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Widespread kelp-derived carbon in pelagic and benthic nearshore fishes suggested by stable isotope analysis

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ABSTRACT

Kelp forests provide habitat for diverse and abundant fish assemblages, but the extent to which kelp provides a source of energy to fish and other predators is unclear. To examine the use of kelp-derived energy by fishes we estimated the contribution of kelp- and phytoplankton-derived carbon using carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopes measured in muscle tissue. Benthic-foraging kelp greenling *(Hexagrammos decagrammus)* and pelagic-foraging black rockfish *(Sebastes melanops)* were collected at eight sites spanning ~35 to 60°N from the California Current (upwelling) to Alaska Coastal Current (downwelling) in the northeast Pacific Ocean. Muscle $\delta^{13}C$ values were expected to be higher for fish tissue primarily derived from kelp, a benthic macroalgae, and lower for tissue primarily derived from phytoplankton, pelagic microalgae. Muscle $\delta^{13}C$ values were higher in benthic-feeding kelp greenling than in pelagic-feeding black rockfish at seven of eight sites, indicating more kelp-derived carbon in greenling as expected. Estimates of kelp carbon contributions ranged from 36 to 89% in kelp greenling and 32 to 65% in black rockfish using carbon isotope mixing models. Isotopic evidence suggests that these two nearshore fishes routinely derive energy from kelp and phytoplankton, across coastal upwelling and downwelling systems. Thus, the foraging mode of nearshore predators has a small influence on their ultimate energy source as energy produced by benthic macroalgae and pelagic microalgae were incorporated in fish tissue regardless of feeding mode and suggest strong and widespread benthic-pelagic coupling. Widespread kelp contributions to benthic- and pelagic-feeding fishes suggests that kelp energy provides a benefit to nearshore fishes and highlights the potential for kelp and fish production to be linked.

1. Introduction

Kelp forests are ubiquitous along temperate and sub-arctic coastlines (Dayton, 1985; Estes and Steinberg, 1988) where they provide habitat and prey for diverse and abundant fish assemblages (Bodkin, 1988; Efird and Konar, 2014; Leaman, 1980; Siddon et al., 2008). Kelp-derived energy may also provide a trophic benefit to fishes (Foster and Schiel, 1985; Koenigs et al., 2015), as is the case for several benthic invertebrates (Duggins et al., 1989; Eckman and Duggins, 1991; Fredriksen, 2003; Salomon et al., 2008; Tallis, 2009). Nearshore marine food webs are complex with energy derived from phytoplankton, macroalgae (e.g., kelp), and terrestrial primary production (Duggins et al., 1989; Dunton et al., 2012; Fredriksen, 2003; Tallis, 2009; von Biela et al., 2013) and changes in the availability of these energy sources appears to influence the growth and production of fishes (Robards et al., 2002; von Biela et al., 2011). Canopy-forming kelps are a conspicuous source of energy with a concentrated biomass of primary production available to food webs by grazers, detritivores, and filter feeders (Kaehler et al., 2006; Steneck et al., 2002). Understanding the extent to which kelp provides energy throughout the nearshore food web is a priority as warming temperatures, rising sea levels, and increased human development have the potential to disrupt the function of ecologically and economically important nearshore ecosystems (Agardy et al., 2005; Harley et al., 2006; Scavia et al., 2002). Critical knowledge gaps include understanding the extent to which kelp

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energy reaches higher trophic level predators, such as fishes, and whether kelp is a routine source of energy for pelagic-, as well as benthic-, feeding species.

Kelp forest fish assemblages include species that are associated with the seafloor and forage benthically and species that occur primarily in the water column and forage pelagically within and along the edge of kelp forests. We define kelp forest ecosystems in this study as subtidal rocky reefs characterized by canopy- and understory-forming kelp (brown algae of the order Laminariales) in the neritic zone and use the term pelagic to refer to water column feeding in nearshore habitats unless otherwise specified. Evidence of kelp-derived energy in nearshore food webs has most often focused on benthic invertebrates (Duggins et al., 1989; Fredriksen, 2003; Salomon et al., 2008; Tallis, 2009) and occasionally benthic fishes or other predators that consume benthic invertebrates (Duggins et al., 1989; McMeans et al., 2013). In these studies, kelp-derived energy enters food webs either through the direct grazing of live kelp by kelp herbivores (e.g., urchins) or more commonly as kelp detritus by filter and suspension feeders (e.g., clams and mussels) (Duggins et al., 1989; Fredriksen, 2003; Salomon et al., 2008; Tallis, 2009). Recently, the tissues of pelagic-feeding fishes in nearshore systems were shown to contain substantial amounts of benthically produced carbon (Kopp et al., 2015) and kelp carbon (Koenigs et al., 2015; Markel and Shurin, 2015).

If kelp-derived energy is an important reason why so many fishes are associated with kelp forests, kelp should be a routine and substantial source of primary production that supplies energy for species that have either benthic or pelagic feeding modes. Energy can be traced through food webs by analyzing carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope values. Kelp generally have higher $\delta^{13}C$ values than sympatric phytoplankton and these differences propagate up the food chain even when predators are separated from primary producers by several trophic levels (Duggins et al., 1989; Fredriksen, 2003; Michener and Kaufman, 2007; Page et al., 2008; Tallis, 2009). When the isotope values of both primary producers (e.g., kelp and phytoplankton) and focal consumers (e.g., fish) are measured, a stable isotope mixing model can estimate the relative carbon contribution of each primary producer (e.g., Parnell et al., 2010). Mixing models also require estimates of consumer trophic level that can be estimated from $\delta^{15}N$ analysis and trophic discrimination factors, defined as the isotopic difference between consumer tissues and that of their prey ($\Delta^{13}C_{tissue\text{-}diet}$ or $\Delta^{15}N_{tissue\text{-}diet}$). Ideally, isotope values of potential energy sources used in mixing models are well constrained, however, $\delta^{13}C$ and $\delta^{15}N$ values of phytoplankton and kelp can vary both spatially and seasonally (Bond and Diamond, 2011; Fox, 2013; Miller and Page, 2012; Page et al., 2008; Simenstad et al., 1993) and may require some considerations.

Black rockfish *(Sebastes melanops)* and kelp greenling *(Hexagrammos decagrammus)* are ideal focal predators for examining the use of both kelp and phytoplankton energy pathways in the northeast Pacific Ocean. Both fishes are widely distributed in nearshore habitats with small individual home ranges (~1 km^2; Love, 2011; Parker et al., 2007), assuring that capture locations reflect foraging grounds. Each species represents one of the two principal feeding modes in aquatic marine ecosystems, pelagic and benthic. Black rockfish are water-column (e.g., pelagic) generalists that consume forage fish, euphausiids, and zooplankton, and often aggregate near steep rocky reefs in relatively shallow water <55 m deep (Brodeur et al., 1987; Love, 2011; Love et al., 2002; Pirtle et al., 2012; Rosenthal, 1983). Kelp greenling are benthic generalists that consume sea cucumbers, brittle stars, crabs, amphipods, shrimp, worms, and snails on or near the seafloor (Love, 2011; Moulton, 1977; Rosenthal, 1983). Based on these feeding modes, we anticipated that each species would acquire carbon contributions from both kelp and phytoplankton pathways, but that kelp greenling would derive substantially larger carbon contributions from kelp than black rockfish. Ontogenetic dietary shifts may occur in either species, thus we considered individual fish size. To determine whether pelagic- and benthic-feeding predators consistently use both kelp and phytoplankton pathways, black rockfish and kelp greenling were collected from eight nearshore sites in the northeast Pacific Ocean from California to Alaska, spanning 25 degrees of latitude (~35 to 60°N) and two large marine ecosystems, the California Current and Gulf of Alaska. The former is a seasonal coastal upwelling system, whereas the latter is predominantly a year-round downwelling system.

2. Methods

2.1. Sample collection and stable isotope analysis

A total of 308 black rockfish and 336 kelp greenling were captured at eight subtidal rocky reef sites in the northeast Pacific Ocean: Katmai National Park and Preserve, AK (KATM); western Prince William Sound, AK (WPWS); Elfin Cove, AK (ELFI); Whale Bay, AK (WHAL); Clayoquot Sound, BC (CLAY); Neah Bay, WA (WASH); Monterey Bay, CA (MONT); and Big Sur, CA (BIGS) (Fig. 1; Table 1). Sea otters were present at all sites; predation by otters increases kelp production and species diversity via top-down control of major kelp grazers, such as sea urchins (*Strongylocentrotus spp.*; Estes and Duggins, 1995; Steneck et al., 2002; Watson and Estes, 2011). Fish were collected using trammel nets, hook and line sampling, or via spear fishing in 2010 and 2011 (Table 1). Most collections occurred between April and September, but some samples were collected in October from WASH ($n = 12$) and November from MONT ($n = 7$). Collection month was not standardized as it is doubtful to influence isotope values because the muscle tissue of slow-growing adult fish (age: 1+) living in cold waters have slow isotopic incorporation rates and likely reflect several months to one year of foraging information (Hesslein et al., 1993; Perga and Gerdeaux, 2005; Weidel et al., 2011). Epaxial muscle was sampled and stored frozen prior to stable isotope analysis.

Epaxial muscle samples were freeze-dried and subsampled for stable isotope analysis at the University of Wyoming Stable Isotope Facility (Laramie, WY). Each sample was analyzed for carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) values using a NC 2500 Carlo-Erba or a Costech 4010 Elemental analyzer (Costech Analytical, Valencia, CA) interfaced with a Thermo-Finnigan Delta Plus XP continuous-flow stable isotope ratio mass spectrometer (Thermo Electron Corp., Waltham, MA). Stable isotope values are reported using standard delta notation, $\delta^{15}N$ or $\delta^{13}C = 1000\,[(R_{sam}/R_{std})\text{-}1]$, where R_{sam} and R_{std} are the $^{15}N{:}^{14}N$ or $^{13}C{:}^{12}C$ ratios of the sample and standard, respectively. Lipids were not extracted prior to analysis because the mean (±SD) ratio of carbon:nitrogen concentration, expressed as [C]/[N] ratios, of fish muscle for both species was 3.2 ± 0.1, which is indicative of pure protein containing negligible lipid content (Logan et al., 2008; Post et al., 2007; Ricca et al., 2007; Sotiropoulos et al., 2004) and previous work found no effect of lipid extraction of muscle $\delta^{13}C$ for black rockfish (Markel and Shurin, 2015) or a closely related greenling species, rock greenling (*Hexagrammos lagocephalus*) (Ricca et al., 2007). The within-run standard deviation of $\delta^{13}C$ and $\delta^{15}N$ reference materials, calibrated to internationally accepted Vienna-Pee Dee Belemnite (V-PDB) and atmospheric N_2, was $\leq 0.2‰$.

2.2. Statistics and stable isotope mixing models

Differences in the size of fish among sites were evaluated using

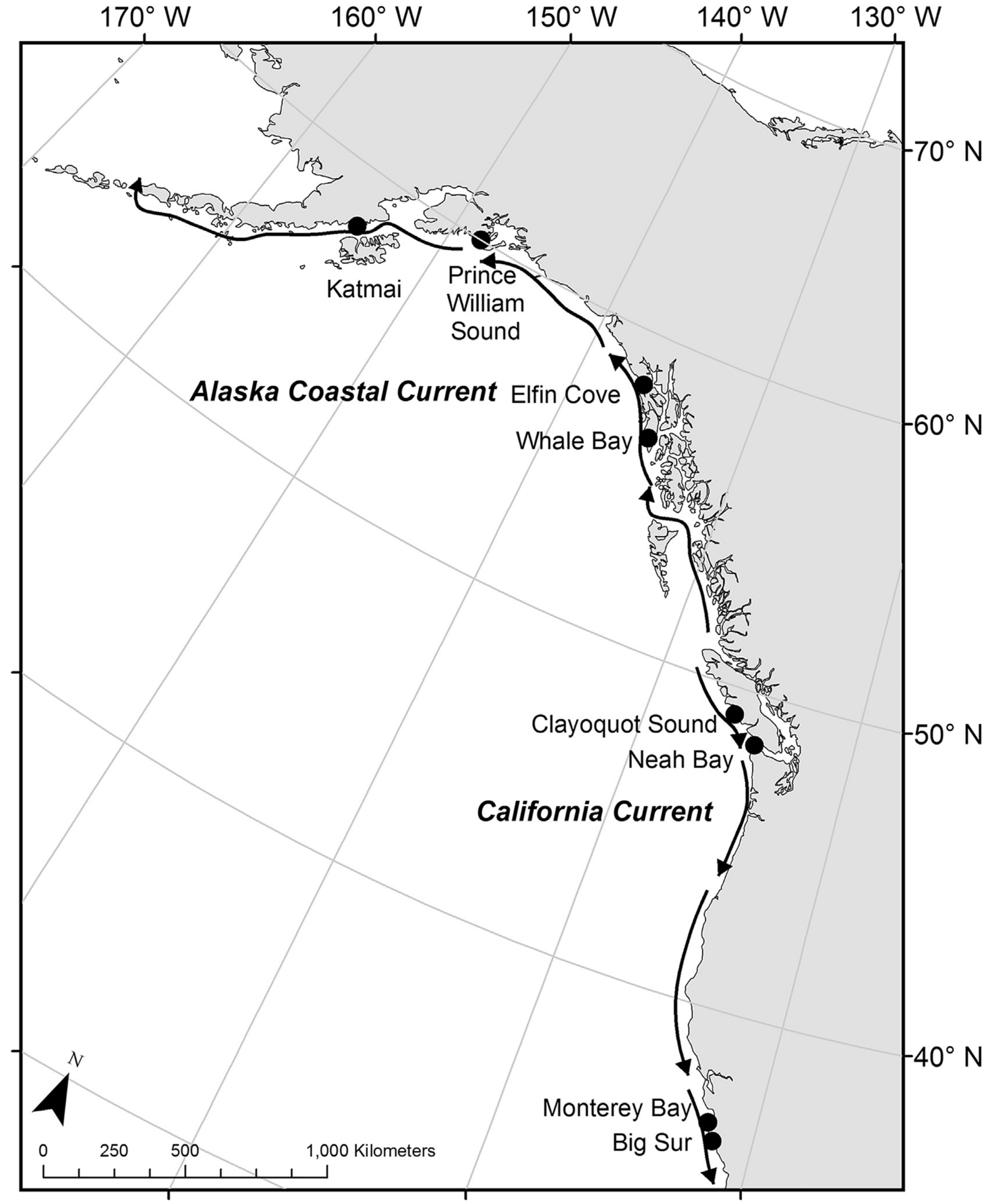

Fig. 1. Nearshore fish collection sites (solid dots) and generalized nearshore current flow in summer (arrows) in the Alaska Coastal Current and California Current.

an analysis of variance with pairwise Tukey's honestly significant difference post-hoc tests ($P < 0.05$) for each species. If fish lengths differed among sites, then the magnitude of the effect of length on δ^{13}C and δ^{15}N values was evaluated prior to comparing primary producer contributions across sites. A set of linear mixed-effect models was used to test the influence of fish length on δ^{15}N and δ^{13}C and for each species. In the full model, δ^{15}N or δ^{13}C is described by fork length (X_i) and random site effects for the intercept and slope:

$$\delta^{15}\mathrm{N}_{\ ki} = (\alpha + a_k) + (\beta + b_k\ )X_i + \varepsilon_{ki},$$

where $\delta^{15}\mathrm{N}_{ki}$ is the nitrogen isotope value of fish i from site k and is estimated by a fixed intercept α, a random site-specific deviation that allows average isotope levels to differ among sites a_k, a fixed length effect β, and a site-specific deviation in the length effect b_k that allows the effect of length on isotope values to vary across sites. The random effects a_k and b_k are assumed to follow a bivariate normal distribution with mean 0, variances σ_a and σ_a and covariance σ_{ab}. Residuals are assumed to be independent of the random effects and normally distributed such that:

$$\varepsilon_{ki} \sim N\left(0,\ \sigma^2\right).$$

The full model was compared to nested models without random length effects (b_k= 0 for all k) and without fixed or random length effects ($\beta = b_k = 0$) using Akaike information criterion (AIC) and likelihood ratio tests. Random site-specific intercepts were

Table 1
Carbon isotope values ($\delta^{13}C$), nitrogen isotope values ($\delta^{15}N$), and kelp-derived carbon contributions in black rockfish (*Sebastes melanops*) and kelp greenling (*Hexagrammos decagrammus*) muscle tissue collected from rocky nearshore habitats throughout the northeast Pacific Ocean. Pairwise differences in mean length among sites are denoted by different numbers for black rockfish and different letters for kelp greenling. Kelp–derived carbon percentages are based on the mean estimates from SIAR mixing models with site-specific $\delta^{13}C$ and $\delta^{15}N$ for phytoplankton and kelp (Table 2) and trophic discrimination factors of 1.0 ± 1.0‰ for $\delta^{13}C$ per trophic level. Kelp-derived carbon contributions were not estimated for fish from Monterey Bay because fish isotope values from this site fell outside the range of kelp and phytoplankton values.

Site	Site code	Collection dates	Species	N	Length ± SD (mm)	$\delta^{13}C$ ± SD	$\delta^{15}N$ ± SD	Kelp-derived carbon ± SD
Katmai National Park, south central Alaska	KATM	July 2010	*S. melanops*	39	404 ± $99^{3,4}$	−17.3 ± 0.5	14.3 ± 0.5	65 ± 3%
			H. decagrammus	47	272 ± 80^{a}	−15.8 ± 0.5	14.6 ± 0.5	89 ± 3%
Western Prince William Sound, south central Alaska	WPWS	June and August 2010	*S. melanops*	38	471 ± 70^{5}	−17.7 ± 0.6	14.9 ± 0.5	63 ± 3%
			H. decagrammus	82	278 ± 85^{a}	−16.8 ± 0.5	14.5 ± 0.6	66 ± 2%
Elfin Cove, Chichagof Island, Southeast Alaska	ELFI	May 2011	*S. melanops*	45	440 ± $44^{4,5}$	−18.0 ± 0.3	14.0 ± 0.5	64 ± 3%
			H. decagrammus	41	323 ± 45^{b}	−17.3 ± 0.7	14.4 ± 0.5	57 ± 3%
Whale Bay, Baranof Island, Southeast Alaska	WHAL	May and June 2011	*S. melanops*	44	384 ± $44^{2,3}$	−17.6 ± 0.3	13.7 ± 0.4	64 ± 3%
			H. decagrammus	41	317 ± 36^{b}	−17.1 ± 0.6	14.6 ± 0.5	63 ± 3%
Clayoquot Sound, Vancouver Island	CLAY	May 2010 and July 2011	*S. melanops*	55	424 ± 37^{4}	−16.2 ± 0.4	14.9 ± 0.4	35 ± 2%
			H. decagrammus	53	316 ± 63^{b}	−15.3 ± 0.4	15.5 ± 0.4	51 ± 2%
Neah Bay, Olympic Peninsula, Washington	WASH	2010 and 2011	*S. melanops*	49	384 ± 55^{2}	−16.6 ± 0.4	14.9 ± 0.7	32 ± 4%
			H. decagrammus	38	386 ± 27^{c}	−16.0 ± 0.7	14.6 ± 0.7	36 ± 4%
Monterey Bay, central California	MONT	September and November 2010	*S. melanops*	13	270 ± 51^{1}	−16.4 ± 0.3	14.9 ± 0.6	
			H. decagrammus	17	324 ± $77^{a,b}$	−14.9 ± 0.4	15.8 ± 0.7	
Big Sur, central California	BIGS	September 2010	*S. melanops*	25	278 ± 50^{1}	−16.5 ± 0.6	14.5 ± 0.5	61 ± 6%
			H. decagrammus	17	340 ± $27^{b,c}$	−16.1 ± 0.7	15.2 ± 0.2	58 ± 8%

included in all models to account for known spatial shifts in the isotopic composition of primary producers (i.e., isotopic baseline) that can vary due to a host of physical and biological variables (Graham et al., 2010). The same set of models was compared for $\delta^{13}C$ values by substituting $\delta^{13}C_{ki}$ for $\delta^{15}N_{ki}$.

The $\delta^{13}C$ of black rockfish and kelp greenling muscle tissue were compared at each site with independent two-sample t-tests that assumed unequal variance following Leven's test. Comparisons of $\delta^{13}C$ between greenling and rockfish at each site reflect differences in carbon source when common assumptions are met, including similar trophic levels, trophic discrimination factors between species, and end-member values (Duggins et al., 1989; Fredriksen, 2003; Miller et al., 2008). Similar trophic levels can be assessed by comparing $\delta^{15}N$ between species; there is no reason to suspect differences in discrimination factors or source (phytoplankton and kelp) values for black rockfish and kelp greenling captured at the same site.

Estimating kelp-derived carbon contributions to fish muscle required the use of site-specific isotope mixing models to account for differences in kelp and phytoplankton $\delta^{13}C$ values at each location. The mean (±SD) $\delta^{13}C$ values from kelp and phytoplankton were based on direct sampling or values at a nearby location reported in the literature (Table 2). Phytoplankton isotope values were measured from samples of particulate organic matter (POM) suspended in the water column 100 m to 3 km offshore (Table 2). End member values were not available for sites in Southeast Alaska (ELFI and WHAL), so values from the northern Gulf of Alaska were applied. Minor shifts (<1‰) in baseline isotope values were anticipated between these localities based on a lack of consistent geographic pattern in weathervane scallop (*Patinopecten caurinus*) isotope values from the northern to eastern Gulf of Alaska (Andrews, 2010). Kelp isotope values were for the dominant canopy kelp species at each site: *Macrocystis pyrifera* at sites in California (BIGS and MONT), Washington (WASH), and British Columbia (CLAY) (Foley and Koch, 2010; Markel, 2011; Tallis, 2009) and *Nereocystis luetkeana* in Alaska (WHAL, ELFI, WPWS, and KATM) (Dean et al., 2000; Lindstrom, 2009). While other kelp species may also be present in these systems, kelp biomass is generally dominated by the canopy kelp forming species (Duggins, 1980; Miller et al., 2011). We analyzed fresh kelp samples, but the majority of kelp likely enters these food webs as detritus (Krumhansl and Scheibling, 2012). Stable isotope values are fairly robust to decomposition

Table 2
Kelp and phytoplankton carbon and nitrogen source values used in mixing models. Phytoplankton was represented by particulate organic matter (POM) suspended in the water column. Sites are abbreviated as follows: Katmai National Park and Preserve, AK (KATM); western Prince William Sound, AK (WPWS); Elfin Cove, AK (ELFI); Whale Bay, AK (WHAL); Clayoquot Sound, BC (CLAY); Neah Bay, WA (WASH); Monterey Bay, CA (MONT); Big Sur, CA (BIGS).

Site	Kelp			Phytoplankton		
	$\delta^{13}C$ (±SD)	$\delta^{15}N$ (±SD)	Source	$\delta^{13}C$ (±SD)	$\delta^{15}N$ (±SD)	Source
KATM	−17.6 ± 1.0	7.4 ± 1.3	*Nereocystis* from Takli Island and Kaflia Bay, KATM (n = 20)	−23.0 ± 1.8	6.5 ± 1.2	Mean POM values collected ~100 m offshore at sites in Katmai and Kenai Fjords National Parks, and western Prince William Sound during summer (n = 11).
WPWS	−17.5 ± 1.0	7.5 ± 1.9	*Nereocystis* from Johnson Bay, WPWS (n = 10)			
ELFI WHAL			Used WPWS source values			
CLAY	−14.8 ± 0.2	6.5 ± 0.3	*Macrocystis* collected between Kyuquot Sound and Nuchatlitz Inlet (n = 44, Markel, 2011)	−20.3 ± 0.9	6.9 ± 0.9	marine POM collected 100–250 m offshore (n = 44, Markel, 2011)
WASH	−13.7 ± 0.3	6.1 ± 3.0	Mixed kelp detritus from Olympic Peninsula sites (n = 2, Tallis, 2009)	−20.2 ± 3.2	6.7 ± 3.2	Summer marine POM collected at river plume edges (n = 46, Tallis, 2009)
MONT	−17.1 ± 3.2	8.0 ± 1.3	Pre-experiment mature *Macrocystis* blades (n = 29, Fox, 2013)	−22.8 ± 1.9	5.1 ± 0.7	Summer marine POM collected 3 km offshore Big Sur coastline (n = 6, Foley, 2009)
BIGS	−17.5 ± 3.0	6.7 ± 1.9	*Macrocystis* from Big Sur coastline (n = 238, Foley, 2009)	−22.8 ± 1.9	5.1 ± 0.7	Summer marine POM collected 3 km offshore Big Sur coastline (n = 6, Foley, 2009)

and minimal influence on isotope values was assumed (Fenton and Ritz, 1988; Kaehler et al., 2006; Schaal et al., 2009). Other kelp species (e.g., *Saccharina* and *Agarum*) exist at our Alaska study sites and have similar isotope values as the dominant species used in our analysis (Dethier et al., 2013).

Trophic level (TL) was calculated based on differences in mean δ^{15}N between primary producers and fish at each site following Post (2002):

$$TL = 1 + \left(\delta^{15}N_{fish} - \left[\delta^{15}N_{phyto} \mathrm{x}\, \alpha + \delta^{15}N_{kelp} \mathrm{x}(1-\alpha) \right] \right) \Big/ \Delta^{15}N.$$

In this equation, $\Delta^{15}N$ is the nitrogen discrimination factor and α is the proportion of phytoplankton derived carbon. We assumed $\Delta^{15}N = 3.4‰$ based on Post (2002). For the trophic level calculation, α was set at 0.5, but estimates are not sensitive to this assumption as δ^{15}N values are similar for kelp and phytoplankton producers relative to the 3.4‰ enrichment per trophic level.

Bayesian mixing models were constructed using package SIAR (Parnell et al., 2010) in R (R Core Team, 2013) statistical software for each site. The SIAR model inputs included the means and standard deviations of δ^{13}C and δ^{15}N values for phytoplankton and kelp, trophic discrimination factors multiplied by the estimated mean trophic level of fish at each site, a standard deviation for the trophic discrimination factors, as well as the δ^{15}N and δ^{13}C values for individual specimens of each species at each site. Allowing errors in discrimination factors and carbon sources (i.e., kelp and phytoplankton) to propagate through the mixing model provides a more accurate measure of uncertainty. Incorporating error affords a buffer against known spatial and temporal variation in δ^{13}C of primary producers and uncertainty in discrimination factors (Bond and Diamond, 2011; Fox, 2013; Miller and Page, 2012; Page et al., 2008; Simenstad et al., 1993). A mean (±SD) trophic discrimination factor of 1.0 ± 1.0‰ for δ^{13}C per trophic level was assumed (Dubois et al., 2007; Elsdon et al., 2010; Kilham et al., 2009). No prior information on the mean percentages for each dietary source or elemental concentration data was included in the model. The SIAR package fits models using Markov Chain Monte Carlo simulations. The mean and standard deviation of kelp and phytoplankton carbon contribution was calculated from the posterior density draws for each species at each site.

Lastly, our mixing models did not consider other possible carbon sources, such as terrestrial plants, non-kelp macroalgae (e.g., green and red macroalgae) or seagrasses. The possibility of terrestrial carbon sources at these sites was minimal due to limited riverine influence and selection for sample sites on exposed coastlines. Similarly, we observed that kelp dominate the macroalgal biomass in subtidal habitats and seagrass beds did not occur along the exposed coastlines sampled in our study. Mixing model results were interpreted broadly and no comparisons among sites were considered given the difficulty of consistently collecting representative end member values to estimate the isotope signatures of phytoplankton and kelp from across the time period integrated by fish consumers. Mixing models were not implemented for fish captured at MONT, as most isotope values for individual fish fell outside the mean δ^{13}C values phytoplankton and kelp. When consumers' isotope values fall outside those of potential sources, it is likely that sources of primary production have been poorly defined and, as a result, mixing models may return nonsensical results (Phillips and Koch, 2002).

3. Results

The average length of black rockfish (one-way ANOVA, F = 35.7, $P < 0.001$) and kelp greenling (one-way ANOVA, F = 13.8, $P < 0.001$) differed among sites (Table 1). Rockfish from BIGS and MONT were the smallest ($P < 0.05$ for pairwise comparisons with all other sites) and those from ELFI and WPWS were largest ($P < 0.05$ for all pairwise comparisons except fish from ELFI were not significantly larger than those from KATM or CLAY), while rockfish from other sites were intermediate in mean length. Greenling from WPWS and KATM were the smallest ($P < 0.05$ for pairwise comparisons with all sites except MONT) and those from WASH were the largest ($P < 0.05$ for pairwise comparisons with all sites except BIGS).

Length of fish at capture was related to δ^{15}N values in both species and δ^{13}C values for black rockfish based on AIC and likelihood ratio tests among competing models (Table 3, Fig. 2). The increase in δ^{15}N values with length was described by a simple fixed length effect in black rockfish (Fig. 2a) and a fixed length effect with random site-specific slope deviations in kelp greenling (Fig. 2b). A model with a fixed fish length effect marginally improved predictions of δ^{13}C values in black rockfish (Fig. 2c, AIC improvement = 3.0 compared to model without a length effect), while length and δ^{13}C values were unrelated in kelp greenling (Fig. 2d, lines represent the differences in the random site-specific intercept effect and are horizontal due to the absence of a length effect). In general, the data suggest that a length effect is much more likely to influence δ^{15}N compared to δ^{13}C values as judged by AIC and likelihood ratios.

Within sites, kelp greenling δ^{13}C values were significantly higher than those of black rockfish at all sites except BIGS (t-tests with unequal variances, $P < 0.001$) (Fig. 3). At BIGS, kelp greenling and black rockfish had similar δ^{13}C values ($P = 0.06$). Within site variance in δ^{13}C values between species was unequal at 4 of 8 sites (MONT, WASH, WHAL, ELFI) based on Levene's test ($P < 0.05$). Trophic level estimates for fish were 2.2 to 2.6 levels above primary producers based on the difference between fish and primary producer δ^{15}N values within sites.

The kelp-derived carbon contributions estimated from mixing models were always >30% across sites for both species (Table 1). In Alaska, the mean percentage of kelp carbon in rockfish captured was ~65% while the mean percentage among kelp greenling ranged from 57 to 89% (Table 1). In the California Current, the contribution of kelp-derived carbon was 30 to 60% for either species (Table 1). On

Table 3
Model selection results for predicting black rockfish (n = 308) and kelp greenling (n = 336) nitrogen or carbon isotope values using individual fish length as a fixed or random site effect. Models in italics provided the best fit for each model group as judged by Akaike information criterion (AIC). Pairwise likelihood ratio tests contrast the best fit model and each of the two alternative models and likelihood ratios and *P* values are reported for this test. The likelihood ratio describes how much more likely the data are under the best fit model as compared to each alternative model.

Model	df	ΔAIC	Likelihood ratio	*P* Value
Nitrogen isotope				
Black rockfish				
Fixed length effect	4	0		
Fixed and random length effects	6	2.1	1.9	0.4
No length effect	3	40.5	42.5	<0.0001
Kelp greenling				
Fixed and random length effects	6	0		
Fixed length effect	4	7.7	11.7	0.003
No length effect	3	69.9	75.9	<0.0001
Carbon isotope				
Black rockfish				
Fixed length effect	*4*	*0*		
Fixed and random length effects	6	2.1	1.9	0.4
No length effect	3	3.0	5.0	0.02
Kelp greenling				
No length effect	*3*	*0*		
Fixed length effect	4	1.2	0.8	0.4
Fixed and random length effects	6	4.9	1.1	0.8

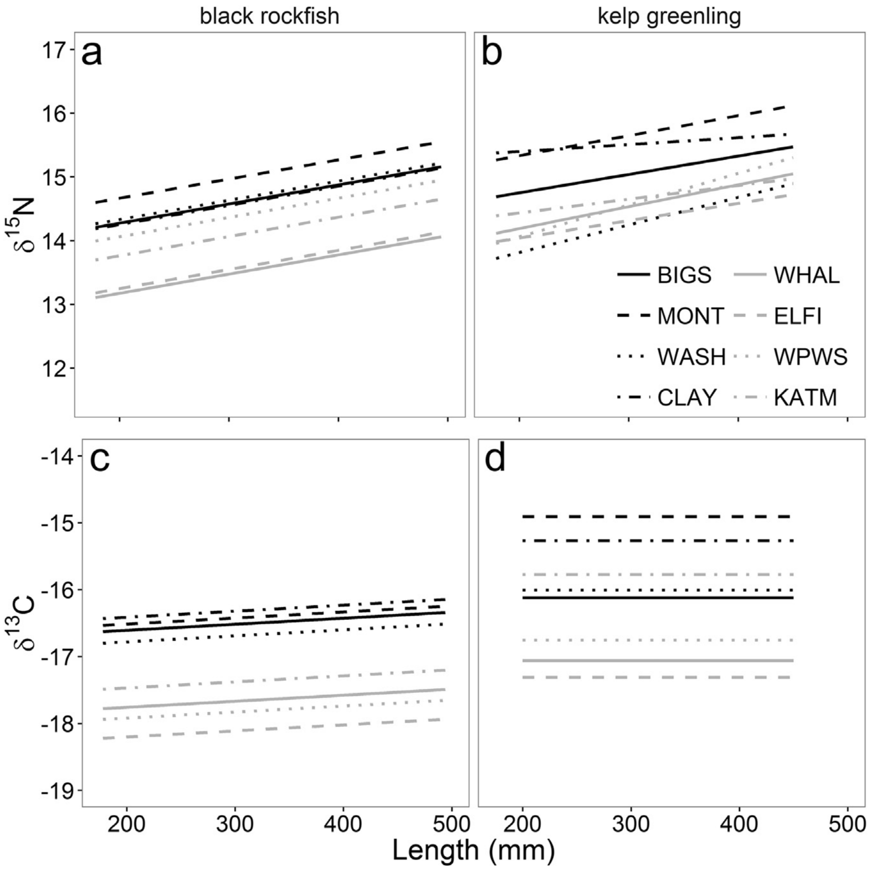

Fig. 2. Predicted change in nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) isotope values with fish fork length. Each line represents a study site. The best models describing the change in $\delta^{15}N$ (a) and $\delta^{13}C$ (c) with length for black rockfish included length as a fixed effect and random site-specific intercept effects. Among kelp greenling, the best models describing the change in $\delta^{15}N$ included length as a fixed effect with random site-specific slope effect that modified the relationship between length and $\delta^{15}N$ by site (b), while length was not related $\delta^{13}C$, as indicated by horizontal lines (d). Length had a minimal effect on isotope values and was not biologically significant. Sites are abbreviated as follows: Katmai National Park and Preserve, AK (KATM); western Prince William Sound, AK (WPWS); Elfin Cove, AK (ELFI); Whale Bay, AK (WHAL); Clayoquot Sound, BC (CLAY); Neah Bay, WA (WASH); Monterey Bay, CA (MONT); Big Sur, CA (BIGS).

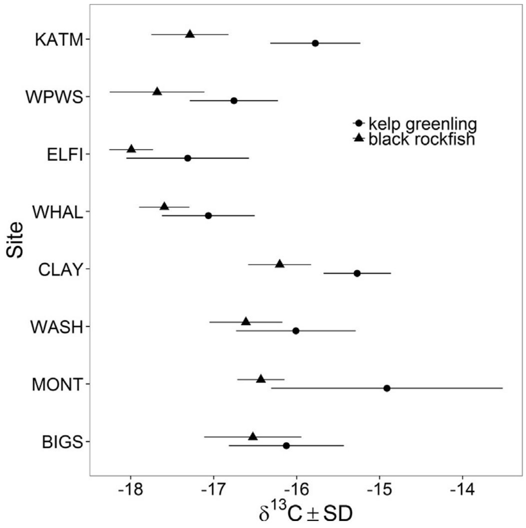

Fig. 3. Mean carbon ($\delta^{13}C$) isotope values of kelp greenling (circles) and black rockfish (triangles) muscle from each study site; error bars represent standard deviation (SD). Sites are ordered geographically from north (top) to south (bottom) within the figure. Within each site, higher $\delta^{13}C$ values indicate higher kelp carbon contributions. Sites are abbreviated as follows: Katmai National Park and Preserve, AK (KATM); western Prince William Sound, AK (WPWS); Elfin Cove, AK (ELFI); Whale Bay, AK (WHAL); Clayoquot Sound, BC (CLAY); Neah Bay, WA (WASH); Monterey Bay, CA (MONT); Big Sur, CA (BIGS).

average, the contribution of kelp-derived carbon (mean ± SD) was 57 ± 15% across all sites and both species. The standard deviations of kelp contributions were <10% across species and sites (Table 1).

4. Discussion

This collection of nearshore fish isotope values provides the first evidence of routine kelp-derived carbon contributions to benthic- and pelagic-feeding nearshore fishes across a wide latitudinal gradient. Kelp forests have been known to benefit fish by providing habitat (Bodkin, 1986; Efird and Konar, 2014; Holbrook et al., 1990; Reisewitz et al., 2006; Siddon et al., 2008), and our data suggests that kelp also provides an important source of primary production for the food webs used by benthic-feeding kelp greenling and pelagic-feeding black rockfish. Overall, our results indicate strong pelagic-benthic coupling in nearshore waters based on the small site-specific differences in $\delta^{13}C$ values between benthic (greenling) and pelagic (rockfish) foraging fishes that produce similar estimates of kelp-derived carbon. Pelagic-benthic coupling and the use of multiple carbon pathways have been associated with increased food web stability and resilience in both aquatic and terrestrial ecosystems (Haddad et al., 2011; McCann et al., 2005; Rooney et al., 2006).

Kelp carbon contributed an average of 57% to the muscle tissue of nearshore fish across sites and species. Uncertainty in the site-specific isotope values of kelp and phytoplankton, as well as the trophic discrimination factors used to model carbon sources, are both important caveats to the interpretation of the mixing model results. Nevertheless, the consistently high kelp-derived carbon contributions and associated low variance (SD) provide compelling evidence that kelp is an important source of production in both benthic and pelagic food webs. In addition, our estimates of kelp carbon contributions are consistent with previous isotope studies (Table 4). Kelp carbon contributions to nearshore predators in more localized regions (e.g., collections from single sites or a cluster of study sites in a particular bay) were 15 to 75% in rock greenling, predatory sea stars, and cormorants at sites in the Aleutian Islands (Duggins et al., 1989), 40 to 70% in fish and birds in a Norwegian kelp forest (Fredriksen, 2003), 45 to 60% in epibenthic fishes in an Antarctic kelp forest (Dunton, 2001), 35 to 65% in black and copper rockfish (*Sebastes caurinus*) off Vancouver Island (Markel and Shurin, 2015), 20 to 40% in fishes near Santa Barbara, CA (Koenigs et al., 2015), 50% in predatory snails in the Beaufort Sea (Dunton and Schell, 1987), and 0 to 42% across a variety of marine predators in the Canadian Arctic (McMeans et al., 2013).

4.1. Variation in δ^{15}N and δ^{13}C with fish length

Fish length was related to δ^{15}N for both species and δ^{13}C for black rockfish only as evident in the inclusion of a slope term in the best model (Table 3), but the effect was weak (Fig. 2). In both species, we observed increase in δ^{15}N with length that represented approximately one-third of a trophic level over the entire length range examined; we observed a ~0.9‰ increase in muscle δ^{15}N values from 200 to 500 mm. Similarly, the increase in δ^{13}C values with black rockfish length was only ~0.3‰ from 200 to 500 mm; no size-related trend in δ^{13}C values was present among kelp greenling. Overall, the influence of length on fish muscle δ^{15}N and δ^{13}C values was not biologically significant and had a minimal effect on comparisons across study sites with different length distributions.

4.2. Differences between black rockfish and kelp greenling

Kelp greenling muscle was composed of more kelp-derived carbon than that of black rockfish at all but one site (Fig. 3). Kelp greenling feed primarily on benthic invertebrates that may derive >50% of their carbon from kelp (Duggins et al., 1989; Eckman and Duggins, 1991; Fredriksen, 2003; Salomon et al., 2008; Tallis, 2009) and thus provide a trophic link between kelp and benthic fish predators. Lower percentages of kelp-derived carbon in black rockfish are consistent with a tendency to feed on zooplankton and forage fish in the water column, which are thought to derive more carbon from phytoplankton (Kline, 1999; Miller et al., 2008). Big Sur was the only site where rockfish and greenling δ^{13}C values were similar. This site has low phytoplankton concentrations year-round as persistent upwelling and offshore advection of surface currents drive phytoplankton blooms offshore (Foley, 2009), perhaps resulting in a higher reliance by rockfish on kelp-derived carbon in the nearshore pelagic food web as compared to other sites. Overall, the differences in isotope values between kelp greenling and black rockfish were relatively small at several sites, as the standard deviations of δ^{13}C values for each species often overlapped.

4.3. Estimating kelp- versus phytoplankton carbon contributions to fishes

Our mixing models suggest widespread kelp-derived carbon contributions to both fish species across sites. Differences in the seasonal availability of phytoplankton and kelp (Duggins et al., 1989; Foley, 2009) may explain why both sources are widely used by fishes and other consumers in coastal food webs. Phytoplankton abundance is highest during the spring and summer months when both nutrients and light are available for pelagic primary producers, while the availability of kelp detritus is likely highest in the winter due to senescing annual species (e.g., *Nereocystis*) or storm damage to perennial species (e.g., *Macrocystis*) (Duggins et al., 1989). Indeed, kelp carbon contributions to filter-feeding mussels and barnacles tend to be higher during winter months (Foley, 2009; Tallis, 2009).

Kelp-derived carbon contributions were moderate to high (36 to 89%) in both kelp greenling and black rockfish (32 to 65%) (Graphical abstract, Table 1). High kelp-derived carbon contributions to kelp greenling were not surprising given their reliance on benthic prey and strong isotopic evidence that benthic invertebrates rely on kelp (Duggins et al., 1989; Fredriksen, 2003; Love, 2011; Moulton, 1977; Salomon et al., 2008; Tallis, 2009). Similar percentages of kelp in black rockfish and kelp greenling is somewhat unexpected, as black rockfish are often assumed to be strongly linked to phytoplankton-based food webs through their zooplankton and forage fish prey (Kline, 1999; Miller et al., 2008). Our results raise questions about how kelp carbon reaches black rockfish. The possibility that pelagic organisms may assimilate kelp detritus has been suggested by others (Dunton and Schell, 1987; Foster and Schiel, 1985), and is supported by the observation that kelp detritus can be entrained in the water column as a component of suspended particulate organic matter (SPOM; Kaehler et al., 2006; Hill et al., 2008) that is eaten by pelagic consumers like zooplankton. Indeed, within-species comparisons of Atlantic herring (*Clupea harengus*) and Atlantic cod (*Gadus morhua*) along onshore-offshore gradients indicated that individuals captured closer to shore contained more benthic carbon than those captured offshore (Fredriksen, 2003; Kopp et al., 2015).

Alternatively, high kelp carbon contributions to black rockfish may reflect omnivory and a higher reliance on benthic prey directly by black rockfish or the forage fish consumed by black rockfish than currently recognized. Black rockfish (Brodeur et al., 1987; Hallacher and Roberts, 1985) and their forage fish prey (Brodeur et al., 1987; Hallacher and Roberts, 1985; Moulton, 1977; Rosenthal, 1983) opportunistically consume benthic prey (e.g., polychaetes and mysids), especially when pelagic prey are less abundant. Still, black rockfish feeding morphology (small mouth, long intestines, and long gill rakers) is more consistent with pelagic foraging (Hallacher and Roberts, 1985; Love, 2011). Because benthic-feeding is likely to be relatively infrequent for black rockfish and the forage fish they often consume, we suggest that kelp detritus contributions to SPOM that is subsequently consumed by zooplankton is a more reasonable pathway for such significant contributions of kelp carbon in black rockfish.

4.4. Isotope mixing model caveats

Miller and Page (2012) suggested that studies of nearshore communities that have concluded kelp is an important source of production for consumers have been consistently biased, because researchers tend to use isotope values from phytoplankton collected 10s–100s of kilometers offshore. In our study, POM was collected in coastal locations just 100 m to 3 km from shore to provide a more realistic representation of phytoplankton available to nearshore consumers. This approach risks contamination from kelp detritus in the form of SPOM, but reduces overestimation of kelp-derived carbon. If our POM samples were routinely contaminated by enriched kelp detritus, it would cause an enrichment bias. An enrichment bias in the depleted end member shrinks the expected range of consumer isotope values and shifts the depleted end member, phytoplankton, closer to the fish values, resulting in a systematic underestimation of kelp-derived carbon.

Table 4
Kelp-derived carbon contributions to various predators in kelp forest systems. Asterisk indicates kelp-derived carbon contributions assessed from a plot provided in the citation when specific numbers were not provided in text.

Taxa	Species	Location	Kelp carbon contribution	Citation
Sea star	Sea stars (various)	Palmer, Antarctic Peninsula	90–100%*	Dunton, 2001
Sea star	*Leptasterias* spp.	Aleutian Islands, AK, USA	15–60% *	Duggins et al., 1989
Snail	*Polinices pallidus*	Beaufort Sea, AK, USA	50%	Dunton and Schell, 1987
Fish	Epibenthic fishes (various)	Palmer, Antarctic Peninsula	45–60%*	Dunton, 2001
Fish	*Brachyistius frenatus*	Santa Barbara, CA, USA	15–30%*	Koenigs et al., 2015
Fish	*Centrolabrus exoletus*	Finnøy, Norway	63%	Fredriksen, 2003
Fish	*Ctenolabrus rupestris*	Finnøy, Norway	65%	Fredriksen, 2003
Fish	*Clupea harengus*	Baffin Island, Canada	0%	McMeans et al., 2013
Fish	*Clupea pallasi* (juv.)	Vancouver Island, BC, Canada	35–45%	Markel and Shurin, 2015
Fish	*Gadus morhua* (open sea)	Finnøy, Norway	40%	Fredriksen, 2003
Fish	*Gadus morhua* (kelp forest)	Finnøy, Norway	59%	Fredriksen, 2003
Fish	*Heterostichus rostratus*	Santa Barbara, CA, USA	15–30%*	Koenigs et al., 2015
Fish	*Hexagrammos decagrammus*	northeast Pacific Ocean	39–99%	This study
Fish	*Hexagrammos lagocephalus*	Aleutian Islands, AK, USA	15–75% *	Duggins et al., 1989
Fish	*Labrus bergylta*	Finnøy, Norway	57%	Fredriksen, 2003
Fish	*Liparis montagui*	Finnøy, Norway	68%	Fredriksen, 2003
Fish	*Mallotus villosus*	Baffin Island, Canada	4%	McMeans et al., 2013
Fish	*Microstomus kitt*	Finnøy, Norway	64%	Fredriksen, 2003
Fish	*Myoxocephalus scorpius* (small)	Baffin Island, Canada	26%	McMeans et al., 2013
Fish	*Myoxocephalus scorpius* (large)	Baffin Island, Canada	42%	McMeans et al., 2013
Fish	*Oxyjulis californica*	Santa Barbara, CA, USA	25–50%*	Koenigs et al., 2015
Fish	*Paralabrax clathratus*	Santa Barbara, CA, USA	30–50%*	Koenigs et al., 2015
Fish	*Pollachius pollachius*	Finnøy, Norway	53%	Fredriksen, 2003
Fish	*Pollachius virens*	Finnøy, Norway	33%	Fredriksen, 2003
Fish	*Salvelinus alpinus*	Baffin Island, Canada	15%	McMeans et al., 2013
Fish	*Sebastes atrovirens*	Santa Barbara, CA, USA	35–45%*	Koenigs et al., 2015
Fish	*Sebastes caurinus*	Vancouver Island, BC, Canada	55–65%	Markel and Shurin, 2015
Fish	*Sebastes melanops*	Vancouver Island, BC, Canada	50–60%	Markel and Shurin, 2015
Fish	*Sebastes melanops* (juv.)	Vancouver Island, BC, Canada	35–45%	Markel and Shurin, 2015
Fish	*Sebastes melanops*	northeast Pacific Ocean	35–81%	This study
Fish	*Sebastes mystinus*	Santa Barbara, CA, USA	10–25%*	Koenigs et al., 2015
Shark	*Somniosus microcephalus*	Baffin Island, Canada	14%	McMeans et al., 2013
Skate	*Amblyraja hyperborea*	Baffin Island, Canada	0%	McMeans et al., 2013
Bird	*Phalacrocorax carbo*	Finnøy, Norway	37%	Fredriksen, 2003
Bird	*Phalacrocorax pelagicus*	Aleutian Islands, AK, USA	30–70% *	Duggins et al., 1989
Bird	*Somateria mollissima*	Finnøy, Norway	49%	Fredriksen, 2003
Mammal	*Phoca groenlandica*	Baffin Island, Canada	20%	McMeans et al., 2013
Mammal	*Phoca hispidia*	Baffin Island, Canada	9%	McMeans et al., 2013

Ideally, primary producers would be collected consistently across sites over the timeframe represented by consumer tissues (Dethier et al., 2013) as the isotopic composition of primary producers can quickly change across space and time (Michener and Kaufman, 2007). Simulations suggest that collecting primary producers during just one season leads to a large decrease in mixing model accuracy if consumers integrate production over longer timeframes (Dethier et al., 2013), as is the case in our study. Therefore, even if phytoplankton and kelp samples had been collected simultaneously with fish samples, our interpretations would still need to be tempered because primary producer isotope values can vary widely over the timeframe represented in fish tissues (Dethier et al., 2013). When studies have made more extensive collections of primary producers in a particular location, the variation in primary producer isotope values increases; e.g., higher sample sizes are often associated with higher standard deviations in isotope values (Table 2). Because of the difficulty associated with obtaining representative primary producer samples, we used a Bayesian mixing model capable of including estimates of uncertainty in the isotopic composition of sources and estimates of trophic discrimination.

Even with our attempts to select the most appropriate source values available, we were unable to estimate the kelp- and phytoplankton-derived carbon contributions for fish collected from Monterey Bay. At this site, the fish $\delta^{13}C$ values fell outside the range of $\delta^{13}C$ for phytoplankton and kelp. Fish $\delta^{13}C$ values at this site were similar to kelp grazers (e.g., kelp crabs and urchins) collected in Monterey Bay (Newsome et al., 2012) and suggests that kelp is an important primary producer for fishes in Monterey Bay. Likewise, mixing model results from Big Sur were puzzling because of large variation in kelp isotope values despite the availability of an extensive data set (Foley and Koch, 2010, $n = 238$). While the mean fish $\delta^{13}C$ values were within the range of kelp at this site, large variation in kelp isotope values resulted in a conservative estimate of ~60% kelp-derived carbon in the muscle tissue of both greenling and rockfish.

Kelp source values were based on isotope values for the dominant canopy-forming kelp species at each study site (*Nereocystis* at sites in Alaska and *Macrocystis* other sites), as canopy-forming kelps dominate biomass compared to understory species (Duggins, 1980; Miller et al., 2011). Still, the kelp-derived carbon contributions described in this study may include other kelp species (e.g., *Saccharina*) or microphytobenthos (unicellular algae and cyanobacteria in the top layer of sediment) with similar $\delta^{13}C$ and $\delta^{15}N$ values as the canopy-forming kelp species in our analysis (Dethier et al., 2013; Sokołowski et al., 2012). Previous studies have shown that these other kelp species (Duggins et al., 1989; Fredriksen, 2003) and microphytobenthos (MacIntyre et al., 1996; Takai et al., 2004) can be important sources of primary production for consumers under some circumstances. Yet, at sites along rocky shores with abundant canopy kelp similar to the ones we studied, canopy kelp production likely dominates over production of understory kelps (Miller et al., 2011) and microphytobenthos (Dalsgaard, 2003) because shading by canopy kelp limits understory kelp production (Miller et al.,

2011) and rocky substrates are associated with sparse microphytobenthos (Paterson and Hagerthey, 2001).

Further investigation of kelp-derived carbon with additional isotope tracers and more extensive field collections is needed. More intensive approaches include (1) increasing the number of isotope systems (e.g., hydrogen isotopes), (2) exploring compound-specific amino and fatty acid $\delta^{13}C$ analysis to better partition kelp from other primary producers, and (3) multi-season sampling of primary producers to better match the timeframe represented by consumer tissues (Dethier et al., 2013; Larsen et al., 2013). Amino acid compound-specific stable isotopes have been particularly successful at constraining the range of $\delta^{13}C$ in the kelp *Macrocystis pyrifera* from more than 5‰ to less than 1‰ (Larsen et al., 2013) and ultimately led to better accuracy in the estimation of kelp carbon contribution.

5. Conclusions

Overall, the high muscle $\delta^{13}C$ values and isotope mixing model results of both kelp greenling and black rockfish strongly suggest that a ^{13}C-enriched carbon source, likely dominated by canopy kelp, contributes substantially to the benthic and pelagic food webs that these species utilize across both coastal upwelling and downwelling systems in the northeast Pacific Ocean. If kelp contributes substantial energy to fishes, it follows that shifts in kelp production could influence fish production in the same way that phytoplankton production has been associated with fish production (Ware and Thomson, 2005). Kelp and other macroalgae are sensitive to changes in temperature, CO_2 concentration, storm frequency, and sea level associated with climate change, but the ultimate influence of changing climate on kelp production remains poorly understood (Harley et al., 2012). The possibility of declines in kelp production and biomass could be particularly problematic in temperate regions where phytoplankton declines are also anticipated (Behrenfeld et al., 2006). The cascading influence of changes in kelp production will not necessarily be limited to the nearshore resident fishes examined here, as many fish species use kelp forests as nursery habitats (Johnson et al., 2012; Laurel et al., 2007).

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