nearshore consumers in areas such as Australasia, where local kelp species have high phlorotannin concentrations, may be less able to feed directly on live kelp tissues as compared to consumers in the temperate Northeast Pacific with relatively more 'palatable' kelp taxa (Estes and Steinberg 1988). Understanding the factors driving the importance of kelp versus phytoplankton production to local consumers is highly topical, as recent reviews have documented that coupling of pelagic and benthic resources can have strong implications for community stability and resilience (Rooney et al. 2006, Rooney and McCann 2012, Wolkovich et al. 2014). Despite this, other than the well-known patterns of trophic cascades in kelp-forest ecosystems (Estes and Palmisano 1974, Steneck et al. 2002), little work has been undertaken to characterize the biogeographic patterns of energy flow within kelp forests (but see Miller and Page 2012).

Here, we review the results of geochemical studies (Box 1) on kelp forests ecosystems globally and evaluate our current understanding of the structure of these food webs. We focus specifically on the use of $\delta^{13}$C analysis to trace the importance of different energy channels to kelp forest consumers. We review the geography of these studies, discuss the distribution of different functional groups that have been examined, and highlight both geographic and ecological areas that are noticeably understudied and represent critical areas for future research. Where sufficient data exist, we explore the patterns of energy flow in these dynamic systems. We also present a dataset of isotopic measurements from kelp, and particulate organic matter (a proxy for local phytoplankton) from around the globe. Finally, we discuss caveats associated with using geochemical techniques in kelp forests, and we highlight cutting-edge techniques that have the potential to fill in key knowledge gaps in our understanding of these dynamic ecosystems.

## Review methods and study criteria

We conducted our literature review using the Web of Science search engine with the following topics: 'kelp forest AND food web', 'kelp forest AND energy', 'kelp forest AND isotope' and 'kelp AND isotope'. We then selected studies which assessed energy flow to one or more food web compartments through stable isotope analysis; our broad criteria were the presentation of isotopic values for both local kelps and consumers (modern). When available, for each region we also included 1–3 studies which examined the natural isotopic variability of kelps in the context of better understanding/constraining consumer isotopic data (Wing et al. 2007, Dethier et al. 2013, Buchholz et al. 2019); we did not include data from experimental manipulations (Fox 2013). If papers presented a combination of field and laboratory data, we recorded only the field data. We likewise excluded papers which relied exclusively on invertebrate endmember proxies, sensu Post (2002), as these studies necessarily make assumptions regarding the energy channels used by benthic consumers. Following this initial selection, we checked the reference lists of all manuscripts for any additional studies that matched the above criteria for inclusion.

From each manuscript, we compiled data on the consumer and primary producer taxa analyzed, the time frame and sampling methodologies employed, and the locales/sites where the research was conducted. We binned studies according to

### Box 1. The use of geochemical tracers in marine food web studies

To understand the dynamics of marine food webs, researchers have increasingly utilized geochemical proxies, particularly the determination of stable isotope ratios of carbon ($\delta^{13}$C) and nitrogen ($\delta^{15}$N) in whole (bulk) tissues of autotrophic and consumer taxa (Newsome et al. 2010, Layman et al. 2012). Isotopic results are reported as delta values ($\delta$) via the following equation:

$$\delta^{13}\mathrm{C} \text{ or } \delta^{15}\mathrm{N} = 1000 \times \left[ \left( \frac{R_{\mathrm{sample}}}{R_{\mathrm{standard}}} \right) - 1 \right]$$

$R_{\mathrm{sample}}$ and $R_{\mathrm{standard}}$ are the $^{13}$C:$^{12}$C or $^{15}$N:$^{14}$N ratios of the sample and standard. The internationally accepted standards for $\delta^{13}$C and $\delta^{15}$N analysis are Vienna-Pee Dee Belemnite (VPDB) and atmospheric $N_2$, respectively. Delta notation units are parts per thousand, or per mil (‰) (Sharp 2017).

The utility of this methodology within kelp forests relies on a few key observations. Firstly, $\delta^{13}$C values in the marine environment vary widely among different clades of primary producers due to differences in the species of inorganic carbon utilized (Maberly et al. 1992), the presence of carbon concentrating mechanisms (Raven 2002), the biochemical structure of tissues (Stephenson et al. 1984, Fox 2013, Buchholz et al. 2019) and growth rates (Laws et al. 1995, Wing et al. 2007). In nearshore environments, kelps and seagrass typically have the highest $\delta^{13}$C values, whereas particulate organic matter (a proxy for phytoplankton) has much lower values; green and red algae can vary substantially along this spectrum (France 1995). Secondly, there are relatively predictable isotopic offsets between the tissues of a consumer and those of its diet which can be accounted for given appropriate knowledge of consumer physiology (Caut et al. 2009). Consequently, $\delta^{13}$C values in consumers provide a record of the basal source of production supporting the local food web. In addition, $\delta^{15}$N values of consumers can be used to provide a picture of trophic structure, as $^{14}$N is preferentially excreted (Vanderklift and Ponsard 2003), and so $\delta^{15}$N values tend to increase with increasing consumer trophic level. Isotopic analysis thus allows researchers to characterize both the overall structure of local food webs as well as the flows of energy from basal production sources through to top consumers.

the Marine Ecoregions of the World framework presented by Spalding et al. (2007); given the small number of studies, we binned by either by province or by realm. When presented by the authors, we recorded the estimated mean (or median) % contribution from kelps to consumer tissues. For several studies, a % contribution for benthic macroalgae was presented, and kelp contributions inferred from other data. To avoid biases based on repeated measures, where multiple % kelp contribution estimates were provided for the same species, we report averages based on the geographic distinctions made in the original study. For example, Ramshaw (2012) presents multiple kelp contribution estimates for consumer taxa in three different localities within British Columbia. For each region, % kelp estimates of each taxon were broken down by variables such as consumer size, or sampling season (Ramshaw 2012). Here, we present binned % kelp estimates for these consumers by each geographic region and report these data as independent means. Details for all such binning can be found in the Supporting information, and the full range of un-binned values for each province is provided in Table 2.

Our objective was to evaluate biogeographic patterns in the importance of kelp-derived energy/carbon to consumer functional groups across the globe. However, there are limitations in the compiled dataset (Supporting information) that precluded fine-scale quantitative analyses. These include 1) the small number of studies that directly quantified the importance of kelp-derived energy to consumers, 2) geographic disparities in research effort and 3) large variability in estimated kelp contributions within functional groups and regions. Indeed, most provinces are highly under-sampled and the estimated average kelp contribution to a regional food web can be changed by more than 50% with the inclusion or exclusion of 5–7 species (Supporting information). Thus, we present a qualitative analysis of the consumer data, along with ANOVA, to explore patterns of kelp contribution to different consumer functional groups at broad biogeographic scales. We analyzed consumer groups with the largest datasets: suspension feeders, carnivores and grazer/herbivores (Supporting information). We used one-way ANOVA to test for differences in the mean contribution of kelp-derived energy (% kelp contribution) among functional groups. We then explored differences in % kelp contribution among realms for each functional group, excluding realms with $n < 10$ for a given group. Finally, we tested for potential effects of oceanographic conditions on the energetic pathways within local kelp forests by comparing % kelp contributions from localities with no major upwelling regimes (e.g. not on an Eastern Boundary Current), versus those with seasonal or consistent upwelling (see Kämpf and Chapman 2016 and the Supporting information for all designations), for each functional group. For carnivores and suspension feeders, we pooled data from upwelling regions for analysis due to small and uneven sample size.

This review also provided the opportunity to assess potential limitations of a bulk tissue stable isotope approach in characterizing energy flow in kelp forests (Stephenson et al. 1984, Miller and Page 2012, Dethier et al. 2013, Fox 2013, 2016, Dyer et al. 2019b). To this end, we examined 1) variability in $\delta^{13}C$ values within and among kelp species, 2) the degree of isotopic overlap between kelps and particulate organic matter (POM; a proxy for pelagic resources) both globally and among regions, 3) variation in $\delta^{13}C$ values of both kelps and POM as a function of local oceanography and 4) the potential effects of study methodology on the reported % kelp contribution to consumers.

To assess isotopic variability and regional overlap among primary producer endmembers, from each study we compiled reported isotopic data of kelps ($n = 284$) and POM ($n = 133$). For all analyses we used the finest-scale data available (e.g. individual replicates or mean values; Supporting information). To examine the taxonomic and geographic patterns of $\delta^{13}C$ values among kelps we compared $\delta^{13}C$ values of blade tissues across species within five of the most widely sampled genera (*Alaria*, *Ecklonia*, *Laminaria*, *Macrocystis*, *Saccharina*). To compare the global and regional overlap of endmembers in carbon isotope space, we used a non-parametric bootstrap resampling approach to conservatively estimate global mean values of kelp and POM $\delta^{13}C$ and their overlap. There was insufficient sampling of offshore versus

Table 1. Isotopic studies on kelp forest food webs.

| Marine region | Marine province° | Studies providing estimates for % kelp, (or kelp + macroalgae) to consumer taxa | Total number of studies |
|---|---|---|---|
| Arctic | 1 | 2* | 8 |
| Northern European Seas and Lusitanian | 2, 3 | 8 | 15 |
| Cold Temperate Northwest Atlantic | 5 | 1* | 6 |
| Temperate Northwest Pacific | 8, 9 | 0 | 7 |
| Cold Temperate Northeast Pacific | 10 | 8 | 15 |
| Warm Temperate Northeast Pacific | 11 | 4 | 10† |
| Temperate South America | 45, 48 | 4 | 9 |
| Temperate Southern Africa | 50, 51 | 1 | 4† |
| New Zealand | 53, 54 | 8 | 10 |
| Southern Australian Shelf | 56, 57, 58 | 4 | 6† |
| Subantarctic Islands | 59 | 3 | 4 |

°As defined by Spalding et al. (2007).
*Denotes one or more papers which determined % kelp contribution with alternative metrics (e.g. gut contents or fatty acid concentrations).
†Includes papers which spans multiple provinces.

Table 2. Contribution estimates of kelp, or a combined kelp + macroalgae endmember, to consumer taxa from surveyed studies.

| Province(s)[°] | Consumer taxa[*] | Realm-wide kelp diversity[•] genera (species) | Range in kelp contribution to consumer tissues (%) | Range in kelp + macroalgae contribution to consumer tissues (%) |
|---|---|---|---|---|
| Arctic | 14 | 5(14) | 0–76 | |
| Northern European Seas, Lusitanian | 65 | 5(11) | 0–100 | 41–100 |
| Cold Temperate Northeast Pacific | 34 | 19(29) | 1–100 | 88–99 |
| Warm Temperate Northeast Pacific | 15[†] | 19(29) | < 1–71[†] | |
| Warm Temperate Southeastern Pacific | 13 | 4(9) | 2–86 | 0–55 |
| Magellanic | 11 | 4(9) | 38–39 | 6–38 |
| Benguela, Aguhlas | 5 | 3(4) | 63–84 | |
| Subantarctic Islands | 2 | 2(7) | 33–41 | |
| Northern, Southern New Zealand | 23 | 3(7) | 24–95 | 19–100 |
| West Central, Southwest and Southeast Australian Shelf | 7 | 3(7) | 42–88 | 17–42 |

[°] As defined by Spalding et al. (2007).

[•] As listed in Bolton (2010).

[*] Includes broader taxonomic groups (e.g. 'Bryozoa, Porifera'), but does not include mixed communities (Kaehler et al. 2000, Queirós et al. 2019, Udy et al. 2019a).

[†] Does not include six fish species from Koenings et al. (2015) as this manuscript used benthic and pelagic invertebrate 'indicator species' (sensu Post 2002) to estimate kelp contributions.

nearshore POM within our reviewed studies to formally compare these sources, and on average their mean $\delta^{13}C$ values are similar (Supporting information). As such, we pooled all local POM data. For each biogeographic province (the finest geographic scale with sufficient data), we randomly sampled $\delta^{13}C$ values with replacement and calculated a mean for kelp, POM and their difference ($\Delta^{13}C_{POM\text{-}Kelp} = \delta^{13}C_{POM} - \delta^{13}C_{Kelp}$). We repeated this process 10 000 times to create a distribution from which we estimated the mean $\delta^{13}C$ value with 75 and 95% confidence intervals. We excluded South Australia because no POM data were available apart from one sample from Hyndes and Lavery (2005), which had an anomalously high $\delta^{13}C$ value ($-12.8$‰) consistent with seagrass contamination. We also pooled data from both islands of New Zealand and combined data from Portugal with the Northern European Seas province to due to low data density. To explore potential drivers of isotopic overlap between kelps and POM we also assessed the effects of oceanography on $\delta^{13}C$ values of these endmembers. We used one-way ANOVA to compare mean $\delta^{13}C$ values of kelps and POM sampled from regions without upwelling, versus areas with strong seasonal, or consistent upwelling (Kämpf and Chapman 2016).

Lastly, we assessed the potential effects of study methodology on the reported estimates of % kelp contribution to consumers. We focused on the methodologies for sampling potential sources (e.g. kelps and POM), and grouped studies according to three parameters: 1) the time frame of kelp sampling – specifically whether this occurred over just a single season and year, or a longer time frame, 2) the time frame of POM sampling using the same criteria and 3) the type of POM sampled – characterized as cultured, nearshore only, mixed (nearshore and offshore) or offshore only. We used ANOVA to examine whether there were systematic differences in the average % kelp contributions to consumers globally, as well as within realms, based on these methodological groupings. We found no significant effect of methodology on reported % kelp contribution to consumers, and thus do not discuss these patterns further (Supporting information).

## Ecological trends in kelp forest food webs

### Geographic and taxonomic gaps in research

With a few exceptions (e.g. Oman, eastern Russia and Argentina), the studies we reviewed span the known global distribution of kelp forests (Table 1, Fig. 2; Bolton 2010). However, strong geographic disparities in research effort are evident. Isotopic studies of kelp-forest food webs were overwhelmingly focused on high latitude regions of the Northern Hemisphere, particularly the temperate Northeast Pacific and Northern European Seas/Lusitanian. We found relatively few studies in Australia/Tasmania, the northeastern United States, South America and Southern Africa (Table 1, Fig. 2). Furthermore, less than half of the reviewed papers provided a quantitative metric of the % contribution of kelp (or kelp + macroalgae) to local consumers (Table 2); the rest relied on either qualitative discussions, or other metrics to infer kelp contribution, such as a shift in consumer $\delta^{13}C$ values (Simenstad et al. 1993, Hamilton et al. 2014), or a back-calculation of dietary isotopic values (Won et al. 2007, 2010).

We also found substantial gaps in the consumer taxa surveyed. In the Supporting information, we present a complete list of all the fauna for which a % contribution of kelp (or kelp + macroalgae) was reported: this is a total of 141 species, 35 broader taxonomic groups and nine mixed communities (e.g. invertebrate benthic meiofauna (Queirós et al. 2019)). Most of the surveyed fauna were invertebrate consumers (> 70% of species), primarily suspension feeders, followed by grazers/herbivores (Fig. 3). In some regions, this reflects the known distribution of biomass among functional groups and trophic levels (Paar et al. 2019). However, this is likely not the case in many areas, and the contribution of kelp-derived

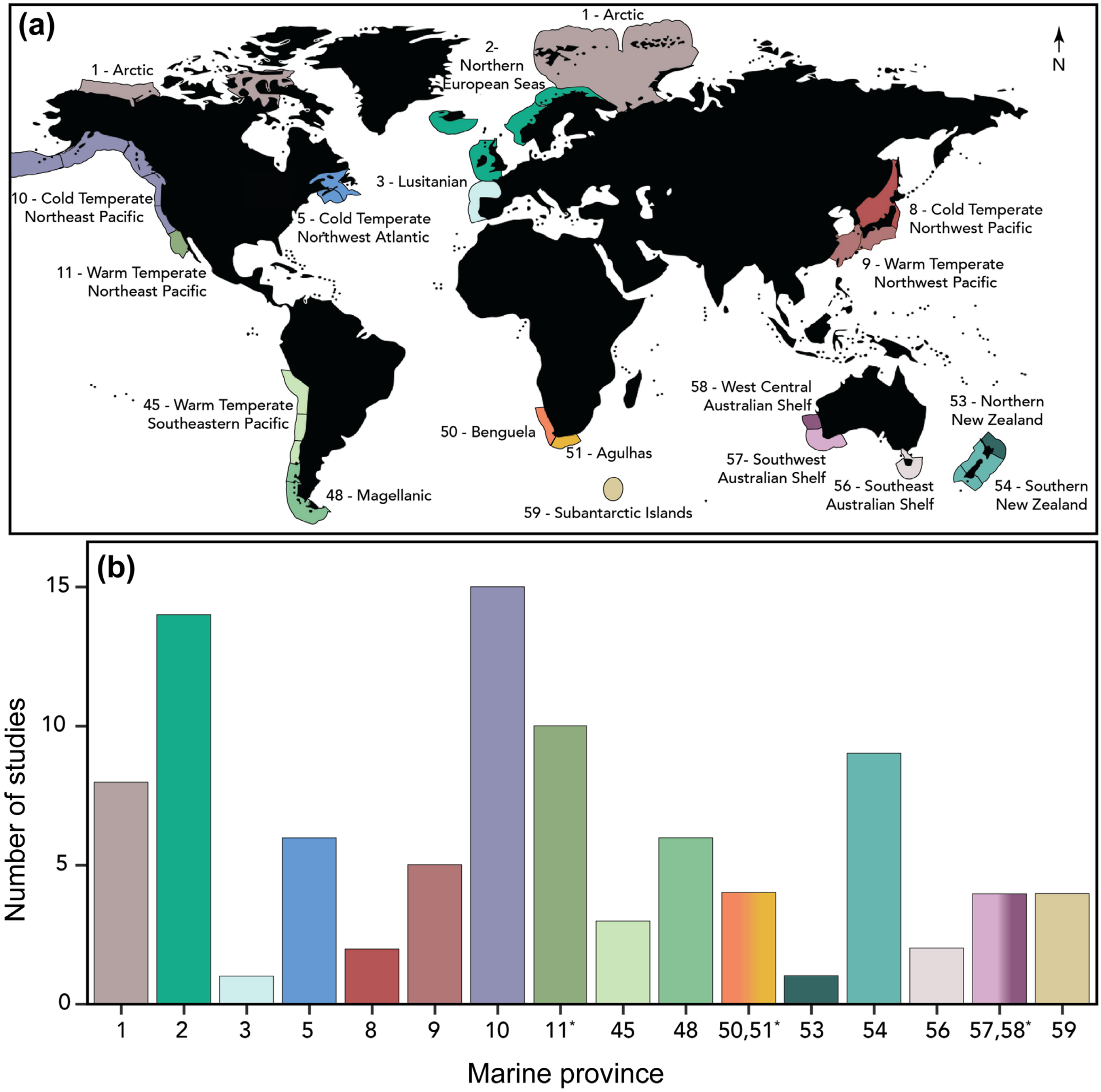

Figure 2. Geographic distribution of kelp forest food web papers utilizing stable isotope analysis. Studies were binned and labeled according to the marine provinces outlined by Spalding et al. (2007). Briefly, the criteria for study inclusion are the presentation of stable carbon isotope values ($\delta^{13}C$) of both local kelps and consumers. Also included are 1–3 papers per region on the isotopic variability in kelps as related to food web studies. See the main text for additional details. (a) shows the location of marine provinces with kelp forest stable isotope studies; colors correspond to provinces, with nested ecoregions indicated by black outlines on the map. (b) shows the distribution of reviewed studies across these provinces. Four studies spanned multiple marine provinces (*). For provinces 57 and 58 this was the case for two of the four papers reviewed, and we thus binned these regions. Similarly, we binned one study which spanned provinces 50 and 51 with three from province 50. In total we reviewed 94 papers from across the globe – the overwhelming majority of these came from studies of kelp forests in the Northern Hemisphere. Supporting information for a complete reference list.

energy to higher order consumers (carnivores) is particularly poorly characterized in many provinces (Fig. 3). Additionally, we found only a single estimated contribution from kelps to a mammalian consumer: in New Zealand, kelp and macroalgae constitute 60–90% of the basal carbon source for the dolphin *Tursiops* sp. (Lusseau and Wing 2006) highlighting both the potential importance of kelp-derived carbon at the highest trophic levels (Lesage et al. 2001) as well as the paucity of data for top predators that forage in kelp forests.

### Energy flow and kelp utilization by consumers

A main goal of this work was to characterize what is known about energy flow in kelp forest food webs across the globe, and to examine biogeographic patterns in the use of kelp-derived energy by consumers. Broadly, we had anticipated that the importance of kelp carbon/energy to local fauna would depend on a combination of consumer functional guild, local oceanographic conditions and kelp physiology. In contrast to these expectations, the data we compiled from the literature show no strong differences among functional groups globally (Fig. 4, ANOVA: $F_{2,222} = 2.306$, $p = 0.102$). Similarly, we did not find strong regional differences among consumers (Fig. 4, carnivores: $F_{2,50} = 0.296$, $p = 0.745$; suspension feeders: $F_{2,97} = 0.434$, $p = 0.649$; herbivores: $F_{3,39} = 3.506$, $p = 0.024$), although herbivores from tTemperate South America had lower mean % kelp contributions than those in Temperate Australasia (Tukey's HSD: $p = 0.036$). The effect of oceanographic region varied by consumer group (Fig. 5, carnivores: $F_{1,57} = 6.002$, $p = 0.017$; suspension feeders: $F_{1,116} = 0.006$, $p = 0.94$; herbivores: $F_{2,45} = 2.144$, $p = 0.129$), with the mean % kelp contribution to carnivore diets highest in areas with no upwelling (Tukey's HSD: $p = 0.023$). However, given the paucity of data in most provinces, and the high variability in the reported % kelp contributions we found for nearly every functional group and region (Fig. 4, 5), it remains unclear whether our findings are a result of low sample size or real ecological patterns. Regional differences observed among herbivores and oceanographic differences among carnivores should thus be interpreted with caution. Previous work suggests that kelp forest dynamics are largely driven by local scale phenomena (Krumhansl et al. 2016). Thus, it is possible that emergent patterns in the use of kelp-derived energy by consumers could be quantified were sufficient data available at more discrete biogeographic scales (e.g. marine 'ecoregion' rather than 'province' or 'realm'). Accordingly, we focus below on the mechanisms and pathways by which kelp-derived energy can support key functional groups, discuss broad patterns in our compiled data, and highlight fruitful avenues for future research.

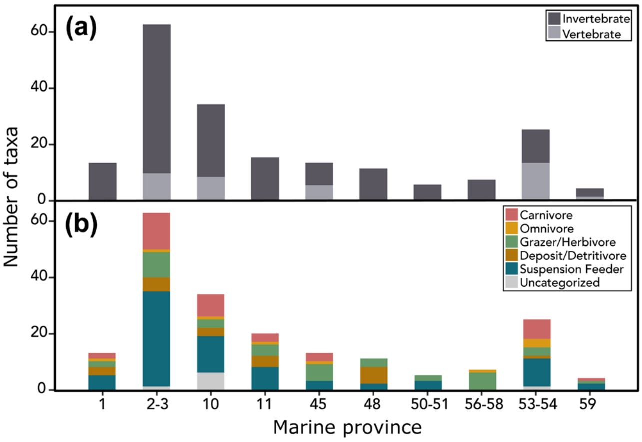

Figure 3. Fauna with quantified kelp contribution estimates. Data are binned by marine province; shown are the taxonomic identities (a), and functional groups (b) for all consumer taxa where quantified estimates of kelp, or a combined kelp + macroalgae endmember, were provided by surveyed studies. We include only the estimates that are based on stable isotope data (Table 1). For each province, we show the number of unique consumers broken down to the lowest taxonomic group; 17 taxa were identified only by broad taxonomic categories (e.g. Decapoda), and nine faunal groupings (see 'Uncategorized' in panel b) were presented as either mixed communities or unidentified beyond basic qualitative descriptions (e.g. benthic meiofauna). See the Supporting information for a list of all consumer species.

Perhaps the most intuitive pathway by which kelp production can support consumers is through direct grazing, where herbivorous taxa ingest fresh material, and then pass kelp-derived energy and nutrients through the food web when consumed by other fauna. The best examples of this come from taxa with well-known associations with kelp, such as sea urchins (Stephenson et al. 1986, Rodriguez 2003, Won et al. 2007, Kang et al. 2008, Wing et al. 2008, Vanderklift and Wernberg 2010, Kelly et al. 2012, Galloway et al. 2013, Zapata-Hernández et al. 2016, Elliott Smith et al. 2018, Paar et al. 2019), and 'saddle-shaped' limpets (Bustamante and Branch 1996, Dauby et al. 1998, Fredriksen 2003, Steinarsdóttir et al. 2009, Schaal et al. 2010, Leclerc et al. 2013b, Reddin et al. 2015). Our data from 40 grazing/herbivorous taxa across the globe found tremendous variability in the degree of kelp-derived energy used by this functional group (Fig. 4, 5). Indeed, the mean (or median) % kelp contribution for individual herbivore species could vary from ~0 to 100% in a single study (Ramshaw 2012, Elliott Smith et al. 2021). Unfortunately, the paucity of data from temperate Australasia (10 estimates from nine herbivorous taxa) precludes our ability to examine the effects of secondary metabolite concentrations in kelp tissues on the utilization of this resource by consumers. However, the data do hint at a potential biogeographic signal in the importance of kelp to nearshore herbivores. The mean % kelp contribution to herbivorous species is higher in regions without predictable upwelling (mean kelp contribution = 57%), relative to areas with seasonal (51%) or consistent (30%) upwelling regimes (Fig. 5). This is likely due to the dataset from temperate South America, which shows the lowest mean % kelp contribution (26.3%; Fig. 4) and includes one of the world's strongest upwelling systems (Thiel et al. 2007). However, there is insufficient data to determine if these patterns are truly a result of the perennial nature of kelp-derived energy in non-upwelling areas or an artifact of the data that are presently available.

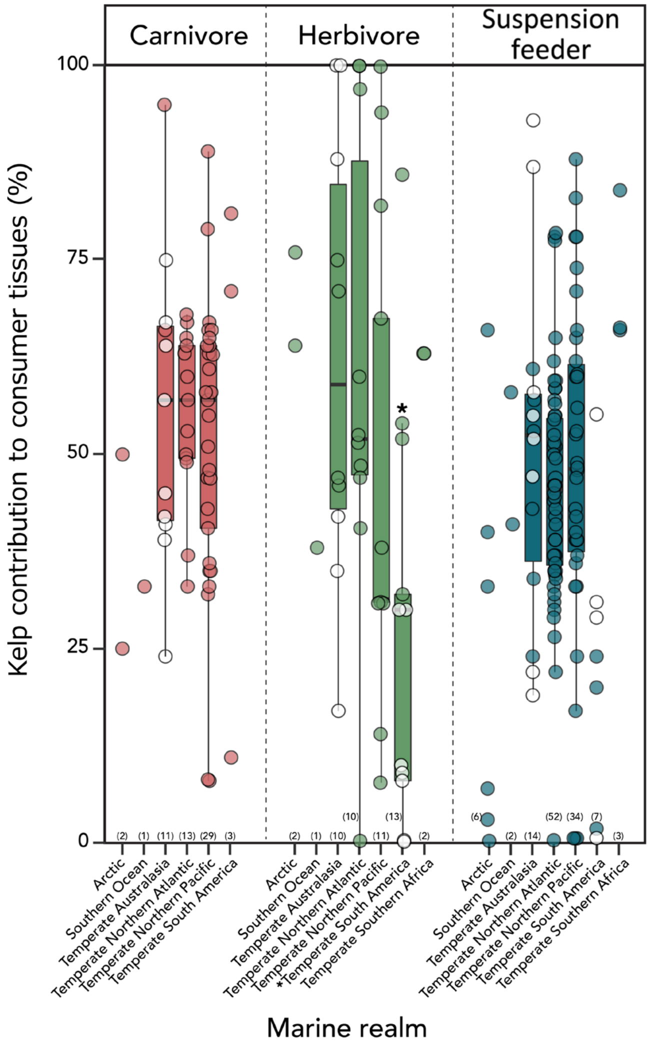

Figure 4. Kelp contributions to consumer functional groups across the globe. Box plots illustrate the spread of data around the median % contribution of kelp (filled circles; n = 189) or a combined kelp + macroalgae endmember (open circles; n = 36) to consumer functional groups with the largest datasets (Supporting information). Each point is a local mean (or median) contribution for a taxon. Consumers are grouped by their ecological identity as well as their geographical location within marine realms; sample sizes for each group provided parenthetically. For realms with sample sizes of < 10 we present the raw data points only. Data for herbivores from the temperate Northern Pacific includes a single estimate of 109% kelp for *Tegula pulligo* from Markel and Shurin (2015) which we have changed here to be 100%. For each functional group, an asterisk (*) indicates mean % kelp contribution estimates for a given realm that differ significantly from one or more regions.

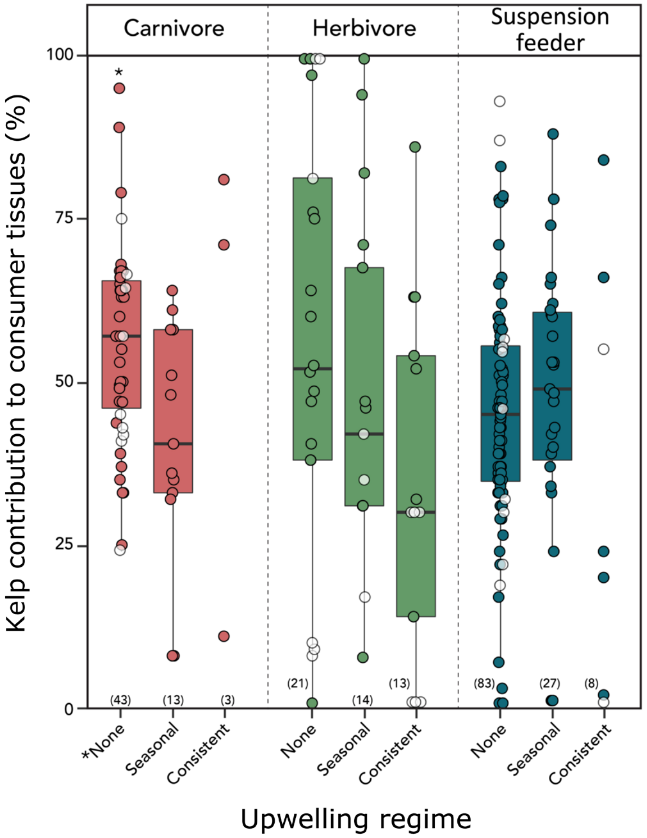

Figure 5. Kelp contributions to consumers across upwelling regimes. Plotted are the estimated contributions of kelp to the tissues of three consumer functional groups, binned by the upwelling regime of the respective province. Box plots illustrate the spread of data around the median % contribution of kelp (filled circles) or a combined kelp + macroalgae endmember (open circles) to these groups; each point is the local mean (or median) contribution for a taxon. Sample sizes for each bin provided parenthetically. For groups with sample sizes of < 10 we present the raw data points only. Data for herbivores from the temperate Northern Pacific includes a single estimate of 109% kelp for *Tegula pulligo* from Markel and Shurin (2015) which we have changed here to be 100%. For each functional group, an asterisk (*) indicates mean % kelp contribution estimates for a given upwelling regime that differs significantly from other regimes. Note that for carnivores and suspension feeders the 'Seasonal' and 'Continuous' upwelling categories were binned for analysis due to low sample size.

A second pathway for kelp-derived energy supporting nearshore consumers comes from the ingestion of kelp detritus. In this scenario, seasonal or continuous degradation of kelp lamina, and sloppy feeding by key herbivores (Yorke et al. 2019), results in a high contribution to the local particulate and dissolved organic material pools (POM and DOM). The 'kelp shrapnel' in POM/DOM can then be utilized by kelp forest fauna, either directly by suspension feeders, or by deposit feeders/detritivores once the detrital material has settled to the benthos. Importantly, reported changes in the isotopic composition of decaying kelp material are small in magnitude (e.g. −1.5‰ to 1.5‰), and generally fall within the range of live kelps (Fig. 6; Stephenson et al. 1986, Markel and Shurin 2015, Buchholz and Wiencke 2016, Buchholz et al. 2019, Gabara 2020). We suspect this is the main route through which kelp-derived energy supports consumers for two reasons. First, kelps produce tremendous amounts of biomass each year (Adin and Riera 2003, Fredriksen 2003, Kang et al. 2008, Paar et al. 2019), most of which enters the detrital pool, rather than being grazed directly (Krumhansl and Scheibling 2012). When this detrital material is available to food webs depends on local kelp taxa, seasonality and hydrodynamic forces (Krumhansl and Scheibling 2012, de Bettignies et al. 2013). Broadly, erosion of kelp lamina occurs in autumn/winter, whereas dislodgement occurs predominantly in spring. Krumhansl and Scheibling (2012) for additional details. Second, kelp detritus may be a higher quality food source for consumers than fresh tissue; C:N ratios and phlorotannin concentrations in kelp detritus decrease quickly, presumably because of microbial activity (Duggins and Eckman 1997, Norderhaug et al. 2003, Krumhansl and Scheibling 2012, Pedersen et al. 2021). This does, however, vary among kelp species (Dethier et al. 2014). Thus, the opportunity for kelp material to be incorporated by suspension or deposit feeders is high, and this pathway should be available to taxa in all marine provinces.

As anticipated, we found evidence for the kelp-detrital pathway in nearly all provinces where suspension, or detrital/deposit feeding taxa were quantitatively examined for kelp contribution (Fig. 4). For example, in the cold temperate Northeast Pacific, detritus from *Macrocystis pyrifera* and *Nereocystis luetkeana* can comprise up to 58% of local POM pools (Ramshaw et al. 2017) and kelp can contribute substantial energetic subsides to local suspension feeders (Duggins et al. 1989, Tallis 2009, Ramshaw 2012, Elliott Smith et al. 2018). Similarly, in the Northern European Seas, the kelp *Laminaria hyperborea* functions as a pseudo-perennial, with blade decay occurring in late summer through fall (Lüning 1979), and aged kelp particles becoming resuspended and incorporated by suspension or deposit feeders living within kelp holdfasts (Schaal et al. 2012, Leclerc et al. 2013a). We found no relationship between the utilization of kelp-derived energy by suspension feeders and the degree of upwelling (Fig. 5; ANOVA: $F_{1,116} = 0.006$, $p = 0.94$). However, as mentioned above, there was substantial variation around these estimates, and this pattern should be reexamined once sufficient data exists at more appropriate biogeographic scales.

Given the small number of stable isotope studies that have been conducted globally (Fig. 2), it is not surprising that we cannot presently draw conclusions regarding biogeographic patterns in kelp forest food web dynamics. However, the dataset we have compiled here is novel and represents a critical step towards a synthetic understanding of kelp forest ecosystems. It is evident that kelps provide substantial energetic subsides to a wide range of fauna, both within coastal food webs, and in adjacent ecosystems (Kaehler et al. 2006, Hansen et al. 2019, Olson et al. 2019, Queirós et al. 2019). Thus, the importance of kelp-derived energy should not be immediately overlooked or presumed negligible, and we anticipate that future research will continue to uncover energetic contributions from kelp to a wide range of consumer species.

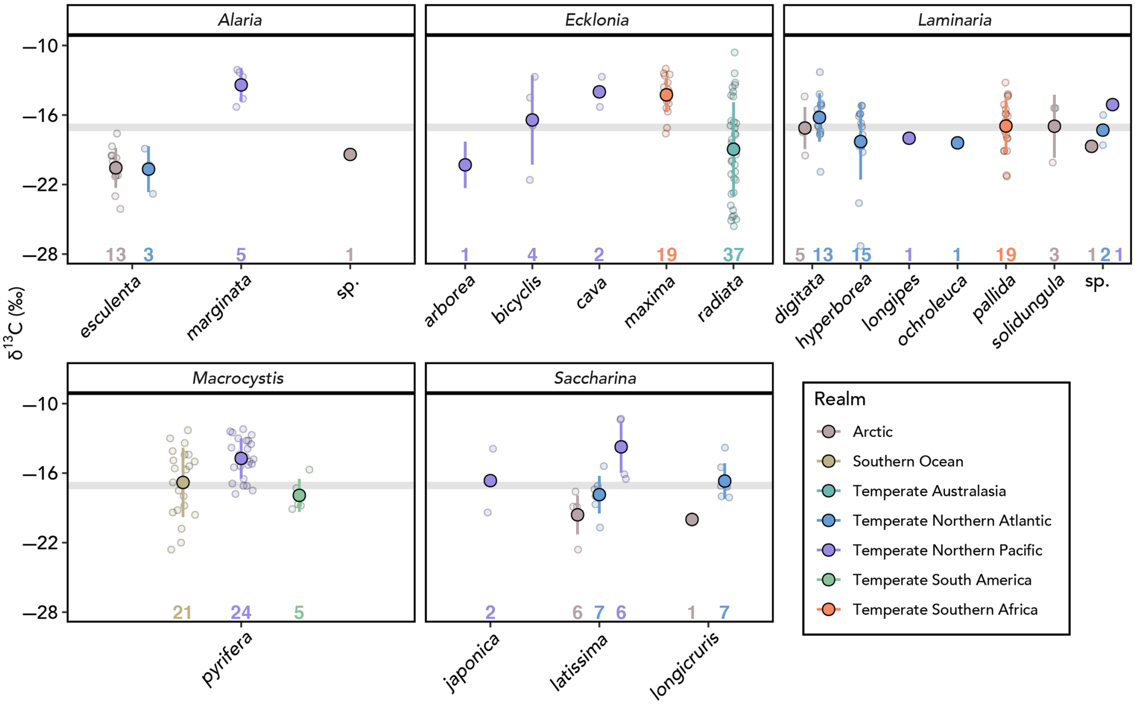

Figure 6. Taxonomic variation in kelp $\delta^{13}C$ values worldwide. Kelp $\delta^{13}C$ values (blades only) are organized by the five most widely sampled genera and presented at the species level. All raw values from the literature are shown as translucent points with larger points representing mean ± SD. For taxa with only one unique observation the data point represents the mean reported in the study. For taxa with only two observations the mean represents the average of those two studies. Points are colored by realm (as defined by Spalding et al. 2007) and the numbers along the x-axis indicate the total number of $\delta^{13}C$ values obtained from the literature.

## Stable isotope analysis in kelp forest food webs

### Isotopic variation in kelp forest primary producer groups

Numerous studies have reported substantial variability in the $\delta^{13}$C values of kelps (Stephenson et al. 1984, Wing et al. 2007, Dethier et al. 2013, Buchholz et al. 2019, Dyer et al. 2019a), and some have even suggested that this variation makes stable isotope analysis of limited use in tracing energy flow through these systems (Stephenson et al. 1984). Indeed, kelp are unique among macroalgae in their capacity to translocate and store carbohydrate reserves (Parker 1963, Chapman and Craigie 1978, Dunton and Schell 1987), which can result in substantial $^{13}$C enrichment and intraindividual variability (Fox 2013, Drobnitch et al. 2018). Kelp $\delta^{13}$C values can also vary substantially among tissue types (Buchholz et al. 2019, Dyer et al. 2019b), and age or decay stage (Stephenson et al. 1986, Buchholz and Wiencke 2016, Buchholz et al. 2019). In addition, many kelps live in dynamic and seasonal environments which can strongly influence their strategies for growth and reproduction (Chapman and Craigie 1978, Lüning 1991, Henley and Dunton 1995), and in turn alter isotopic values (Wing et al. 2007, Fox 2016, Drobnitch et al. 2018, Dyer et al. 2019a). These factors likely contribute to the high degree of spatial and taxonomic variability in isotopic values that we found among kelp species (Fig. 6; Supporting information). Broadly, kelps from the Temperate North Pacific, including *Alaria marginata*, *Saccharina latissima* and *Ecklonia cava*, show the highest $\delta^{13}$C values (> −14‰; Fig. 6). Interestingly however, despite the greater diversity of kelp species in this region (Table 2) we do not find a greater degree of isotopic variation in Temperate Pacific kelps compared to other regions (Fig. 7). The genus *Laminaria* exhibited remarkable consistency across seven species and four geographic provinces, with most having $\delta^{13}$C values similar to our estimated global mean (−17.0‰; Fig. 6, 7). We also found evidence of an oceanographic signal (Supporting information); kelp growing in realms with strong or consistent upwelling have higher $\delta^{13}$C values, by 1.8‰ and 2.2‰ respectively, than those in non-upwelling areas ($F_{2,281} = 15.02$, $p < 0.001$).

Another frequently cited issue with an isotopic approach to characterizing energy flow in kelp forest food webs is the degree of isotopic overlap among the two dominant primary producer groups: kelps and phytoplankton (POM). Generally, kelps have higher $\delta^{13}$C values than phytoplankton (and other macroalgae) due to their reliance on carbon concentrating mechanisms and isotopically heavy $HCO_3^-$ (Wendt 1968, Maberly et al. 1992, Raven et al. 2002). However, the ability to distinguish isotopically between kelps and other primary producer groups is dependent on the species in question and their mode of inorganic carbon acquisition (Maberly et al. 1992, Raven et al. 2002). The $\delta^{13}$C values of phytoplankton can also vary substantially due to a variety of abiotic and biotic factors (Supporting information; Laws et al. 1995, Popp et al. 1998, Tagliabue and Bopp 2008), which can confound clear separation and compromise estimates of the contributions of these basal carbon sources to higher trophic levels. Furthermore, the contribution of kelps to dissolved organic, and inorganic nutrient pools can alter local seawater chemistry (Pfister et al. 2019) and may result in 'kelp-like' POM $\delta^{13}$C values if phytoplankton taxa are recycling kelp-derived DIC (Miller and Page 2012).

Despite these potential confounding factors, we found that at a global scale co-occurring POM and kelps differ in mean $\delta^{13}$C values by nearly 5.0‰ ([95% CI] = [−7.5‰, −0.5‰]; Fig. 7). This pattern held at every marine province we examined, and the isotopic offset was in the anticipated direction (France 1995), with kelps having higher mean $\delta^{13}$C values than POM. The magnitude of $\Delta^{13}C_{POM\text{-}Kelp}$ varied among regions, with the largest offset in the Warm Temperate Northwest Pacific, and the smallest offset in the Warm Temperate Southeastern Pacific (Fig. 7). The latter was the only province for which $\Delta^{13}C_{POM\text{-}Kelp}$ was not significantly different than zero, indicating that bulk tissue isotope analysis may be of limited use in this region; but we note that only a limited number of local studies met our review criteria ($n = 3$). The regional variability in $\Delta^{13}C_{POM\text{-}Kelp}$ may relate to the shifts in $\delta^{13}$C values we found in both kelp ($F_{2,281} = 15.02$, $p < 0.001$) and POM ($F_{2,130} = 16.53$, $p < 0.001$) as a function of upwelling regime (Supporting information). Notably, POM $\delta^{13}$C values increased to a greater extent than those of kelps (4.1‰ versus 2.2‰, respectively) when collected from areas of consistent upwelling which strongly suggests that local oceanography plays a key role in setting regional $\Delta^{13}C_{POM\text{-}Kelp}$. However, the small sample size for POM from consistent upwelling regions ($n = 5$) means that this result should be verified with additional research.

Broadly, our synthesis of the $\delta^{13}$C values of kelp and POM suggests that in most cases these important coastal endmembers are isotopically distinct and $\delta^{13}$C analysis is therefore useful for partitioning energetic contributions to kelp forest consumers. However, the seasonal, spatial and physiological sources of variability in both kelp and POM isotopic values that we describe and show (Fig. 6, 7; Supporting information) should be taken into consideration when designing field studies of kelp forests ecosystems, and researchers should avoid relying on producer isotope values from disparate time periods and localities (Dethier et al. 2013).

### Analytical advances

Although bulk tissue stable isotope analysis is a powerful tool in characterizing marine food web dynamics (Box 1), it requires careful consideration of the isotopic variability of relevant endmembers (Fig. 6, 7), and selection of appropriate trophic discrimination factors; for many species these data may be difficult to come by. Cutting-edge isotopic techniques offer potential solutions to these issues and are rapidly becoming more affordable and accessible to ecologists (Whiteman et al. 2019). The isotopic analysis of molecular components from organic tissues, termed compound-specific stable isotope analysis (CSIA), has strong potential to trace

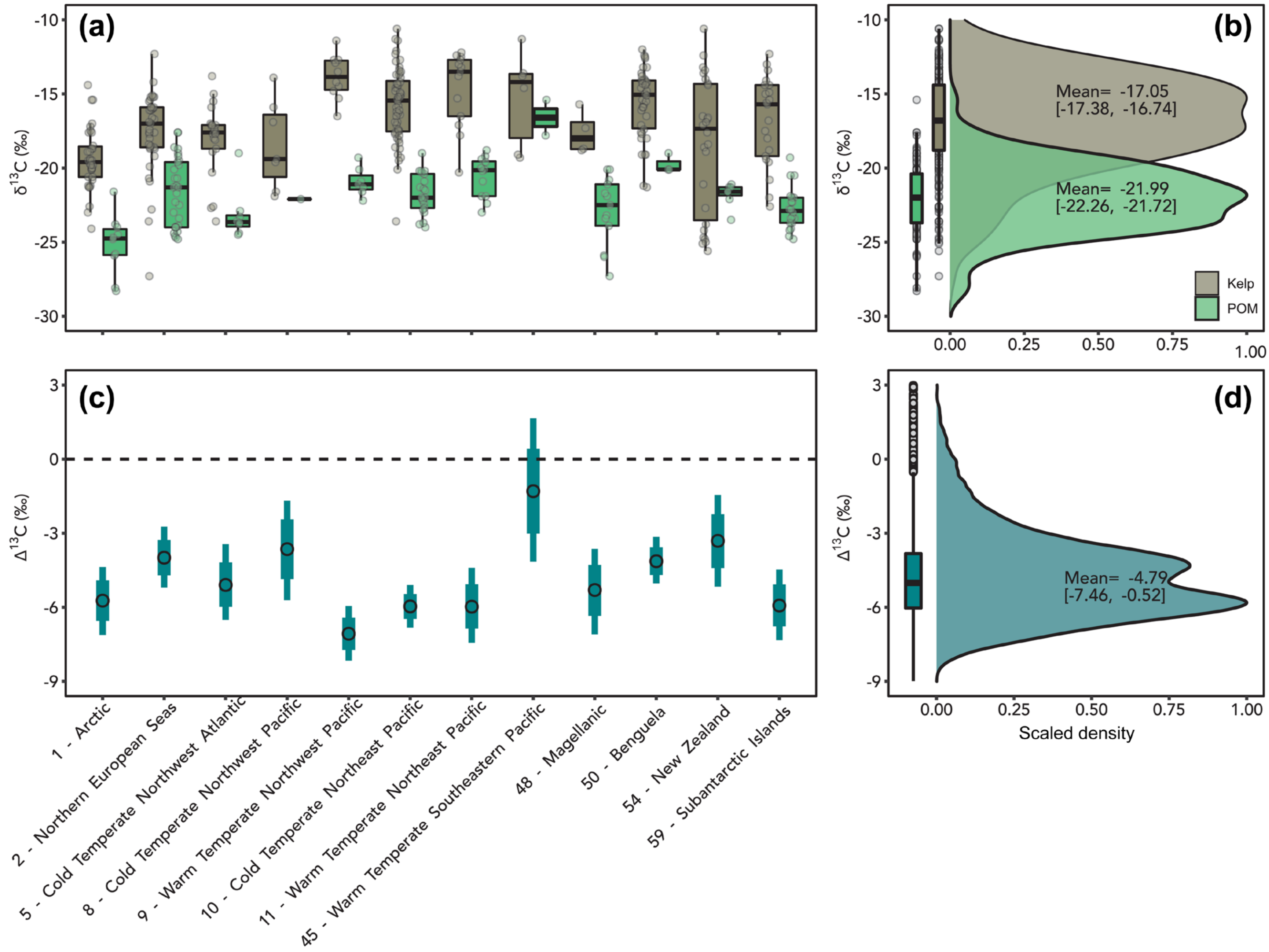

Figure 7. Global patterns of kelp and particulate organic matter (POM) $\delta^{13}C$ values. (a) shows all data from the literature plotted by marine province and summarized with boxplots. (b) shows pooled $\delta^{13}C$ values across all provinces highlighting the distribution of values for each resource type. This is shown as a scaled density distribution with boxplots illustrating the spread of all individual $\delta^{13}C$ values. The mean $\delta^{13}C$ value ± 95% CI are based on bootstrap resampling of global values for each resource type. (c) shows regional differences in kelp and POM $\delta^{13}C$ values ($\Delta^{13}C = \delta^{13}C_{POM} - \delta^{13}C_{kelp}$) estimated from bootstrap resampling within each region. Error bars denote 75% (thick) and 95% (thin) CI around the mean. (d) shows the global distribution of estimated $\Delta^{13}C$ values from the resampling analysis with overall mean $\Delta^{13}C$ and 95% CI presented. The province numbers correspond to Fig. 2.

the flow of energy and nutrients through food webs. Unlike bulk tissue isotopic analysis which represents a weighted average of all macromolecules in each sample, CSIA measures the isotopic composition of individual monomers, such as amino- or fatty acids (Whiteman et al. 2019). These compounds can then be classified within established biochemical pathways, allowing researchers to disentangle organismal physiology from ecological processes.

Within kelp forests, recent studies exemplify the utility of CSIA – particularly essential amino acid (EAA) $\delta^{13}C$ measurements – as a method of quantifying the sources of production supporting consumers. First measured in samples of *Macrocystis pyrifera* from California (Larsen et al. 2013), the unique physiologies of kelps appear to impart a highly distinct and identifiable 'fingerprint' on EAA $\delta^{13}C$ values. This has been corroborated by studies in southcentral Alaska (Elliott Smith et al. 2018), and northern Chile (Elliott Smith et al. 2021), where EAA $\delta^{13}C$ analysis distinguished local kelps (*Laminaria*/*Saccharina*, *Macrocystis*, *Lessonia*) from co-occurring POM, green algae (*Ulva* sp.) and red algae with between 75 and 90% accuracy. In the Chilean case study, bulk tissue isotopic values of local kelps and POM were indistinguishable (Fig. 7a), which would have made food web analysis impossible with traditional isotopic methods (Elliott Smith et al. 2021). Importantly, EAA also serve as conservative tracers of proteinaceous energy flow, as they are minimally altered isotopically through trophic transfers (Fantle et al. 1999, Howland et al. 2003, Newsome et al. 2011, McMahon et al. 2015). This negates the need for researchers to 'correct' consumer EAA $\delta^{13}C$ for trophic discrimination factors when comparing consumers to potential energy producers. EAA $\delta^{13}C$ analysis thus allow researchers a method for reliably tracing kelp-derived energy and nutrients through complex nearshore food webs. However, this technique is not without limitations. Notably, this technique is only able to track proteinaceous molecular components through food webs and is thus unable to trace the fate of carbohydrate heavy kelp exudates (Abdullah and Fredriksen 2004), or recycled carbon. In addition, variation in EAA $\delta^{13}C$ values among diverse phytoplankton taxa have not been thoroughly investigated (Rowe et al. 2019), and the role of other microbial taxa in synthesizing EAA, either within consumer digestive tracts (Newsome et al. 2011), or benthic biofilms (Phillips et al. 2020) is poorly understood. For detailed reviews on the use of CSIA see Close (2019) and Whiteman et al. (2019).

## Unlocking kelp forest ecology – future steps

### Recommendations for future research

We have highlighted here the pressing need for additional research into the flows of energy through kelp forest communities. Notably, research into kelp forest food web structure – through stable isotope analysis – has been overwhelmingly focused in high-latitude regions of the Northern Hemisphere, leaving many of the world's kelp forests understudied. Furthermore, even within regions of relatively high study density, there are critical gaps in our understanding of the importance of kelp to consumer groups. In considering future research best practices, our analysis of isotopic variability within and among kelps and planktonic resources indicated generally good separation between these endmember groups. This result supports the use of a stable isotope perspective in studying energy flow within these systems. However, we have also highlighted a cutting-edge isotopic technique that alleviate many of the concerns associated with bulk tissue stable isotope analysis. Based on our review, we make the following recommendations for future research into kelp forest food web dynamics:

1) The highest priority for future research is within marine provinces that are currently both data deficient (Fig. 2) and undergoing kelp deforestation (Krumhansl et al. 2016, Smale 2020). These include the Warm Temperate Southeastern Pacific, Magellanic, Southern Australia and the Cold Temperate Northwest Atlantic.
2) When designing and conducting field studies in kelp forests, efforts should be made to sample consumers from higher trophic levels and a broad range of taxonomic groupings alongside local primary producer endmembers. Best practice would involve surveys of the most abundant, or functionally important, fauna followed by sampling and isotopic measurements. Special attention should be paid to predatory vertebrate taxa (especially mammalian), as these groups are drastically underrepresented in current studies of kelp forest food webs (Fig. 3). For source collections, we recommend kelp samples be taken from both live sporophytes and decaying material, to provide representation of the isotopic composition likely to be incorporated by different functional groups. POM should be sampled over similar time and spatial scales as other endmembers, with care to minimize contamination by local detritus which confounds accurate $\delta^{13}C$ estimates for planktonic contributions.
3) Researchers should provide empirical estimates for the contribution of kelp versus pelagic energy to local consumers. For regions with consistently large $\Delta^{13}C_{POM\text{-}Kelp}$ (Fig. 7) bulk tissue stable isotope analysis may be sufficient in this regard, presuming primary producers are sampled over appropriate timescales (Dethier et al. 2013), and trophic discrimination factors for local consumers can be constrained (Caut et al. 2009). In areas with small, or highly variable $\Delta^{13}C_{POM\text{-}Kelp}$, researchers may want to consider employing amino acid $\delta^{13}C$ 'fingerprinting' (Larsen et al. 2009, 2013) to characterize the flow of energy in kelp forest ecosystems (Elliott Smith et al. 2018, 2021).
4) Finally, though we have focused here on the importance of kelp-derived energy to consumers, this line of inquiry is not mutually exclusive to studies of kelps as habitat. Future research should attempt to quantify the importance of kelps both as habitat and as a source of energy/nutrients for consumers. A handful of studies suggest that these factors may intersect in interesting ways, particularly for species with ontogenetic ecological shifts (Markel and Shurin 2015, Olson et al. 2019).

Kelp forests have been important to human communities for millennia (Erlandson et al. 2007, Kobluk et al. 2021, Mouritsen et al. 2021), and the energetic subsidies provided by kelps extend far beyond the coastal realm. Kelp-derived energy can support consumers in deep waters (Bernardino et al. 2010, Galloway et al. 2013, Filbee-Dexter et al. 2018, Queirós et al. 2019), in remote habitats kilometers from the nearest kelp bed (Kaehler et al. 2006), and even in terrestrial environments (e.g. reindeer (Hansen et al. 2019)). Taking the steps outlined here will lead to robust, local-scale datasets regarding the flows of energy, and the importance of kelp-derived carbon to consumers across the globe. Kelp forests are changing rapidly in response to ocean warming (Filbee-Dexter and Wernberg 2018, Smale 2020, McPherson et al. 2021), habitat degradation (Krumhansl et al. 2016) and disease (Rogers-Bennett and Catton 2019). Characterizing patterns of energy flow in these dynamic systems is thus vital for the development of effective conservation and management plans and for improved understanding of how these changes will impact adjacent ecosystems or highly dependent consumers.

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### Author contributions

**Emma A. Elliott Smith**: Conceptualization (lead); Data curation (lead); Formal analysis (equal); Writing – original draft (lead); Writing – review and editing (lead). **Michael D. Fox**: Conceptualization (supporting); Data curation (supporting); Formal analysis (equal); Writing – original draft (supporting); Writing – review and editing (supporting).

### Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.n02v6wwxd> (Elliott Smith and Fox 2021).

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