# Pelagic–benthic coupling in kelp forests of central California

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ABSTRACT: Pelagic–benthic coupling in the marine environment influences productivity, trophic interactions, and community structure in nearshore ecosystems. It is also intrinsically variable as oceanographic conditions, species abundances, and the availability of basal resources shift. Kelp forests are home to a nearshore fish assemblage that accesses not only energy derived from kelp but also from pelagic, phytoplankton-based primary production, providing a clear example of pelagic–benthic coupling. Here, I used a combination of stomach content analysis and carbon and nitrogen stable isotope analyses to explore rockfish use of kelp- and phytoplankton-based carbon in kelp forests in central California from 2013–2016. I examined connections between rockfish diet and 2 large-scale events that influence the influx of pelagic-based energy to the kelp forest: seasonal upwelling and the recruitment of juvenile rockfish. I show that phytoplankton-based carbon use was higher in species that forage in the water column (~65 %) as opposed to species on or near benthic substrates (~50 %), and that both pelagic and benthic foragers consumed a diversity of prey taxa advected to the kelp forest from pelagic environments. Furthermore, multiple lines of evidence indicate the importance of variable juvenile rockfish recruitment in understanding rockfish use of phytoplankton-based energy. This research advances our understanding of how ecosystem connectivity influences species′ diets and the many ways that cross-ecosystem subsidies shape the marine environment. Results suggest that to truly understand how kelp forest communities function, we must give more attention to the dynamics of pelagic energy sources and the conditions that lead to variability in pelagic–benthic coupling.

KEY WORDS:  Pelagic–benthic coupling · Kelp forest · Trophic ecology · *Sebastes* spp.

## 1.  INTRODUCTION

Pelagic–benthic coupling in the marine environment links the food webs and dynamics of open ocean habitats to those in the coastal ocean (Docmac et al. 2017). Carbon and other nutrients move between these ecosystems, subsidizing production and structuring recipient ecological communities (Stasko et al. 2016, Morais & Bellwood 2019). The wide-ranging impacts of subsidies moving from the open ocean to benthic, nearshore environments can be profound. The foraging ecology, interactions, growth, and survival of benthic species or species that consume open ocean subsidies are all influenced by the delivery of carbon and nutrients produced externally (Udy et al. 2019). Understanding the dynamics of energy subsidies and how they vary is therefore essential for a complete understanding of the trophic structure of a nearshore ecosystem (Kopp et al. 2015). While the drivers and outcomes of pelagic–benthic coupling have been extensively documented in polar systems (Renaud et al. 2008, Darnis et al. 2012), in the open ocean (Alldredge & Silver 1988, Smith et al. 1994), and for organisms near the base of the food chain (Krenz et al. 2011), fewer studies have explored these dynamics in temperate systems or for higher-level consumers.

Temperate kelp forests are among the most productive ecosystems in the world, supporting a diverse

range of species (Schiel & Foster 2015). This productivity stems largely from 2 sources, both of which vary in space and time: dense stands of macroalgae producing energy within the kelp forest and phytoplankton-based energy that enters the ecosystem from adjacent pelagic habitats (Duggins et al. 1989, Miller et al. 2011, Carr & Reed 2016). In kelp forests on the Pacific coast of California, the macroalgal-based carbon pool is produced primarily by canopy-forming kelps (generally *Macrocystis pyrifera* south of Santa Cruz and *Nereocystis luetkeana* north of Monterey Bay), with additional contributions from understory kelps and benthic red and green algae (Graham et al. 2007, Carr & Reed 2016). This energy enters the kelp forest food web through one of 2 pathways. Invertebrate kelp grazers serve as conduits of energy derived from live kelp up the food chain, while detritivores and filter- and suspension-feeders consume drift kelp, suspended kelp particulates, and dissolved organic matter (Miller & Page 2012, Carr & Reed 2016, Duffill Telsnig et al. 2019). The second major source of energy for the kelp forest food chain is phytoplankton. Suspension-feeders and planktivores inhabiting kelp forests directly consume phytoplankton, much of which is delivered to the kelp forest on currents, internal waves, and other oceanographic events (Miller & Page 2012, Dyer et al. 2019, Yorke et al. 2019). In addition, a wide diversity of trophic subsidies from the pelagic ocean that derive energy from phytoplankton (i.e. organisms which feed on phytoplankton-based food webs) are delivered to kelp forests, where many of them are consumed. These include invertebrates such as gelatinous zooplankton that can be swept into nearshore habitats, juvenile invertebrates and fishes recruiting back to the kelp forest after a pelagic larval phase, and schooling fishes that move in and out of nearshore systems, among other organisms (Zuercher & Galloway 2019). Phytoplankton species and the diversity of additional pelagic subsidies result in a wide range of pathways for pelagic energy to enter kelp forest food webs and impact the many consumers that feed on them.

Accessing energy from pelagic primary producers is not uncommon for fish dwelling in nearshore marine ecosystems. Stable isotopes and stomach content methods have revealed that the majority of fish species residing in mangrove habitats rely predominately on external sources of energy (Igulu et al. 2013), that salt marsh infauna receive large dietary contributions from phytoplankton-based sources, and that higher trophic-level consumers in seasonally ice-covered coastal fjord habitats rely predomi-

nately on phytoplankton-based carbon (McMeans et al. 2013). However, despite being ecologically connected to pelagic ecosystems, higher trophic levels in the nearshore Dutch Wadden Sea rely predominately on benthic primary production, emphasizing that the relative contribution of these components is context- and system-dependent (Christianen et al. 2017).

While some kelp forest consumers feed entirely on either kelp-based or phytoplankton-based trophic pathways, many of the fish species residing in nearshore kelp forests are generalist feeders that utilize both energy sources (Koenigs et al. 2015, von Biela et al. 2016, Docmac et al. 2017). And though much remains to be explored, patterns concerning the importance of macroalgal- or phytoplankton-based energy for kelp forest fishes are beginning to emerge from field and experimental studies. The relative importance of these 2 energy sources varies among consumers: by species, functional group, and with consumer traits. Stable isotope evidence from southern California suggests that higher-level predators are more reliant on kelp-based carbon and planktivores more reliant on pelagic-based carbon (Koenigs et al. 2015). However, similar studies have shown kelp forest fishes from a range of trophic levels and functional groups to predominately use phytoplankton-based energy sources (Chilean kelp forests: Docmac et al. 2017; Australian rocky reefs: Truong et al. 2017), kelp-based energy sources (Norwegian kelp forests: Fredriksen 2003) or to exhibit considerable variability in their energic intake (New Zealand/Aotearoa kelp forests: Udy et al. 2019), highlighting the complexity in food webs subsidized through pelagic–benthic coupling. Evidence suggests that relative use of macroalgal-based carbon can also vary with consumer traits, such as a fish species' feeding mode (von Biela et al. 2016) or foraging position in the water column (Koenigs et al. 2015). Though trophic level, functional group, and several other traits seem to be useful predictors of the use and importance of kelp- versus phytoplankton-based energy in some contexts, additional studies can help to bolster evidence and uncover additional patterns and predictors of energy pathways.

A second central source of variation related to the importance of phytoplankton-based energy to a kelp forest consumer is the spatio-temporal variation in the production of macroalgae, phytoplankton, and other pelagic subsidies (Broitman & Kinlan 2006, Page et al. 2008, Dyer et al. 2019). The relative importance of an energy source for a consumer might vary by oceanographic regimes. For instance, on the west coast of North America, the relative contribution of kelp-based energy to predatory fish species

seems to vary between the California Current (a seasonal upwelling system) and the Alaska Coastal Current (a year-round downwelling system), apparently reflecting differences in the persistence of coastal upwelling (von Biela et al. 2016). Seasonal and annual variation in a consumer's use of pelagic energy could also result from changes in the ocean environment, especially those that directly influence the abundance of basal resources or the delivery of phytoplankton to the kelp forest (Markel & Shurin 2015, Udy et al. 2019). In central California, upwelling represents a major and seasonally predictable shift in oceanographic conditions that is likely to influence pelagic–benthic coupling (Foley 2009). Upwelling conditions trigger system-wide shifts influencing sea surface temperatures, water movement, primary and secondary production, and ecosystem structure (Bograd et al. 2009). Similarly, the annual pulse of juvenile rockfishes recruiting to the kelp forest from the open ocean is an annual ecological event likely to influence energy flow to kelp forests. Juvenile rockfishes exhibit strong variability in recruitment strength — virtually absent in some years and recruiting in dense aggregations in others (Caselle et al. 2010). Because juvenile rockfishes are a high-protein and high-energy prey item, there is the potential for this variation in recruitment (which is ultimately driven by oceanography and other environmental factors) to cause shifts in the diets of kelp forest consumers (Wilson et al. 2008, Zuercher & Galloway 2019).

To better understand the sources and outcomes of variation in energy source use in the kelp forest, I examined the trophic ecology of a subset of species in a kelp forest fish assemblage. The (non-cryptic) nearshore fish assemblage in central California is dominated by rockfishes in the genus *Sebastes.* They are ecologically important as meso-predators with diverse diets and occupy habitats from the kelp forest canopy to the midwater environment to benthic cracks and crevices of the rocky reef (Hallacher & Roberts 1985). They typically have small home ranges, making them vulnerable to changes in the local prey assemblage (Freiwald 2012). I focused on 4 species of nearshore rockfishes (blue rockfish *Sebastes mystinus*, black rockfish *S. melanops*, kelp rockfish *S. atrovirens*, and black-and-yellow rockfish *S. chrysomelas*) that represent a diversity of traits that may influence energy use: trophic strategies, foraging habitats, and feeding morphologies. While all 4 are generalist predators with overlapping diets, studies show clear interspecies diet variation (Love & Ebeling 1978, Hallacher & Roberts 1985, Hobson & Chess 1988, Hobson et al. 2001).

This research combined multiple lines of evidence to describe the diet of these 4 species in terms of phytoplankton- and macroalgal-based carbon contributions and to test for temporal variability in their diets resulting from changes in the ocean environment. Stable isotope analyses were used to estimate the importance of pelagic–benthic coupling (as quantified by the proportion of energy derived from phytoplankton-based carbon) for each rockfish species. This analysis was combined with stomach content analysis to give species-level information about diet composition, allowing for identification of particular prey species that contribute macroalgal- and/or phytoplankton-based carbon to a fish's diet. Using these methods, I first tested the following 2 hypotheses: (H1) rockfish species that forage in the water column (blue and black rockfishes) consume higher proportions of dietary carbon from phytoplankton and phytoplankton-based sources than do benthic foragers (kelp and black-and-yellow rockfishes). (H2) Species consuming higher proportions of phytoplankton-based carbon rely more heavily on prey species delivered to the kelp forest as pelagic subsidies. Secondly, I examined 2 notable events hypothesized to be drivers of variation in rockfishes' use of phytoplankton-based carbon: seasonal coastal upwelling and the recruitment of juvenile rockfish from the pelagic ocean to the kelp forest. I tested 2 additional hypotheses related to seasonal and annual variation in phytoplankton-based carbon use: (H3) there is a positive relationship between the magnitude of annual juvenile rockfish recruitment (a pelagic subsidy), the importance of fishes as prey for adult rockfishes, and the importance of phytoplankton-based energy for focal fish species that are shown to consume juvenile rockfishes. I expected that adult fishes would switch to a diet heavier in fish during large recruitment years and show a corresponding shift in $\delta^{13}C$ (to reflect a more pelagic-based diet) and increase in $\delta^{15}N$. (H4) Rockfishes that feed on pelagic subsidies will consume a higher proportion of phytoplankton-based carbon during seasonal upwelling. For fishes that forage on the influx of pelagic prey such as gelatinous zooplankton, the relative importance of phytoplankton-based carbon will vary seasonally, as upwelling dynamics influence delivery of pelagic carbon.

## 2. MATERIALS AND METHODS

To test the 4 hypotheses stated above, I collected stomach content and fish tissue samples from each of the 4 focal rockfish species during both upwelling

and non-upwelling seasons and across years with variable rockfish recruitment (2013–2016).

## 2.1. Study area

I collected all fish samples in kelp forests of southern Monterey (36° 38′ N, 121° 55′ W) and Carmel bays (36° 33′ N, 121° 56′ W) in central California, where a narrow shelf positions kelp forests in close proximity to open ocean habitats. The majority of collections were done at sites dominated by *Macrocystis pyrifera*, though some collections were done in patches of *Nereocystis luetkeana* adjacent to *M. pyrifera* forests. Collection site depth ranged from approximately 5–20 m and took place within 350 m of shore. Surface water temperatures in the region range from approximately 13–16°C, and kelp forests here experience strong, seasonal upwelling in the spring and early summer months (Graham & Largier 1997, Pennington & Chavez 2000). Fishes were collected in haphazardly selected kelp forest patches that represented a range of swell and wave exposure.

## 2.2. Estimating the relative importance of phytoplankton-based carbon

I used both stomach contents and stable isotope ratios to examine the relative importance of phytoplankton-based carbon in the diets of nearshore rockfishes. Stomach content samples were collected opportunistically in 2013 (July–November), 2014 (June–October), 2015 (April–September), and 2016 (March–September). Tissue for $\delta^{13}C$ analysis was collected at uneven intervals throughout 2014 (June–October), 2015 (May–September), and 2016 (March–September). Fish samples were collected during daylight hours using either hook and line gear (squid bait was excluded from stomach content analysis), spear on SCUBA, or were salvaged from the local recreational fishery in cases where an accurate location of capture could be specified. To limit variation in diet due to ontogenetic dietary or habitat shifts, only fishes 22 cm and larger (20 cm and larger for black-and-yellow rockfish) were included in the analysis.

Non-lethal sampling for stomach contents using gastric lavage was done when lethal sampling for other tissues was not required. Gastric lavage was performed using a 100 ml syringe attached to a 20 cm section of flexible polyethylene tubing to pump seawater into a fish's stomach until water forced back through the esophagus was free of prey items

(Hartleb & Moring 1995). Prey items were immediately preserved in 95% ethanol. Fishes that showed any signs of regurgitated stomach contents or stomach extrusion upon capture were excluded from the study. Fishes sampled for stable isotope analysis were euthanized immediately following capture (except those salvaged from recreational fisheries) and put directly on ice. A ~2 cm³ section of anterior dorsal muscle was removed from each rockfish and immediately frozen.

### 2.2.1. Stomach content analysis

Whole and partial prey items were enumerated and identified to the lowest taxonomic level possible using a dissecting scope. Because many prey items could not be identified to species, most were aggregated into broad taxonomic groups. Bryozoan species (e.g. *Membranipora* spp.) encrusting kelp were quantified as bryozoans. After sorting, prey items were blotted dry and weighed. Only stomachs with identifiable prey items were included in the analysis. For stomachs that contained identified prey items, unidentified material was sorted and weighed (to contribute to total weight) but excluded from subsequent analysis. For each prey item, prey-specific abundance (by weight and number), frequency of occurrence (FO), and the prey-specific index of relative importance (PSIRI) were calculated (Brown et al. 2012). Prey-specific number and weight were calculated as:

$$\%PX_{i,j} = \frac{\sum_{j=1}^{n} \%X_{i,j}}{n_i} \tag{1}$$

where $i$ is a given prey item in stomach sample $j$, $n_i$ is the total number of stomachs containing prey $i$, X is either the number (N) or weight (W), and PX is the prey-specific number or weight. Percent PSIRI values were calculated as:

$$\%PSIRI_i = \frac{\%FO_i(\%PN_i + \%PW_i)}{2} \tag{2}$$

$\%FO_i$ was calculated as the number of stomach samples containing prey $i$ divided by the total number of stomach samples.

### 2.2.2. Stable isotope sample preparation and analysis of muscle tissue

To examine basal carbon sources for each fish sampled, I measured $\delta^{13}C$ in muscle tissue. All tissue

samples were dried for 48 h in a Labconco FreeZone 4.5 lyophilizer. Lipid extraction was not done for muscle tissue, as the C:N ratios for those samples were found to be less than 3.5 (Pinnegar & Polunin 1999, Post et al. 2007, Markel & Shurin 2015). Dried samples were pulverized and homogenized with a ceramic mortar and pestle before a 0.5 mg portion of each sample (weighed to the nearest 0.001 mg) was placed in a tin capsule for analysis. I used a Carlo-Erba 1108 elemental analyzer coupled to an isotope ratio mass spectrometer (ThermoFinnigan Delta Plus XP IRMS) at the University of California Santa Cruz Stable Isotope Laboratory to analyze all samples for $\delta^{15}N$, $\delta^{13}C$, %N and %C. Data are reported in standard delta notation (‰) relative to the standards Vienna Pee Dee Belemnite for carbon and atmospheric $N_2$ for nitrogen, as:

$$\delta S = \left[\left(\frac{R_{sample}}{R_{standard}}\right) - 1\right] \times 1000 \qquad (3)$$

where $S$ is either carbon or nitrogen and $R$ is the ratio $^{13}C/^{12}C$ or $^{15}N/^{14}N$ (Peterson & Fry 1987). Five percent of samples were run in duplicate with a mean difference between duplicate samples of $0.07 \pm 0.07$‰ for $\delta^{13}C$, $0.12 \pm 0.12$‰ for $\delta^{15}N$, and $0.1 \pm 0.39$ for C:N ratio. For duplicate samples, means were used in subsequent analyses. Assumptions of normality (assessed with Shapiro-Wilks tests) and homogeneity of variance (assessed with Levene's test) in this data set were not met. As such, $\delta^{13}C$ values were compared among species with a Kruskal-Wallis test followed by a post hoc Dunn's test for pairwise comparisons.

### 2.2.3. Mixing models

I developed 2-source Bayesian mixing models using the package 'simmr' in R (v.3.6.3) to estimate the proportion of carbon from each of 2 sources: kelp and phytoplankton (Parnell et al. 2010, Parnell & Inger 2016, R Core Team 2018). Inputs to mixing models include mean and SD of isotope values for primary producers, mean and SD of isotope values for the focal species of nearshore rockfish, trophic level estimates for each fish species, and the mean and SD of trophic discrimination factors. I used the commonly cited $1.0 \pm 1.0$‰ $\delta^{13}C$, allowing error in these estimates to propagate through the model (Vander Zanden & Rasmussen 2001, Post 2002, Elsdon et al. 2010). Due to the challenge in categorizing many kelp forest prey items as either kelp-based or phytoplankton-based, stomach content data were not used to inform priors for the mixing models.

Kelp and phytoplankton end members have been shown to be well-separated globally (Miller & Page 2012, Elliott Smith & Fox 2021), including in studies conducted in California where $\delta^{13}C$ of giant kelp has been estimated between −12.2 and −13.8‰ (Page et al. 2008) and phytoplankton (as measured in coastal particulate organic matter) at −20.5‰ (Miller et al. 2013). However, because primary producers in nearshore marine systems exhibit large spatial and temporal variability in isotopic values, primary consumers were used in this study as baseline trophic species (Foley & Koch 2010, Parnell et al. 2010, Kurle & McWhorter 2017). Drobnitch et al. (2018) showed more than 2‰ of seasonal variation in $\delta^{13}C$ values for giant kelp and up to 6‰ within a single individual, in addition to variability by depth and location in a kelp bed. Foley & Koch (2010) reported $\delta^{13}C$ values ranging from −25 to −13‰ and $\delta^{15}N$ ranging from 2−10‰ for giant kelp. Research has also documented variability among kelp species and other kelp forest algae (Fredriksen 2003). To integrate this variation, kelp isopods *Idotea resecata*, which graze directly on kelp, were used as a proxy in mixing models to represent macroalgae. They were collected haphazardly from a boat in kelp forests of Carmel Bay in June 2014, June and September 2015, and July 2016. *I. resecata* samples were acidified following drying to eliminate inorganic carbon (Carabel et al. 2006, Jaschinski et al. 2008). Pelagic-grazing pyrosomes, common components of the plankton in the study region that were especially prevalent during the study years, were used as a proxy in the mixing models to represent phytoplankton (Sutherland et al. 2018, Miller et al. 2019). They were collected in midwater trawls in open ocean environments at the mouth of Monterey Bay (Site 1: 36° 44.77′ N, 121° 59.87′ W; Site 2: 36° 35.95′ N, 122° 3.5′ W) in April−May 2016 (Perissinotto et al. 2007). Whole pyrosomes were dried, crushed, and weighed for isotopic analysis.

To measure the trophic level of each fish species for the mixing models, the same fish muscle samples described in the previous section were sampled for $\delta^{15}N$. Trophic position was estimated from $\delta^{15}N$ data according to the following equation:

$$TL_{consumer} = \lambda + [\delta^{15}N_{consumer} - (\delta^{15}N_{macroalgal\ end\ member} \times$$
$$\alpha + \delta^{15}N_{phytoplankton\ end\ member} \times \beta)] / \Delta \qquad (4)$$

where end members (at the reference trophic level) are at the primary consumer level ($\lambda = 2$), $\Delta$ is the $\delta^{15}N$ trophic enrichment factor from prey to predator, $\alpha$ is the proportion of macroalgal-based prey eaten by the consumer, and $\beta$ is the proportion of phytoplankton-based prey eaten by the consumer, with $\alpha$ and $\beta$ sum-

ming to one. Based on previous experiments on non-herbivorous fishes, I used a value of 3.4‰ as the nitrogen isotope trophic enrichment factor (Vander Zanden & Rasmussen 2001, Sabo & Power 2002, Sweeting et al. 2007, Elsdon et al. 2010).

## 2.3. Quantifying temporal variability in rockfish use of phytoplankton-based carbon

To explore temporal shifts in rockfish diet and energy use related to juvenile rockfish recruitment (annual variation) and upwelling (seasonal variation), I drew on the previously described stomach content analysis, documented $\delta^{13}C$ and $\delta^{15}N$ in 3 life phases of juvenile rockfishes, and analyzed $\delta^{13}C$ and $\delta^{15}N$ ratios in liver tissue of adult rockfishes.

### 2.3.1. Diet variability and juvenile rockfish recruitment

To characterize the relationship between rockfish recruitment and adult rockfish diet, I used stomach content data contextualized with $\delta^{13}C$ and $\delta^{15}N$ for juvenile rockfishes and compared those with juvenile rockfish recruitment surveys. Recruitment indices were obtained from the Partnership for the Interdisciplinary Study of Coastal Oceans (PISCO; www.piscoweb.org). Anomalies were calculated based on the long-term average density of all species of juvenile *Sebastes* (<10 cm total length) across Carmel Bay sites on benthic and midwater fish surveys. Because these surveys take place before some species (i.e. the kelp, gopher, black-and-yellow rockfish complex) migrate from kelp canopies deeper into the kelp forest, the data used do not reflect the annual influx of these particular species (Caselle et al. 2010). The majority of recruits that are captured in the PISCO survey data are black rockfish, blue rockfish, and olive rockfish *S. serranoides*. For more information on PISCO methods, see Malone et al. (in press). To clarify how juvenile rockfishes might be impacting isotopic values of adult nearshore rockfishes that prey on them, $\delta^{13}C$ and $\delta^{15}N$ were measured for 3 life phases: pelagic juveniles, newly recruited juveniles (arrived in the kelp forest from the pelagic ocean fewer than 3 d prior), and kelp forest juveniles. Pelagic juveniles were collected in mid-water trawls in open ocean environments at the mouth of Monterey Bay in April and May (see Ralston et al. 2013), newly recruited juveniles were captured with SMURFs (Ammann 2004), and kelp forest juveniles were captured

in Carmel Bay, on SCUBA with BINCKE nets (Anderson & Carr 1998). Muscle tissue was collected from all juvenile rockfish specimens, immediately frozen, then processed using the same stable isotope sample processing methods described above for adult rockfish muscle tissue. Because the data set did not meet assumptions of normality and homogeneity of variance, a Kruskal-Wallis test followed by post hoc Dunn's test for pairwise comparisons was conducted to compare stable isotope results among life phases.

I used a multivariate statistical approach (permutational analysis of variance; PERMANOVA) paired with ordination analyses to look at diet content differences among *Sebastes* spp. and for interannual variability within each individual species. PERMANOVA analyses were performed in PRIMER 6 with untransformed data. A Type III sum of squares was used to account for the unbalanced design (Clarke & Gorley 2006). Similarity percentages (SIMPER) were used to examine pair-wise comparisons between species and years, and to explore the prey species driving differences shown in PERMANOVA results. These relationships were plotted and visualized using an ordination analysis with Bray-Curtis dissimilarity used to quantify distance.

### 2.3.2. Seasonal and annual shifts in diet as measured using stable isotopes

To test the hypotheses regarding juvenile rockfish recruitment and upwelling-related shifts, stable isotope samples were collected over 3 yr and during both upwelling (April–July) and non-upwelling (Jan–Mar, Aug–Dec) seasons. Because muscle tissue integrates diet over a long time period, annual and seasonal differences in carbon contribution and trophic level were tested using the more metabolically active liver tissue. A ~2 cm$^3$ section of liver was removed from each rockfish and immediately frozen before undergoing the same stable isotope sample preparation described above for muscle tissue. Livers have a higher lipid content, and because lipid synthesis leads to lower values of $\delta^{13}C$, lipids were extracted from a subset of liver samples (kelp rockfish, n = 23; black-and-yellow rockfish, n = 24; black rockfish, n = 21; blue rockfish, n = 19) by accelerated solvent extraction using petroleum ether. Several of these samples (n = 10) underwent 2 lipid extractions to sufficiently eliminate lipids. Samples measured after lipid extraction reflect carbon assimilation more accurately (Kiljunen et al. 2006). The $\delta^{13}C$ and C:N ratio values from liver samples analyzed both before and after lipid extraction

were used to generate arithmetic lipid correction equations to mathematically normalize samples that did not undergo lipid extraction (Sweeting et al. 2006, see Text S1 in the Supplement at www.int-res.com/articles/suppl/m682p079_supp.pdf). Lipid-extracted liver samples were analyzed for $\delta^{13}$C, while livers that had not undergone lipid extraction were analyzed for $\delta^{15}$N, %N, and %C. Liver tissue sample sizes were as follows: kelp rockfish, n = 35; black-and-yellow rockfish, n = 35; black rockfish, n = 36; and blue rockfish, n = 33. Differences between isotope values and season or year were tested with 2-sample $t$-tests (season) or a 1-way ANOVA followed by pairwise Tukey's honest significant post hoc tests (year) where data sets met assumptions of normality (assessed with Shapiro-Wilks tests) and homogeneity of variance (assessed with Levene's tests). Where assumptions were violated, differences were tested using either Mann-Whitney $U$-tests (season) or Kruskal-Wallis tests followed by post hoc Dunn's tests for pairwise comparisons (year). Turnover time, estimated at 6 mo for liver tissue, was considered when categorizing liver samples as 'upwelling' or 'non-upwelling' (Buchheister & Latour 2010, Matley et al. 2016, Barton et al. 2019). For example, a liver sample from a fish captured in July was assumed to reflect prey consumed approximately 6 mo earlier (i.e. in January) and as such, categorized as non-upwelling.

## 3. RESULTS

### 3.1. Relative importance of phytoplankton-based carbon

To examine basal food sources for each species, I measured $\delta^{13}$C of muscle tissue for 60 kelp rockfish (mean ± SD total length: 31.3 ± 2.5 cm), 57 black-and-yellow rockfish (27.6 ± 2.9 cm), 59 black rockfish (31.5 ± 2.7 cm), and 52 blue rockfish (30.5 ± 3.7 cm). Trophic level of each focal rockfish species was calculated to parameterize mixing models as follows: (mean ± SD) blue rockfish: 3.39 ± 0.13; kelp rockfish: 3.57 ± 0.08; black rockfish: 3.62 ± 0.10; black-and-yellow rockfish: 3.65 ± 0.09. Additionally, isotopic values were measured for kelp isopods (mean ± SD; $\delta^{13}$C: −14.2 ± 1.9‰; $\delta^{15}$N: 9.7 ± 1.2‰) and pyrosomes ($\delta^{13}$C: −22.9 ± 1.3‰; $\delta^{15}$N: 8.8 ± 1.0‰) to serve as model end members. Because these organisms are both primary consumers grazing directly on macroalgae (isopods) and phytoplankton (pyrosomes), the $\delta^{15}$N difference reflects a baseline difference between nearshore and offshore systems and was used to scale

trophic level calculations (Foley & Koch 2010). Isopods were collected across 3 yr, and ANOVA revealed no significant difference in $\delta^{13}$C across years ($F_{2,13}$ = 0.48, p = 0.63). The posterior distributions of dietary contributions revealed that pelagic-based carbon contributed approximately 50% to the diets of benthic foraging black-and-yellow rockfish and kelp rockfish, with these more demersal species relying essentially equally on macroalgal- and phytoplankton-based carbon sources (Fig. 1). Pelagic-based carbon was more important for mid-water feeding black (~ 60%) and blue (~ 64%) rockfishes, supporting the hypothesis (H1) that species foraging in the water column rely more heavily on pelagic-based energy relative to those foraging on or near the benthos. $\delta^{13}$C values differed between species (Kruskal-Wallis; $\chi^2$ = 137.96, df = 3, p < 0.001), with all pairwise comparisons significant (p < 0.001) with the exception of kelp and black-and-yellow rockfishes (p = 0.06).

### 3.2. Pelagic prey items in nearshore rockfishes' diets

To evaluate the contribution of various pelagic subsidy prey species, I identified stomach contents from a total of 117 kelp rockfish (mean ± SD total length: 30.7 ± 3.1 cm), 112 black-and-yellow rockfish (27.3 ± 3.0 cm), 72 black rockfish (30.9 ± 2.9 cm), and 64 blue rockfish (30.5 ± 4.4 cm). The percentage of empty stomachs for all years and all species was relatively high at 45.8%, though stomachs with very little prey material were categorized as empty due to the potential that stomach contents were regurgitated during hook-and-line capture. Cumulative prey curves generated using the 'vegan' package in R and following Ferry & Cailliet (1996) indicated that sampling was sufficient to characterize diet by rockfish species (Oksanen et al. 2016) (Fig. S3).

Black and blue rockfishes were shown in the stable isotope analysis of muscle tissue to consume the highest proportion of phytoplankton-based carbon. Thus, these were the species predicted to rely most heavily on pelagic prey. This hypothesis (H2) was borne out in stomach content analysis results (Table 1, Text S2). Blue rockfish relied on prey associated with phytoplankton-based food chains, including tunicates (predominately pelagic salps), cnidarians, fishes, and kelp-encrusting bryozoans. Additionally, crab megalopae and zoea and ctenophores, prey items feeding on phytoplankton-based food chains, were found in blue rockfish diets. These prey items include both pelagic subsidy organisms (organisms delivered to
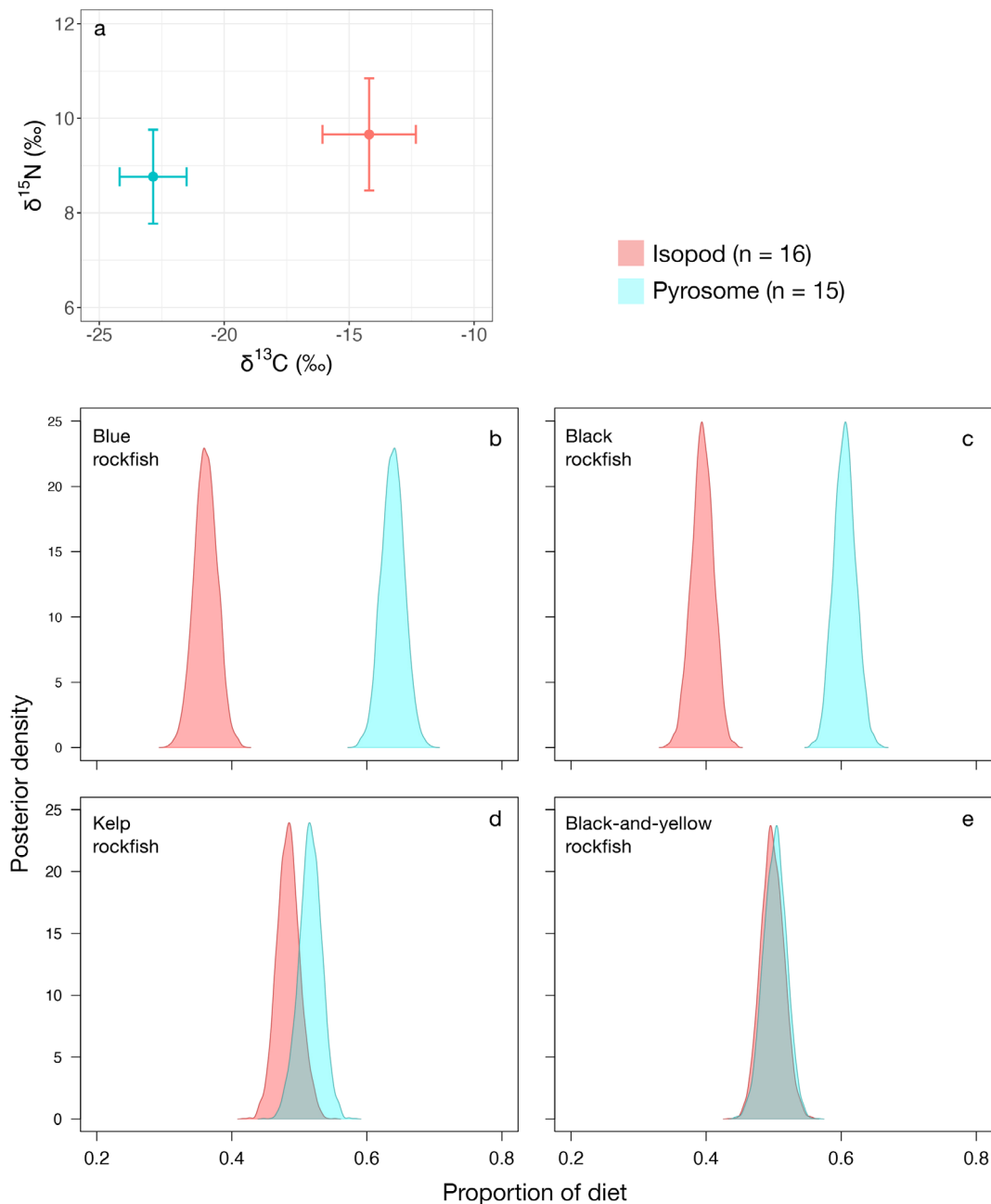
Fig. 1. (a) Biplot of mean (±SD) values for primary consumer end members of phytoplankton-based (*Pyrosoma atlanticum*) and macroalgal-based (*Idotea resecata*) food chains and (b−e) posterior density probabilities from a 2-source Bayesian mixing model using $\delta^{13}C$ values derived from rockfish muscle tissue for the 4 studied rockfish species

the kelp forest from the pelagic ocean; e.g. pelagic tunicates) and kelp forest organisms that feed directly on phytoplankton (e.g. kelp-encrusting bryozoans). Though most important for blue rockfish, tunicates were among the 5 most important prey taxa for 3 of the 4 focal species (excluding the benthic black-and-yellow rockfish).

Fishes were the most important prey item for black rockfish (with a substantially higher PSIRI value than any other prey category) and kelp rockfish, and within the top 5 for blue and black-and-yellow rockfishes. Prey species associated with macroalgae-based food chains were widespread in the diets of nearshore rockfishes, highlighting the importance of both basal energy sources for this group of species. Isopods (predominately *Idotea resecata*) that live on kelp fronds and within the kelp canopy played a large role in the diet of black rockfish, likely contribut-

Table 1. Diet composition of 4 species of nearshore *Sebastes* rockfish by percent frequency of occurrence (%FO), percent prey-specific number (%PN), percent prey-specific weight (%PW), and percent prey-specific index of relative importance (%PSIRI). Diet data with prey categorized at a higher taxonomic resolution can be found in Table S2

| Prey category | %FO | %PN | %PW | %PSIRI |
|---|---|---|---|---|
| **Blue rockfish *S. mystinus* (mid-water forager)** | | | | |
| Tunicate | 20.31 | 82.37 | 74.95 | 15.98 |
| Algae | 28.13 | 51.10 | 47.10 | 13.80 |
| Fish | 26.56 | 43.31 | 48.71 | 12.22 |
| Cnidarian | 17.19 | 66.74 | 68.40 | 11.61 |
| Bryozoan | 14.06 | 62.17 | 58.35 | 8.47 |
| Other or unidentified arthropod | 15.63 | 28.03 | 23.19 | 4.00 |
| Cephalopod | 6.25 | 52.08 | 72.57 | 3.90 |
| Crab megalopa/zoea | 9.38 | 52.10 | 25.42 | 3.63 |
| Brachyuran crab | 4.69 | 50.00 | 57.77 | 2.53 |
| Amphipod | 10.94 | 30.17 | 0.63 | 1.68 |
| Ctenophore | 1.56 | 90.90 | 84.46 | 1.37 |
| Caridean shrimp | 4.69 | 44.44 | 13.77 | 1.36 |
| Polychaete | 3.13 | 50.00 | 5.60 | 0.87 |
| Mollusc (excluding Cephalopoda) | 1.56 | 50.00 | 5.60 | 0.87 |
| Copepod | 1.56 | 33.33 | 0.81 | 0.27 |
| **Black rockfish *S. melanops* (mid-water forager)** | | | | |
| Fish | 55.56 | 69.95 | 82.32 | 42.30 |
| Isopod | 31.94 | 46.26 | 42.31 | 14.15 |
| Tunicate | 11.11 | 83.39 | 63.56 | 8.16 |
| Cephalopod | 8.33 | 62.78 | 97.11 | 6.66 |
| Other or unidentified arthropod | 22.22 | 30.04 | 16.13 | 5.13 |
| Amphipod | 16.67 | 31.46 | 10.36 | 3.48 |
| Crab megalopa/zoea | 11.11 | 35.70 | 14.18 | 2.77 |
| Polychaete | 6.94 | 37.33 | 37.52 | 2.60 |
| Mollusc (excluding Cephalopoda) | 5.56 | 43.59 | 37.28 | 2.25 |
| Barnacle | 2.78 | 33.33 | 68.93 | 1.42 |
| Ctenophore | 1.39 | 100.00 | 100.00 | 1.39 |
| Brachyuran crab | 4.17 | 31.33 | 33.18 | 1.34 |
| Cnidarian | 2.78 | 38.33 | 4.68 | 0.60 |
| Caridean shrimp | 4.17 | 24.44 | 2.00 | 0.55 |
| Krill | 4.17 | 20.51 | 1.89 | 0.47 |
| Anomuran crab | 1.39 | 50.00 | 13.35 | 0.44 |
| Bryozoan | 1.39 | 50.00 | 0.11 | 0.34 |
| Copepod | 1.39 | 33.33 | 12.31 | 0.32 |
| Algae | 2.78 | 3.78 | 2.83 | 0.09 |
| **Kelp rockfish *S. atrovirens* (demersal forager)** | | | | |
| Fish | 36.75 | 47.07 | 71.72 | 21.83 |
| Amphipod | 48.72 | 38.99 | 19.31 | 14.20 |
| Tunicate | 14.53 | 82.50 | 74.71 | 11.42 |
| Other or unidentified arthropod | 29.91 | 27.95 | 33.14 | 9.14 |
| Caridean shrimp | 32.47 | 27.75 | 28.17 | 9.08 |
| Brachyuran crab | 13.68 | 44.50 | 58.30 | 7.03 |
| Isopod | 33.33 | 21.66 | 18.91 | 6.76 |
| Cephalopod | 10.26 | 36.77 | 71.82 | 5.57 |
| Crab megalopa/zoea | 18.80 | 38.38 | 15.38 | 5.05 |
| Barnacle | 3.42 | 39.09 | 46.23 | 1.46 |
| Mollusc (excluding Cephalopoda) | 7.69 | 23.36 | 10.83 | 1.31 |
| Anomuran crab | 2.56 | 32.32 | 32.29 | 0.83 |
| Polychaete | 4.27 | 25.58 | 4.42 | 0.64 |
| Cnidarian | 1.71 | 18.95 | 22.11 | 0.35 |
| Algae | 3.42 | 14.91 | 1.91 | 0.29 |
| Copepod | 1.71 | 26.85 | 0.20 | 0.23 |
| Krill | 0.85 | 33.33 | 0.04 | 0.14 |
| Bryozoan | 1.71 | 5.32 | 0.27 | 0.05 |

ing to the ~40% macroalgal-based carbon in their diet (see Table S3 for information on isotope values of common prey items). Amphipods, a taxon generally abundant in microhabitats throughout the water column, were most important to the kelp rockfish. Black-and-yellow rockfish relied on hard-bodied benthic invertebrates on the reef surface such as brachyuran crabs, shrimps, and other arthropods in addition to octopus (predominately *Octopus rubescens*).

### 3.3. Temporal variability

#### 3.3.1. Juvenile rockfish recruitment

Multiple lines of evidence were used to understand the relationships among variation in rockfish recruitment, diets of the 4 focal nearshore rockfish species (especially focusing on the importance of fishes as prey items), and overall use of phytoplankton-based energy (H3). The magnitude of rockfish recruitment to central California varied substantially over the study period (2013–2016), with a historically large recruitment event in 2013 and a more average recruitment year in 2015 that represents a study period low (Fig. 2).

Differences in diet among the 4 species (as quantified using prey-specific abundance by number in a stomach sample) were consistent across the 4 sampling years, with the exception of 2015 when black, blue, and kelp rockfishes all exhibited more similar diet compositions to each other than each species exhibited with itself in other years (Fig. 3). In other words, diet differed by species in all years except 2015, when the diets of black, blue, and kelp rockfishes converged. The 2015 diet was distinguished from the other years by the importance of crab megalopae and zoea, tunicates, brachyuran crabs, and the relative unimportance of fishes and cephalopods. The impor-

Table 1 (continued)

| Prey category | %FO | %PN | %PW | %PSIRI |
|---|---|---|---|---|
| **Black-and-yellow rockfish *S. chrysomelas* (benthic forager)** | | | | |
| Brachyuran crab | 44.64 | 60.34 | 61.15 | 27.12 |
| Cephalopod | 25.00 | 63.10 | 80.29 | 17.92 |
| Other or unidentified arthropod | 22.32 | 51.74 | 54.35 | 11.84 |
| Caridean shrimp | 20.54 | 56.99 | 46.96 | 10.67 |
| Fish | 18.75 | 45.77 | 57.81 | 9.71 |
| Anomuran crab | 12.50 | 50.68 | 60.18 | 6.93 |
| Mollusc (excluding Cephalopoda) | 10.71 | 39.98 | 34.44 | 3.99 |
| Polychaete | 8.04 | 41.20 | 34.18 | 3.03 |
| Echinoderm | 4.46 | 44.00 | 43.63 | 1.96 |
| Tunicate | 1.79 | 70.00 | 55.97 | 1.12 |
| Algae | 5.36 | 22.68 | 9.44 | 0.86 |
| Bryozoan | 3.57 | 39.58 | 3.47 | 0.77 |
| Amphipod | 6.25 | 21.34 | 1.14 | 0.70 |
| Cnidarian | 1.79 | 45.00 | 32.71 | 0.69 |
| Barnacle | 1.79 | 47.78 | 22.88 | 0.63 |
| Isopod | 1.79 | 35.00 | 18.78 | 0.48 |
| Nematode | 0.89 | 50.00 | 17.08 | 0.30 |
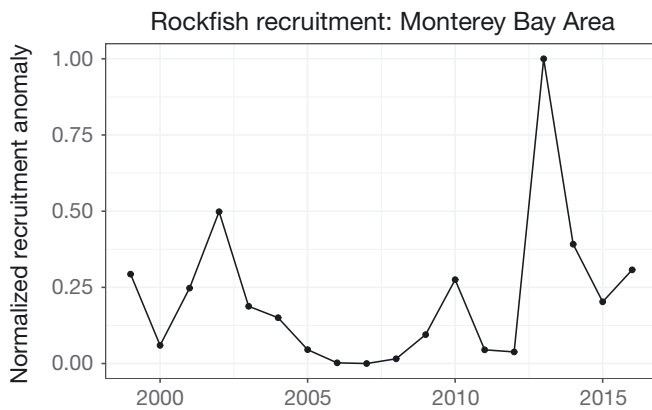


Fig. 2. The rockfish recruitment anomaly (normalized to a 0–1 scale) for 1999–2016 for PISCO sites in Monterey and Carmel bays

tance of tunicates in rockfishes' diet increased from 2013–2015 before decreasing again in 2016 (PSIRI for all species combined, 2013: 2.9; 2014: 13.9; 2015: 19.7; 2016: 2.7; Fig. S4). Crab megalopae and zoea spiked in importance in 2015, though were relatively unimportant in other years (PSIRI for all species combined, 2013: 0.4; 2014: 3.1; 2015: 9.1; 2016: 2.1). The importance of fishes showed an opposite pattern to that of tunicates, with high importance in 2013 and 2014, a drastic decrease in 2015, and subsequent increase in 2016 (PSIRI for all species combined, 2013: 25.7; 2014: 27.6; 2015: 4.0; 2016: 12.6). In contrast, for the most strongly benthic-associated of the fish species sampled, the black-and-yellow rockfish, diet remained static across the sampling years, with a heavy reliance on benthic invertebrates driving the similarity.

To further clarify the contributions of juvenile rockfishes in particular, stable isotope samples were collected for 3 life phases. Pelagic juveniles had a carbon isotope signature consistent with their open ocean diet and significantly different than juveniles in the other 2 life phases (p < 0.001; Fig. 4). Conversely, juvenile rockfishes that had been in the nearshore habitat for several weeks and resided closer to the benthos had a more macroalgal-based carbon signature. The mean $\delta^{13}C$ value of new recruits likely reflects an intermediate between their larval feeding period in the open ocean and nearshore prey consumed more recently. The well-known baseline difference in $\delta^{15}N$ between nearshore and offshore marine environments (approximately 1‰) is partially responsible for the differences in $\delta^{15}N$ among life phases. However, with a 1‰ correction, mean $\delta^{15}N$ of pelagic juveniles was still significantly different from kelp forest juveniles (p < 0.001). It follows that while consumption of new recruits would lead to lower $\delta^{13}C$ values, consumption of kelp forest juveniles would yield the opposite effect. Results from the liver tissue stable isotope analysis support this expectation.

The only species with $\delta^{13}C$ values (measured from liver tissue) that varied by year was the blue rockfish, a midwater forager with a narrow gape likely to prey on small, new recruits (Fig. 5a, Table S4). Mean values of $\delta^{13}C$ for blue rockfish increased from 2014 to 2015 before dropping significantly from 2015 to 2016 (p < 0.001) as juvenile rockfish recruitment increased from the 2015 low. This result may be indicative of the blue rockfish's heavier use of macroalgal-based carbon when fewer newly recruited juvenile rockfishes are available to prey upon.

The final piece of evidence for annual variation in diet related to juvenile rockfish recruitment is seen in the analysis of $\delta^{15}N$: black (p = 0.03), blue (p = 0.02), and kelp rockfish (p = 0.005) liver tissue $\delta^{15}N$ decreased in 2015, the year with the lowest rockfish recruitment during the study period, potentially the result of a diet more reliant on lower trophic level, pelagic-based prey (such as crab megalopae). It then increased again in 2016 for kelp (p < 0.001), black (p = 0.007), and black-and-yellow (p = 0.003) rockfishes. This pattern was not seen in blue rockfish, though they did exhibit an increase in trophic level in 2016 (Figs. 5b & S4).
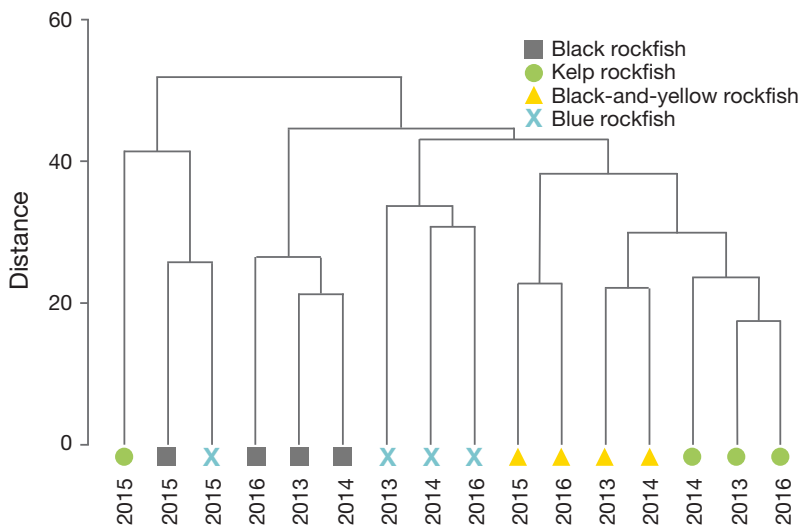
Fig. 3. Similarity in rockfish diets among species and between the years 2013–2016. Clustering is based on Bray-Curtis dissimilarity of the prey-specific abundance by number of each prey category identified in a stomach

### 3.3.2. Seasonal upwelling

Liver tissue samples were used to examine the diet consumed by each species of focal rockfish during both upwelling (April–July) and non-upwelling seasons. Despite hypothesizing (H4) that $\delta^{13}C$ and $\delta^{15}N$ of liver tissue from black and blue rockfishes (species more likely to prey upon incoming pelagic subsidy organisms) would reflect a more phytoplankton-based diet during seasonal upwelling, the results

were mixed. None of the species sampled showed significant seasonal variability in $\delta^{13}C$ values ($p > 0.05$; Figs. 6a & S5). However, kelp (Mann-Whitney $U$, $W = 54$; $p = 0.01$) and black-and-yellow ($W = 57$, $p = 0.002$) rockfishes did show a seasonal difference in $\delta^{15}N$, occupying a lower trophic level in upwelling season (Figs. 6b & S5).

## 4. DISCUSSION

### 4.1. Phytoplankton-based carbon and pelagic prey in the diets of nearshore rockfishes

Carbon derived from the primary production of phytoplankton plays a major role in the nearshore fish assemblage in the Monterey Bay area of central California. My results indicate that the use of phytoplankton-derived carbon differs by species, making up approximately 50–65% of muscle tissue (Fig. 1). Koenigs et al. (2015) found an approximately 60% phytoplankton-based carbon contribution for kelp rockfish and >80% for blue rockfish. Though I found similar relative proportions, small differences could stem from the distinct oceanographic conditions of southern versus central California that influence pelagic–benthic coupling. Similar relative pro-

Fig. 4. Mean (±SD) carbon and nitrogen isotopic values for juvenile rockfish muscle tissue. Less negative $\delta^{13}C$ values indicate kelp-derived carbon. Species comprising pelagic juvenile samples include blue rockfish (n = 11) and members of the KGBC rockfish complex (n = 20; *Sebastes atrovirens*, *S. carnatus*, *S. chrysomelas*, *S. caurinus*). Species comprising new recruit samples include KGBC complex (n = 14) and the OYT rockfish complex (n = 2; *S. flavidus*, *S. serranoides*). Species comprising kelp forest juvenile samples include the KGBC complex (n = 43), OYT complex (n = 15), and blue rockfish (n = 21)
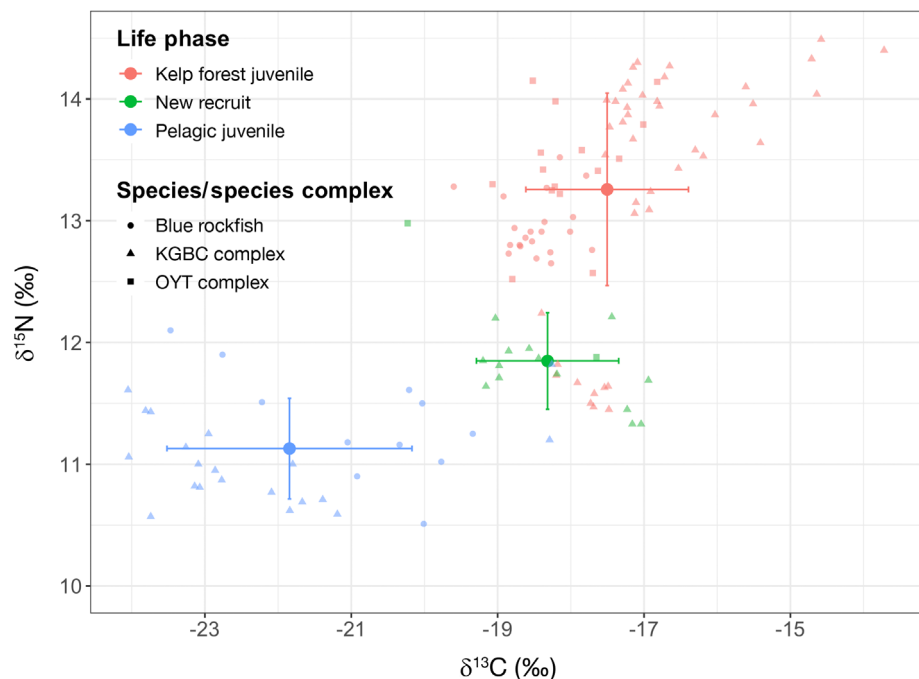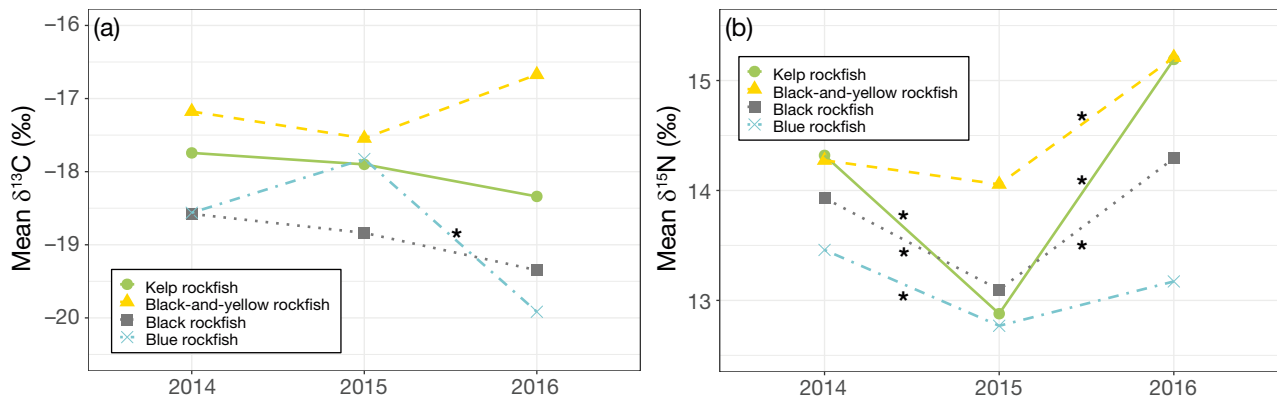
Fig. 5. Mean (a) δ$^{13}$C and (b) δ$^{15}$N for rockfish liver tissue samples in 2014, 2015, and 2016. (*) signifies significance between points to the left and right (α = 0.05). Mean values, SD, and sample sizes can be found in Table S4
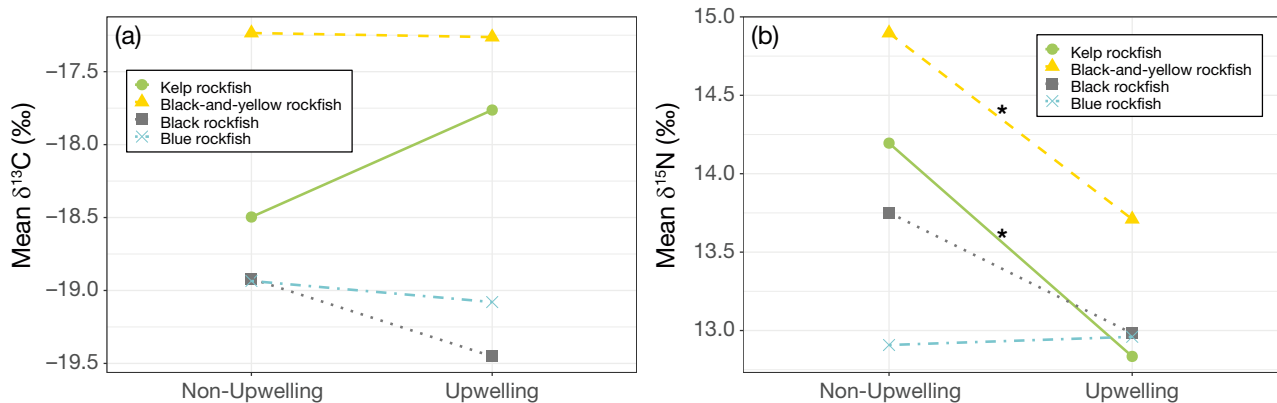


Fig. 6. Mean (a) δ$^{13}$C and (b) δ$^{15}$N for rockfish liver tissue samples in upwelling season (April–July) and non-upwelling (all other months). (*) signifies significance between points to the left and right (α = 0.05). Mean values, SD, and sample sizes can be found in Table S5

portions of kelp-based and phytoplankton-based carbon in rockfishes' tissue were also found by von Biela et al. (2016) and Markel & Shurin (2015). However, a high-resolution stomach content analysis allowed me to further explore dietary contributions from phytoplankton-based food webs.

Gelatinous organisms that typically live in the open ocean are advected to the kelp forest during downwelling or relaxation events. Though tunicates (both salps and pyrosomes) were the most common gelatinous organisms observed, both cnidarians and ctenophores were also identified. I suspect that many of the prey items classified as 'unknown' (and thus excluded from further analysis) also fell into the category of gelatinous organisms. These prey items digest quickly and are likely underestimated in the PSIRI results. Previous studies have found thaliaceans (pelagic salps) to be important prey for blue rockfish, especially during the upwelling season, but that they are not typically consumed by kelp, black, and black-and-yellow rockfishes (Hallacher & Roberts 1985,

Hobson & Chess 1988). My results suggest that the importance of salps as prey for the nearshore fish assemblage extends beyond blue rockfish during certain conditions and, in fact, that gelatinous zooplankton may play a substantial role in nearshore food webs. As we build our understanding of temporal diet variability, future research should focus on the role that gelatinous pelagic subsidies (and resource pulses) play in rockfishes' survival, growth, and overall resilience, especially as climate change alters the pelagic zooplankton assemblage. Metabarcoding may provide a feasible approach for targeting gelatinous prey species in future studies (e.g. Günther et al. 2021).

Recruiting juvenile rockfishes and crabs represent another influx of pelagic energy into the kelp forest (Zuercher & Galloway 2019). The juvenile life phase makes both rockfish young-of-the-year and crab megalopae vulnerable to predation, especially during years of high recruitment (such as 2013 and 2014 for juvenile rockfishes, when adults seemed to shift

toward fishes as prey items; Fig. S4). The $\delta^{13}C$ results suggest that new juvenile rockfish recruits are contributing phytoplankton-based carbon to the kelp forest food web, but that after only a short period, their stable isotope ratio shifts to reflect a more heavily macroalgal-based diet (Fig. 4). As such, the ways that prey fishes, especially juvenile rockfishes, contribute to the isotopic composition of adult rockfishes depends on the life phase and trophic ecology of the prey. Newly recruited juvenile rockfishes residing in the kelp canopy and water column (and contributing relatively more phytoplankton-based carbon) are likely more vulnerable to predation by blue or black rockfishes that show an affinity for mid-water habitats. This was most apparent in the diets of the small-gaped blue rockfish that likely only consume small, newly recruited pelagic juveniles. Adult blue rockfish showed an annual shift toward macroalgal-based carbon in 2015 when few new recruits were available as prey. Conversely, kelp and black-and-yellow rockfishes, which were also shown to prey widely on fishes, forage nearer the benthos where slightly more mature juvenile rockfishes would contribute relatively more macroalgal-based carbon.

A wide variety of benthic organisms contributed to the macroalgal signal detected in adult rockfishes. Brachyuran and anomuran crabs, isopods, amphipods, benthic shrimps, and juvenile fishes that have transitioned to a kelp forest diet all move kelp-based carbon up the food chain. Black-and-yellow rockfish forage almost entirely on benthic organisms and might be expected to have shown even larger contributions of macroalgal-based carbon. However, they prey heavily on octopus, which has $\delta^{13}C$ values indicating use of phytoplankton-based energy (Table S3). This trophic relationship highlights the significance of energy flow via pelagic−benthic coupling for even benthic invertivores. Benthic suspension- and filter-feeding organisms such as tunicates, sponges, barnacles, and bryozoans also likely consume substantial phytoplankton-based energy that is then passed up the food chain to nearshore fishes (Miller & Page 2012).

While I constructed a 2-source mixing model for this work, it is possible that a portion of the $\delta^{13}C$ signal that I interpreted as pelagic instead reflects energy derived from red algae (a potential third source). A wide diversity of red algae species reside in California kelp forests and provide food for benthic invertebrates via direct grazing and through detrital pathways (Mahoney 2014). A sample of red algae from Carmel Bay (n = 5) collected in September 2015 had $\delta^{13}C$ values that were more $^{13}C$-depleted than those typically reported for phyto-

plankton ($\delta^{13}C$: −28.9 ± 5.0‰; $\delta^{15}N$: 7.5 ± 0.8‰) (R. Zuercher unpubl. data). These values are consistent with those measured in Norwegian kelp forests where 2 multi-species groups of red algae were analyzed; one group with $\delta^{13}C$ values ranging from −18.9 through −22.3‰ and another group with even lower values of −32.9 through −34.4‰ (Raven et al. 2002, Fredriksen 2003). Mahoney (2014) showed that the most common epifaunal species group living (and likely feeding) on red algae in Monterey Bay's nearshore ecosystem are gammarid amphipods, a common prey item for kelp rockfish. This could lead to an overestimation of phytoplankton-based carbon in kelp rockfish tissue and should be the focus of future research.

## 4.2. Temporal dynamics in diet and pelagic contributions to the benthic food web

Though 2013 did not see strong El Niño or La Niña conditions, a major shift occurred when 2014 brought 'The Blob' ocean conditions to the west coast of the USA (Joh & Di Lorenzo 2017). Warm water temperatures of 2014 persisted through 2015, a year with strong El Niño conditions, before the ocean returned to more average conditions in 2016. Cumulative upwelling (quantified by the Bakun Upwelling Index) was below average in 2015, likely contributing to the low rockfish recruitment in that year (Bakun 1973; Figs. 2 & S5). Vertical nitrate flux, or the concentration of nitrate upwelled to or downwelled from nearshore surface waters (quantified by the Biologically Effective Upwelling Transport Index, BEUTI), was below average for all 3 years. Cumulative BEUTI was especially low in 2015 (Jacox et al. 2018; Fig. S5). The anomalous ocean conditions of 2015 are reflected in the diet analysis, which showed 3 rockfish species that typically have distinctive diets converging on a 'warm year' diet (Fig. 3). Notably, this diet consisted of a relatively high proportion of tunicates and seemingly benefited from a large crab recruitment event. Again, this highlights the importance of pelagic subsidies, which often come as resources pulses, when typical food sources are less available. It is not known whether the dietary convergence across species in 2015 was the result of a lower abundance of juvenile rockfishes or the presence of other nutritious, energy-dense, and easy to capture prey (e.g. crab megalopae and zoea). If the convergence (and associated low reliance on fishes as prey) resulted from the presence of tunicates and recruiting crabs in 2015 rather than lower numbers of juvenile rockfishes, this may help

to explain why diets of the 4 focal species did not converge in 2013 (a year with very high rockfish recruitment).

With very little rockfish recruitment on the central coast of California in 2015, fewer newly recruited juveniles would have been available as prey. As such, I expected that rockfish $\delta^{13}C$ signatures would reflect a more macroalgal-based diet in 2015. However, the switch away from fishes as prey in 2015 was not accompanied by a corresponding shift in $\delta^{13}C$ to reflect a more kelp carbon-heavy diet, except in blue rockfish. This perhaps indicates that blue rockfish, widely considered a mid-water planktivore, switches to consuming juvenile rockfishes only in years of high recruitment (i.e. in a low-recruitment year like 2015, blue rockfish consumed a more typical diet for a mid-water planktivore). Because the 3 other species switched from fishes to tunicates and other recruiting species (e.g. crabs), these large pelagic contributions may have offset the lack of energy-rich recruiting juvenile rockfishes, leading to little change in their $\delta^{13}C$ signatures. Alternately, because 2015 was the study year with the lowest vertical nitrate flux, this could suggest that blue rockfish are most sensitive to these upwelling-driven shifts in nearshore water nitrate concentration (Fig. S5).

Results from the analysis of $\delta^{15}N$ ratios in liver tissue gave further insight into annual diet variability related to juvenile rockfish recruitment. Trophic levels of all species except the black-and-yellow rockfish fell in 2015; this was especially evident for black and kelp rockfishes. The 2015 downward shift in trophic level may reflect these species' switch from fishes to gelatinous invertebrates. Because the species in this study typify different feeding ecologies, these results provoked an additional observation regarding feeding morphology and the use of phytoplankton-based carbon. Gape width (measured by maxillary length) varies among the 4 focal species, with black-and-yellow at the largest (39.8 mm), kelp (38.8 mm), black (37.3 mm), then blue rockfish at the smallest (30.7 mm) (Roberts 1979). Because larger-gaped fishes likely have a wider range of prey available to them, the effects of large deliveries of pelagic subsides (e.g. juvenile rockfishes or gelatinous zooplankton) might be dampened. This seems to be the case for black-and-yellow rockfish, though this benthic-feeder also may simply encounter prey such as gelatinous zooplankton less frequently.

Finally, because the trend for all rockfishes (including black-and-yellow rockfish) was a decrease in $\delta^{15}N$ in 2015, a shift in baseline $\delta^{15}N$ in either the nearshore or offshore systems in that year could be at least partially responsible. Foley & Koch (2010) showed 3‰ changes in the $\delta^{15}N$ values of *Macrocystis pyrifera* (giant kelp) between samples collected in spring to early summer and those collected in late summer to winter, suggesting that the apparent decrease in trophic level reported here may be the result of a baseline shift. Moreover, while the shift from fishes to pelagic salps and other pelagic prey in 2015 is also supported in the diet content data, there are other possible drivers of the shift toward more phytoplankton-derived carbon. Kelp production typically declines with increasing water temperatures and reduced nitrate availability, such as occurred with the onset of the marine heatwave in 2014 and 2015, potentially limiting kelp-based carbon in the entire system. Moreover, kelp production declined during these years as kelp forests were deforested by sea urchin grazing in central (Beas-Luna et al. 2020, Smith et al. 2021) and northern California (Rogers-Bennett & Catton 2019, McPherson et al. 2021). Ongoing research on the wide-ranging ecological impacts of a phase shift from kelp forest to urchin barrens on the US West Coast will provide additional context with which to interpret my results.

Results regarding seasonal shifts in the relative proportion of phytoplankton-based carbon in rockfishes' tissue were not as conclusive. I found no significant differences in $\delta^{13}C$ values between upwelling and non-upwelling seasons, with high variance in the data relative to the expected effect size (Table S5). These results may also have resulted from underlying trophic and ecological dynamics or might point to uncertainties regarding the turnover rate of liver tissue, which has not been experimentally determined for *Sebastes* spp. It is possible that liver tissue is not appropriate to characterize dietary shifts at seasonal intervals. However, $\delta^{15}N$ values did differ between seasons. The only species that did not exhibit a seasonal shift in trophic level was the blue rockfish. All others occupied a lower trophic level during upwelling season. This is contrary to the expectation that trophic level would increase during upwelling-mediated pulses of rockfish recruitment. However, the seasonal shift may not be related to rockfishes' diet at all. The shift could be due to a seasonal decrease in baseline $\delta^{15}N$ values of *Macrocystis* during the upwelling season that is only reflected in species that have more macroalgal-dominated diets (Foley & Koch 2010). Blue rockfish use less macroalgal-based carbon than any of the other species, and as such, a seasonal baseline shift in *Macrocystis* is perhaps not as strongly reflected.

# 5. CONCLUSIONS

Kelp forest ecosystems are known for extremely high productivity as a result of accessing both benthic and pelagic sources of energy, and the diet of nearshore kelp forest fishes highlights this pelagic−benthic coupling. Though the focal species in this study spend their entire adult lives in the kelp forest ecosystem, the results presented here suggest that their productivity is likely affected by variation in the availability of resources originating in the pelagic ocean. Whether changes in the relative use of macroalgal- versus phytoplankton-based energy by nearshore fishes translates to changes in growth rate is a fruitful topic for future research. It is clear, however, that the contributions of pelagic carbon not only vary by a species' foraging ecology but also as environmental conditions fluctuate and cause changes to the influx of offshore waters that bring phytoplankton-based nutrients and energy to the kelp forest. Though the 4 focal species coexist in central California, kelp forests throughout the world typically support a set of fish species in the same functional guilds (i.e. planktivores, generalist demersal predators, and invertivores). As such, results presented here can inform our understanding of the ways that oceanographic variability and shifts in pelagic subsidies interact with fishes' diets and food web dynamics elsewhere.

This study has advanced our wider understanding of the importance of pelagic−benthic coupling to the productivity of species and ecosystems. Marine systems are constantly changing, and food webs follow suit. Changes to habitat structure, such as is occurring on the west coast of the USA through the loss of giant kelp, and variation in circulation patterns will likely drive further changes in the importance of phytoplankton-based energy to the nearshore fish assemblage (Filbee-Dexter & Wernberg 2018, Beas-Luna et al. 2020). The results presented here suggest that connectivity with open ocean habitats and subsidy prey availability may infer resilience on nearshore rockfishes, especially those associated with water column habitats, as they respond to localized kelp forest loss. Annual dietary shifts characterized here highlight the role that phytoplankton- and kelp-based energy sources play in maintaining the high productivity (i.e. high increase in biomass of an organism per unit time and space) of kelp forest fish assemblages in a highly variable marine environment. Whether this ability to access more than one basal energy source infers resilience and/or stability on the kelp forest ecosystem remains a fruitful area of research

(Rooney et al. 2006, McMeans et al. 2013). Using multiple carbon pathways could exacerbate stress in years of low productivity or could buffer against this stress. The 4 focal species, and many of the other nearshore rockfishes, are generalist predators with the ability to prey-switch to capitalize on available resources. While this behavior has likely contributed to the success of the *Sebastes* genus in the past, it may also prove important in the future as these species adapt to major climate and ecosystem changes. To truly understand how kelp forest communities function, we must give more attention to the dynamics of pelagic energy sources, the conditions that lead to changes in the influx of this energy to the nearshore environment, and the ecosystem-level consequences of these changes.

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