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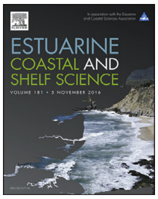

Widespread kelp-derived carbon in pelagic and benthic nearshore fishes suggested by stable isotope analysis

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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.

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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