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Trophic structure and potential carbon and nitrogen flow of a rhodolith bed at Santa Catalina Island inferred from stable isotopes

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Abstract

In many coastal marine systems with low productivity, cross-habitat exchange of subsidies has been shown to have significant bottom-up effects. California rhodolith beds (*Lithothamnion australe* Foslie) support invertebrate communities whose biomass doesn't appear to be supported by the limited productivity of rhodoliths. Detrital subsidies from the water column and adjacent giant kelp *Macrocystis pyrifera* forests may supplement the base of the food web in these beds. Stable isotope analyses were conducted using seawater organic matter, sediment organic matter, and macroalgae as endmembers to determine their relative importance to consumers and create trophic structure of a rhodolith bed off Santa Catalina Island. Using cluster analysis on carbon $\delta^{13}C$ and nitrogen $\delta^{15}N$ values of 13 invertebrate consumer taxa, five trophic groups were identified: planktivore, zoo-planktivore, detritivore, herbivore, and carnivore. The isotope ratios of sediment organic matter from within rhodoliths were similar to benthic and drifting kelp *M. pyrifera* tissue, suggesting neighboring kelp habitats, or other unmeasured sources, may contribute to the organic matter within rhodoliths. Detritivores, herbivores, and carnivores appeared to consume particulate organic matter from the water column directly or indirectly through prey. Follow-up experiments indicated that increasing surface area of giant kelp pieces increased drift rates while smaller kelp material moved less and may have greater potential to be retained within rhodolith beds during periods of increased water motion. Overall, temporal fluctuations in the supply and export of suspended particulate organic matter from the water column and drift macroalgal subsidies from adjacent kelp forests may have considerable effects on secondary production and community structure of rhodolith beds.

Introduction

Movement of nutrients among habitats involves material fluxes from a donor system to recipient systems and is increasingly recognized as an important factor influencing

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populations, communities, and food web structure (Polis et al. 1997; Kelly et al. 2012; Filbee-Dexter et al. 2018). The relative importance of macroalgal detritus in supporting secondary production in aquatic food webs has long been debated (Mann 1988). In polar and temperate marine systems, highly productive kelps periodically slough tissues either through erosion or dislodgement (Krumhansl and Scheibling 2012b). Senescing kelp individuals produce fragmented pieces of kelp as particulate organic matter, or parts, such as blades, or entire thalli (Krumhansl and Scheibling 2012a; Filbee-Dexter and Scheibling 2016). The resulting kelp material termed "detritus" is drifting material that can be consumed locally or exported to adjacent low-productivity habitats such as beaches (Ince et al. 2007), the rocky intertidal (Rodríguez 2003), offshore areas (Kelly et al. 2012), and submarine canyons (Vetter 1995; Vetter and Dayton 1998, 1999) where it can be utilized by infaunal and epibenthic macroinvertebrates (Duggins et al. 1989; Ince et al. 2007; Kelly et al. 2012). The role of detrital subsidies can be particularly important to low productivity habitats

where the communities there may be more reliant on imports (Britton-Simmons et al. 2012).

Multiple factors can influence the flux of material from donor systems. These factors include productivity, temporal patterns in storm frequency and intensity, local geomorphology and current patterns, proximity of recipient systems to donor systems, and the perimeter-to-area ratio of recipient systems (Gerard 1976; Gerard and North 1984; Polis et al. 1996, 1997; Kelly et al. 2012). Kelp detritus supply and dispersal is particularly dependent on local geomorphology, substrate rugosity, currents, wind and wave motion, and winter storm activity (Gerard 1976; Harrold and Reed 1985). For example, shelter from currents reduces the amount of drifting kelp detritus exported from an area, and stable isotope analysis suggested consumers assimilate more benthic algae in more protected sites (Leclerc et al. 2013). The unidirectional Antarctic circumpolar current may transport kelp-derived suspended particulate matter tens of kilometers away from kelp forests and is detected in invertebrate assimilated diet (Kaehler et al. 2006); however, this is debated (Miller and Page 2012).

Rhodoliths (Corallinales, Rhodophyta) are poorly studied foundation species composed of free-living coralline algal nodules from one to tens of centimeters in diameter that form beds when aggregated (Foster et al. 2013). These rhodolith beds can be many individuals deep, with a gradient into dead rhodolith fragments, and carbonate and terrigenous sediment (Foster et al. 2013). Rhodolith beds are globally distributed (Foster 2001) and can support highly diverse communities composed of macroalgae, infaunal and epifaunal invertebrates, and fishes (Foster 2001; Steller et al. 2003; Foster et al. 2007).

Rhodoliths provide increased habitat complexity to the benthos, through branching that creates interstitial spaces within and among rhodoliths (Foster 2001; Steller et al. 2003). In addition to providing habitat, these interstitial spaces may affect food availability and retention, similar to kelp holdfasts that increase small scale heterogeneity and influence particulate macroalgal retention (Schaal et al. 2012). It has been suggested that invertebrates resident to rhodolith beds are reliant on suspended and settling particulate organic matter from the water column and sediment organic matter, which can be composed of many sources including benthic diatoms and biofilms (i.e. microphytobenthos, Grall et al. 2006). Rhodolith architecture may increase retention of particulate organic matter, leading to a community assemblage supported by detritus, first utilized by detritivores and transferred to consumers at higher trophic levels (Kelly et al. 2012). While prior research has enumerated taxa within rhodolith communities, little work has examined carbon and nitrogen flow and trophic structure in this habitat or determined whether communities are supported by internal primary production or rely on subsidies from other habitats (but see Grall et al. 2006).

Carbon and nitrogen flow through natural systems has traditionally been examined by studying consumer gut contents. This approach alone, however, can be inadequate as gut contents give a short-term measure of ingested food, potentially over-representing indigestible food items, and identification of partially digested prey items can be inaccurate and require expert taxonomic knowledge (Jaschinski et al. 2011). Stable isotope analysis can be a powerful tool for the study of trophic relationships as it can integrate diet over longer time scales, and if prey sources are isotopically distinct, it can identify the relative contribution of prey (Fry 2006). Ratios of heavier to lighter carbon (C^{13}/C^{12}) and nitrogen (N^{15}/N^{14}) isotopes, whose ratios are denoted by $\delta^{13}C$ and $\delta^{15}N$ respectively, are often used to explore food web relationships. Generally, carbon isotope ratios indicate the source of primary production as they change little through food webs and nitrogen isotope ratios indicate trophic level as their ratios increase from primary producers to consumer tissues up food webs (reviewed in Fry 2006). Algal isotopic ratios are influenced by primary producer size, boundary layer formation, and photosynthetic pathways (Raven et al. 2002), with phytoplankton carbon isotopic values potentially having lower C^{13}/C^{12} values relative to the higher C^{13}/C^{12} values of benthic macroalgae (Raven et al. 2002). Due to this isotopic separation, the relative importance of pelagic (phytoplankton) versus benthic (micro- and macroalgae) production to a consumer and ultimately a community may be evaluated. However, spatial and temporal characterization of nearshore particulate organic matter and benthic macroalgae are needed to accurately estimate source contributions to consumers (Miller and Page 2012).

All rhodolith beds (*Lithothamnion australe* Foslie) around Santa Catalina Island off southern California, USA occur in shallow, sheltered coves adjacent to giant kelp *Macrocystis pyrifera* forests (Tompkins 2011; Tompkins and Steller 2016) which seasonally export detrital kelp material (Gerard and North 1984; Harrold and Reed 1985). Kelp forests are an important source of food subsidies to herbivorous invertebrates in adjacent habitats, especially autumn through winter when kelp individuals senesce and/or are removed by storm activity (Kelly et al. 2012). The present study proposes the first model for sources of primary productivity supporting rhodolith bed communities in California. Because rhodoliths have low organic content (~6%) relative to calcium carbonate (~94%), the contribution of rhodoliths to the food web was hypothesized to be low relative to other organic sources as suggested in Grall et al. (2006). In the present study, I examined the dynamics of food subsidies from kelp forests to adjacent rhodolith beds off Santa Catalina Island. I hypothesized that

rhodoliths act as substrate for epiphytic macroalgae and may trap phytoplankton and detrital algal particulates, and that these sources may support herbivorous and detritivorous consumers. Specifically, I sought to (1) determine the main trophic groups structuring the rhodolith community food web and the primary trophic pathways connecting them and (2) determine if there is any potential for giant kelp blade pieces to be retained within the rhodolith bed. This is the first trophic study of this ecosystem in the Pacific, and the first to quantify variability in stable isotope values of flora and fauna in a Pacific rhodolith bed food web.

Methods

Study site

Santa Catalina Island is part of the Channel Islands archipelago off the coast of Southern California in the Northeastern Pacific. The island sits in a Northwest-Southeast orientation and is exposed to warm water from the Southern California Countercurrent. Rhodoliths propagate over sand and develop beds in protected coves 4–21 m deep on the Northeast-facing leeward side of the island with giant kelp *M. pyrifera* forests adjacent to all beds. These rhodolith beds are patchy aggregations of live and dead rhodolith (non-pigmented) carbonate sand, with less carbonate and increasing amounts of silicate sand at bed edges (Gabara et al. 2018). Rhodolith bed food web structure was examined from 2012–2013 at the Isthmus Cove rhodolith bed (area = 1148 m^2), which had high average live rhodolith cover (~ 50 percent, Tompkins 2011, Tompkins and Steller 2016) and less secondary macroalgal cover on rhodoliths relative to other sites (Gabara et al. 2018). I used a rhodolith bed with fewer potential sources to detritivores and herbivores (lower epiphytic macroalgal diversity) to better identify the potential contribution of phytoplankton, sediment organic matter, and kelp.

To construct a rhodolith bed food web and quantify carbon and nitrogen flow through this system, potential food sources and community members were collected. SCUBA was used to haphazardly sample suspended particulate organic matter from offshore and nearshore areas. Samples of suspended particulate organic matter (hereafter SPOM), sediment organic matter (SOM) within rhodoliths, epiphytic macroalgae on rhodoliths, fresh and drifting kelp tissue, and invertebrate consumers from areas of high rhodolith cover within the Isthmus Cove rhodolith bed were collected. All collections were processed at the USC Wrigley Institute for Environmental Studies (WIES). These samples of potential food sources (SPOM, SOM, macroalgae) and consumers were collected across four sampling times: February 2012, August 2012, April 2013, December 2013 (Table 1).

Water and sediment collection and preparation

To estimate the isotopic signature of SPOM within the water column and after it settles to the benthos, 3.78 l water samples were collected using seawater from 4 km offshore and within Isthmus Cove above the rhodolith bed. Seawater samples were taken using SCUBA at 3 m and 7 m water depths using pre-rinsed plastic zip bags.

Sediment organic matter (SOM) within the branches of rhodolith individuals may be an important food resource for rhodolith communities and is potentially isotopically distinct from other sources (Grall et al. 2006). To estimate an isotopic signature of SOM within rhodoliths, rhodoliths were haphazardly collected and individually stored in plastic zip bags. At WIES, rhodoliths were transferred into 50 ml centrifuge tubes and agitated in 50 ml of filtered seawater for 30 s using a VWR multi-tube vortexer to suspend SOM from within the branched rhodolith matrix. SPOM and SOM samples were filtered through precombusted (500 °C for 4 h) 47 mm glass microfiber filters (grade GF/F, 0.7 μm, Whatman) under low pressure (~ 5–7 mmHg) using a vacuum pump.

Organism collection and preparation

Samples of macroalgae were collected to estimate the importance of local attached epiphytic algae and macroalgal drift subsidies to the system. Macroalgae sampled included the epiphytic red alga *Polysiphonia* spp. and giant kelp *M. pyrifera*, including drift tissue found within the rhodolith bed and fresh attached tissue found outside of the rhodolith bed as a reference. The isotope values of this reference were compared to those of an herbivore with a preference for kelp blade tissue *Norrisia norrisii* (Wakefield and Murray 1998); however, this grazer may be indiscriminately consume epibionts on the kelp blade and stipe surface (Graham 2004). Samples of attached *M. pyrifera* thalli (1 m above the holdfast) were haphazardly collected in the adjacent kelp bed, approximately 30 m from the Isthmus rhodolith bed. The brown algae *Dictyopteris undulata* and *Dictyota binghamiae* were present (3.1% ± 3.1% cover) within the Isthmus Cove rhodolith bed; however, with low abundance, they were assumed to not contribute greatly to community member diets (Gabara 2014; Gabara et al. 2018).

Common consumers selected for stable isotope analysis were used to examine the importance of different food sources to the community. Samples of 13 abundant conspicuous invertebrates were collected during community surveys from the rhodolith bed surface (hereafter epibenthic) by hand and from within the sediment (hereafter infauna) using sediment cores (6.5 cm diameter × 10 cm, Gabara et al. 2018). Epibenthic invertebrates included the gastropods *Californiconus californicus*, *Lirularia* spp., *Megastraea*

Table 1 Stable isotope ratios, $\delta^{13}C$ and $\delta^{15}N$, for potential food sources and consumers from Isthmus Cove by sampling time: Feb-12 (February 2012), Aug-12 (August 2012), Apr-13 (April 2013), and Dec-13 (December 2013)

Taxonomic group or species	Feb-12 (n)	$\delta^{13}C$	SD	$\delta^{15}N$	SD	Aug-12 (n)	$\delta^{13}C$	SD	$\delta^{15}N$	SD	Apr-13 (n)	$\delta^{13}C$	SD	$\delta^{15}N$	SD	Dec-13 (n)	$\delta^{13}C$	SD	$\delta^{15}N$	SD	Pooled Food Web (n)	$\delta^{13}C$	SD	$\delta^{15}N$	SD	Guild assignment	Citation
Suspended particulate organic matter																											
offshore (3 and 7 m)						6	−23.27	0.32	6.63	0.34	6	−22.77	0.51	7.94	1.1						12	−23.02	0.5	7.39	1		
Rhodolith (3 and 7 m)	3	−23.87	0.66	7.88	0.44	6	−21.92	0.40	8.59	0.77	6	−2237	0.37	7.88	0.8	3	−23.87	0.7	7.68	0.4	18	−2232	0.8	8.1	0.7		
Sediment organic matter (SOM)						4	−19.54	1.16	1045	1.23	4	−17.93	0.2	9.53	0.5	4	−16.18	1.00	10.62	0.6	12	−1738	1.7	10.2	0.9		
Macroalgae																											
Macrocystis pyrifera (drift)						6	−15.50	1.97	10.17	0.70	7	−15.85	2	9.64	0.6	8	−14.77	2	10.84	1.1	21	−1533	1.9	10.25	1		
Macrocystis pyrifera (fresh)						6	−16.57	1.28	9.69	0.09	7	−16.58	2.1	9.55	0.54	8	−1636	1.6	11.62	0.3	21	−1649	1.6	10.36	1.1		
Polysiphonia spp.						2	−27.60	0.47	9.78	0.08						3	−28.97	0.8	10.91	04	5	−2842	1	10.46	0.7		
Annelida																											
Polychaeta						6	−17.62	0.33	1341	0.13											6	−17.62	0.3	13.41	0.1	Carnivore	N/A
Arthropoda																											
Gammaridae																3	−16.6	0.9	10.36	0.4	3	−16.6	0.9	10.36	0.4	Detritivore	Martin (1966)
Podochela hemphilli											3	−17.05	0.7	133	0.8						3	−17.05	0.7	13.3	0.8	Carnivore	N/A
Tanaldacea																6	−1441	0.6	11.69	0.2	6	−1441	0.6	11.69	0.2	Herbivore/omnivore	Blazewicz-Paszkowycz and Ligowski (2002)
Bryozoa																											
Eurystomella spp.											2	−19.25	0.1	10.51	1.0	5	−1934	0.6	11.08	0.7	7	−1931	0.5	10.92	0.8	Zooplanktivore	N/A

Table 1 (continued)

Taxonomic group or species	Feb-12					Aug-12					Apr-13					Dec-13					Pooled Food Web					Guild assignment	Citation
	(n)	$\delta^{13}C$	SD	$\delta^{15}N$	SD	(n)	$\delta^{13}C$	SD	$\delta^{15}N$	SD	(n)	$\delta^{13}C$	SD	$\delta^{15}N$	SD	(n)	$\delta^{13}C$	SD	$\delta^{15}N$	SD	(n)	$\delta^{13}C$	SD	$\delta^{15}N$	SD		
Echinodermata																											
Lytechinus pictus						1	−14.84		1133		8	−15.71	0.9	9.13	0.6	5	−16.65	0.6	9.41	0.7	14	−15.98	0.9	9.39	0.8	Detritivore/Herbivore	Dean et al. (2009)
Parastichopus parvimensus											2	−16.99	0.6	10.77	0.6						2	−16.99	0.8	10.77	0.6	Detritivore	Yingst (1982)
Dendraster excentricus											4	−17.54	0.60	10.21	0.5						4	−1734	0.60	10.21	0.5	Detritivore	Tlmko (1976)
Mollusca																											
Americardia biangulata	15	−14.42	0.62	14.05	0.54						5	−20.47	0.3	6.91	0.3						5	−20.47	0.3	6.91	0.3	Phytoplanktivore	Hobson and Chess (1984)
Callfomconus califomlcus						6	−15.73	0.47	14.15	0.16						6	−15.84	0.7	13.71	0.4	27	−15.03	0.9	14	0.5	Carnivore	Graham (2004)
Limaria hemphilli											3	−21.29	0.3	8.51	0.3						3	−21.29	0.3	8.51	03	Phytoplanktivore	Hobson and Chess (1984)
Lirularia spp.	15	−13.54	1.05	11.87	0.61	9	−14.41	0.43	12.19	0.42	2	−13.53	0.6	9.80	0.1	8	−14.93	0.6	11.12	04	34	−14.09	1.0	11.66	0.8	Herbivore	N/A
Megastraea undosa	15	−13.54	1.69|	11.64	0.45	6	−18.22	1.02	11.79	0.30	14	−17.54	1.2	10.34	0.60	8	−14.98	0.9	11.25	0.4	33	−16.68	1.6	11.24	0.6	Detritivore	Cox and Murray (2005)
Norrisia norrisii (within kelp forest)	4	−12.91	0.43	11.50	0.33																4	−12.91	0.4	11.50	03	Herbivore (in kelp)	Wakefield and Murray (1998)

Samples were pooled (220 samples total) to produce an overall rhodolith bed food web depiction. Citations for guild assignment listed in last column

undosa, and *Norrisia norrisii* from the adjacent kelp bed, the urchin *Lytechinus pictus*, the cucumber *Parastichopus parvimensis*, the decapod *Podochela hemphilli;* infauna included the bivalves *Americardia biangulata* and *Limaria hemphilli*, the sand dollar *Dendraster excentricus*, polychaetes, and gammarid and tanaid crustaceans. Epibenthic and infaunal invertebrates were held for 24 h in flowing filtered seawater to clear gut contents and were then sacrificed via freezing at WIES. Isotope samples of infauna including gammarids ($n = 16$–44 per sample) and tanaids ($n = 37$–96 per sample) were composed of pooled individuals from the same core to meet minimum mass requirements for stable isotope analysis.

SPOM and SOM filters and organism samples were stored at $-80\ ^{\circ}C$ until being thawed for isotope preparation (Gabara 2014). Filters were acidified with dilute HCl fumes to remove carbonates. Samples of fleshy algae were rinsed with deionized water and gently scrubbed to remove epiphytes, and fauna were extracted from their shell, test, cuticle, or tube, or ran whole for infauna. All samples were dried at $60\ ^{\circ}C$ for 48 h, ground to a fine powder using an agate mortar and pestle, then weighed in tin capsules (Costech Analytical Technologies, Inc. Valencia, CA) using a microbalance. See Table 1 for sample sizes of potential food sources and consumers.

Stable isotope analysis

Isotopic analysis was conducted by the Interdisciplinary Laboratory for Elemental and Isotopic Analysis lab, Idaho State University. Stable isotope ratios were determined using an Elemental Combustion System 4010 interfaced to a Delta V advantage mass spectrometer through the ConFlo IV system. The ratios of heavier to lighter stable isotopes for carbon and nitrogen were determined. Data were expressed in the standard δ unit, where $\delta X = [(R_{sample}/R_{standard}) - 1] \times 10^3$. These values were reported as parts per thousand (‰).

$$\delta^{13}C = \left(\frac{^{13}C/^{12}C_{sample}}{^{13}C/^{12}C_{VPDB}} \right)$$

Carbon ratios ($^{13}C/^{12}C$) were relative to the global standard Vienna PeeDee Belemnite (VPDB).

$$\delta^{15}N = \left(\frac{^{15}N/^{14}N_{sample}}{^{15}N/^{14}N_{air}} \right)$$

Nitrogen ratios ($^{15}N/^{14}N$) were reported relative to atmospheric N_2. In-house standards (ISU Peptone, Costech Acetanilide, and DORM-3) were calibrated against international standards. Based on standards, the isotope measurement error (SD) was estimated to be ± 0.07‰ $\delta^{15}N$ and ± 0.08‰ $\delta^{13}C$ for ISU Peptone, 0.07‰ $\delta^{15}N$ and 0.10‰ $\delta^{13}C$ for

Costech Acetanilide, and 0.11‰ $\delta^{15}N$ and 0.13‰ $\delta^{13}C$ for DORM-3.

Data analysis

A hierarchical cluster analysis using Ward's minimum variance method separated carbon and nitrogen stable isotope ratios of consumers into trophic groups based on similarity (Davenport and Bax 2002; Grall et al. 2006; Madigan et al. 2012).

To determine the relative contribution of sources to a consumer, consumer isotopic signatures must first be corrected for trophic enrichment. Carbon and nitrogen stable isotope ratios increase as they move through a food web and are altered by consumers that more readily lose the lighter ^{12}C and ^{14}N isotopes during assimilation and protein synthesis (Fry 2006). This enrichment of $\delta^{15}N$, called isotopic enrichment or fractionation, can create a reliable indicator of the trophic level of a consumer, while $\delta^{13}C$ fractionates much less and is therefore a reliable indicator of primary production and used to infer a prey source or sources (Fry 2006). Trophic Enrichment Factors (TEFs) are used in a mixing model to yield an estimation of source contributions for each trophic group, however, these TEFs may vary among taxa. Species- or taxa-specific TEFs require controlled laboratory studies, which have not been conducted for this system (Moncreiff and Sullivan 2001; Jaschinski et al. 2011).

To address the uncertainty in TEF values, two scenarios using different TEFs were used to estimate potential contributions of sources to consumers. For scenario (1) a $\delta^{15}N$ enrichment ($\Delta^{15}N$) of 2.5‰ (Vanderklift and Ponsard 2003; Ouisse et al. 2012) and a $\delta^{13}C$ enrichment ($\Delta^{13}C$) of 1‰ (Zanden and Rasmussen 2001; Ouisse et al. 2012, Vafeiadou et al. 2013) were used on planktivores, detrivivores, and herbivores. For scenario (2) the difference in the average values of a potential kelp herbivore, the gastropod Norris's top snail *Norrisia norrisii* (11.3 ± 0.2 for $\delta^{15}N$, -13.3 ± 0.3 for $\delta^{13}C$, $n = 2$), and that of canopy *M. pyrifera* tissue from the same time of collection (11.9 ± 0.5 for $\delta^{15}N$, -13.0 ± 1.7 for $\delta^{13}C$, $n = 8$) were used to create enrichment factors. Enrichment factors for nitrogen of 0.4‰ $\Delta^{15}N$ and for carbon 0.2‰ $\Delta^{13}C$ were applied to planktivore, detrivivore, and herbivore isotope values to correct for enrichment. Both scenarios applied a TEF of 3.4‰ for nitrogen ($\Delta^{15}N$) and 1‰ for carbon ($\Delta^{13}C$) to the zooplanktivore and carnivore guilds (Vanderklift and Ponsard 2003; Ouisse et al. 2012).

MixSIAR (R package, Stock et al. 2018), a Bayesian mixing model package for R, was used with concentration dependence (Phillips 2002; Brauns et al. 2019; Mehner et al. 2019, see Table 2 for values) to determine the relative importance of different food sources to the trophic groups identified by cluster analysis (Semmens et al. 2009; Parnell et al. 2010). The MixSIAR model incorporates variability

of isotope values from sources and consumers, as well as trophic enrichment (Parnell et al. 2010; Stock et al. 2018). A MixSIAR mixing model was used to estimate diet contributions of nearshore suspended particulate organic matter (SPOM), sediment organic matter (SOM), and drift kelp tissue (kelp sporophytes were not present within the rhodolith bed) to the planktivore, detritivore, and herbivore groups. The SPOM, planktivore, and SOM groups were used as potential sources for the zooplanktivore guild. The zooplanktivore, detritivore, and herbivore guilds were used as potential sources for both carnivore groups. The urchin *Lytechinus pictus* was removed from the mixing model as their stable isotope values fell outside of the mixing space formed by the potential sources. This suggests a source to this consumer was not in the model.

A second MixSIAR mixing model determined the contribution of SPOM and drift giant kelp tissue to SOM. The red alga *Polysiphonia* spp. was not abundant in April 2013, so samples from the other two sampling periods were used to approximate an isotopic signature for that time point. The estimated percent cover of *Polysiphonia* spp. at Isthmus Cove was low ($5.3 \pm 5.3\%$) and was assumed to contribute little to faunal diet and was therefore excluded from the mixing models (Gabara et al. 2018).

Drift kelp export experiment

An experiment was conducted September 2013 within Isthmus Cove to understand the relationship between kelp blade surface area and retention within rhodolith beds. Fresh kelp blades were collected from an adjacent *M. pyrifera* kelp forest to create drift kelp pieces spanning a range of surface areas and weight (5–100 cm^2 and 1–30 g). Surface area was estimated from photos and wet weight was estimated using a balance in the lab. Small plastic clothing tags were applied to kelp blades to later identify pieces. Drift kelp pieces were released near a PVC stake placed in the center of the rhodolith bed and relocated after 1.5–2 h. Direction and distance from the release point was recorded using a compass and

transect tape. This experiment was repeated three times, each on a different day to incorporate variation in environmental conditions (wind direction, wind speed, wave height, wave direction). ANCOVA was used to compare the retention of kelp blades within the rhodolith bed among trials and understand the relationship between drift kelp blade surface area and retention time.

Results

Potential food sources

The main sources initially considered in this study included pelagic-based offshore and nearshore suspended particulate organic matter (SPOM), rhodolith bed sediment organic matter (SOM), the epiphytic red algae *Polysiphonia* spp., and giant kelp *M. pyrifera* drift tissue present within the rhodolith bed. Potential source carbon values spanned a wide range, $\sim 13\%$ $\delta^{13}C$, from -28.4 to -15.3 ‰. Sources had different carbon isotope values (ANOVA, $F_{5,86} = 115.26$, $P < 0.001$); *Polysiphonia* spp. had the lowest carbon value ($-28.4 \pm 1.0\%$, $n = 5$, Tukey HSD, $P < 0.001$). Carbon isotope values of offshore ($-23.0 \pm 0.5\%$, $n = 12$) and nearshore ($-22.5 \pm 0.9\%$, $n = 18$) SPOM were similar (Tukey HSD, $P = 0.355$). The sources with the highest $\delta^{13}C$ values were SOM (-17.9 ± 1.7, $n = 12$), fresh kelp ($-16.5 \pm 1.6\%$, $n = 21$), and drift kelp tissue ($-15.3 \pm 1.9\%$, $n = 21$). Surprisingly, carbon isotopic values for SOM within rhodoliths and the drift and fresh kelp were similar (Tukey HSD, $P > 0.05$). This similarity suggests organic matter from fresh or decaying kelp may contribute to SOM within rhodoliths (Fig. 1a, Table 1). A MixSIAR mixing model estimated that drift kelp contributed $70.7\% \pm 8.1$ and SPOM contributed $29.3\% \pm 8.1$ to SOM within rhodoliths. Nitrogen isotopic values varied by source (ANOVA, $F_{5,86} = 115.26$, $P < 0.001$). Nearshore and offshore SPOM had similar and relatively low nitrogen values (Tukey HSD, $P = 0.369$). These low values contrast the greater and similar nitrogen isotopic values of *Polysiphonia* spp., SOM, drift kelp tissue, and fresh kelp tissue (Tukey HSD, $P = 0.985$).

Consumer trophic groups

A representation of the trophic structure of the Isthmus Cove rhodolith bed was created using isotope values from 13 consumer taxa. Cluster analysis revealed that the 13 consumer taxa were best described by 5 distinct trophic groups (Fig. 1a). Using published studies on diet, isotopic values of consumers in other isotope studies, and isotopic values from the present study, the groups were assigned a feeding guild: planktivore, zooplanktivore, detritivore,

Table 2 The elemental concentrations of nitrogen and carbon for sources used to incorporate concentration dependence in the mixing model

Source	%N	%N (SE)	%C	%C (SE)
SPOM	0.33	0.15	1.89	0.93
Planktivore	12.05	0.66	39.46	0.74
SOM	0.37	0.11	2.4	0.77
Drift kelp	1.51	0.33	31.76	4.73
Zooplanktivore	3.46	1.2	18.9	7.93
Detritivore	9.79	1.37	32.6	3.17
Herbivore	8.9	1.13	34.02	4.07

Fig. 1 $\delta^{13}C$ versus $\delta^{15}N$ biplot of invertebrate consumer isotope values (mean ± SD) and potential food sources pooled across sampling periods from the Isthmus Cove rhodolith bed. **a** Isotope values for trophic consumer groups colored based on the cluster analysis shown on right. On right, a dendrogram with each node representing a taxon. The gastropod *Norrisia norrisii* (11) was found within the adjacent kelp forest and was included as a stable isotope reference for a kelp herbivore. **b** Potential food sources displayed with isotope values of consumers. Potential sources are generated from points: the red alga *Polysiphonia* spp. (red), nearshore suspended particulate organic matter SPOM (light blue), sediment organic matter (SOM, light brown), and *M. pyrifera* drift kelp (green)
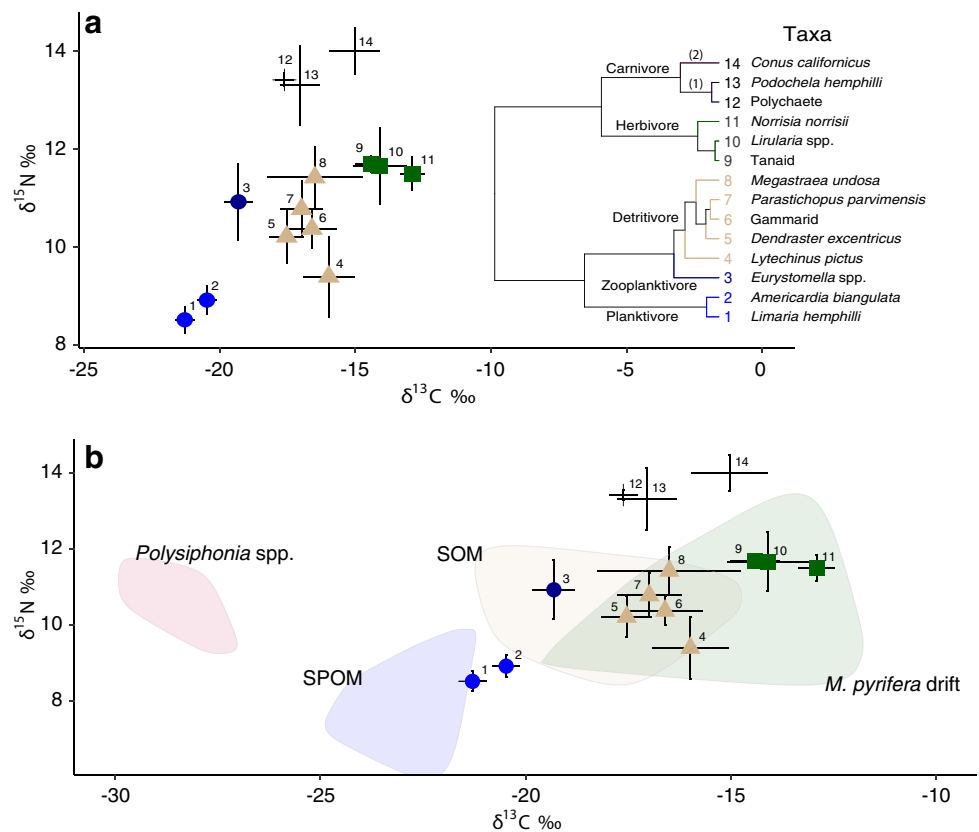
herbivore, or carnivore. The stable isotope ratios of planktivores had the lowest $\delta^{15}N$ values, followed by the zooplanktivore group, followed by the detritivore group, followed by herbivores, and then leading to the highest $\delta^{15}N$ values of the carnivore group. The results from cluster analysis identified a planktivore group composed of the bivalves *Americardia biangulata* and *Limaria hemphilli*. The zooplanktivore group was composed of the bryozoan *Eurystomella* spp. The detritivore group was constituted by the echinoderms *Dendraster excentricus* and *Parastichopus parvimensus,* gammarid amphipods, the gastropod *Megastraea undosa*, and the urchin *Lytechinus pictus.* The herbivore group was composed of the gastropod *Lirularia* spp. and tanaid crustaceans. The isotope values of these herbivores are similar to a known kelp consumer from an adjacent kelp bed, the Norris's top snail *Norrisia norrisii*. This similarity of isotope values suggests these taxa are also herbivores. Carnivores were divided into two groups. Polychaetes and the decapod *Podochela hemphilli* composed the Carnivore (1) group with lower carbon isotope ratios and the gastropod *Californiconus californicus* composed the Carnivore (2) group with higher carbon isotope values (Fig. 1a).

Contributions of sources to consumer trophic groups

A MixSIAR model revealed differences in source contributions to trophic groups which varied by scenario (Fig. 2). In scenario 1, SPOM contributed most the diet of planktivores (96.9% ± 1.7) with little contribution from SOM (2.0% ± 1.6) and *M. pyrifera* drift (< 1%). Detritivore diet was characterized by more SPOM (80.1% ± 8.9) with a moderate amount of SOM (12.1% ± 9.8) and little from *M. pyrifera* drift (7.8% ± 1.5). Herbivore diet was composed of mixed sources including SPOM (63.6% ± 7.5), *M. pyrifera* drift (30.8% ± 6.5), and SOM (5.6% ± 5.6). In scenario 2, SPOM again contributed most to the diet of planktivores (86.0% ± 5.3) with a greater contribution from SOM (12.3% ± 5.4) and little from *M. pyrifera* drift (< 2%). Detritivore diet had a much greater contribution from SOM (85.4% ± 6.1) a moderate contribution from SPOM (10.4% ± 5.0) with little contribution from *M. pyrifera* drift (4.2% ± 2.0). Herbivore diet was composed of mixed sources again but with a higher contribution from *M. pyrifera* drift (69.3% ± 13.3) and relatively similar contributions to scenario 1 from SOM (18.2% ± 13.8) and SPOM (12.5% ± 5.7).
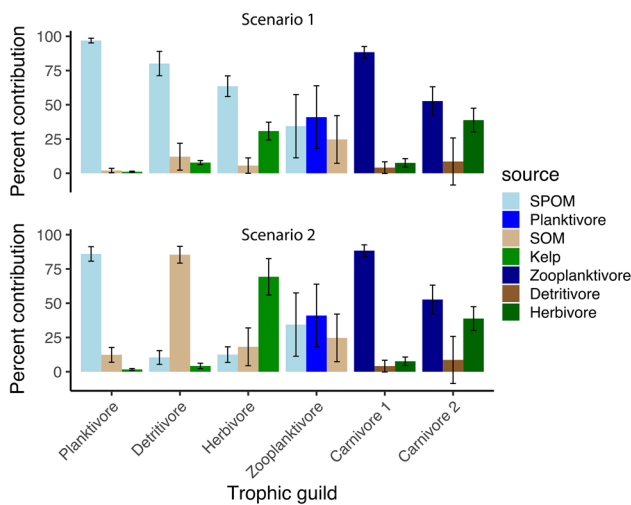
Fig. 2 Contributions of potential food sources (mean ± SD) from MixSIAR models based on two scenarios with different Trophic Enrichment Factors (TEFs) for primary consumers (planktivore, detritivore, herbivore). Primary consumer TEFs differed between scenario 1 (Δ^{15} N of 2.5‰ and Δ^{13}C of 1‰) and scenario 2 (Δ^{15} N of 0.41‰ and Δ^{13}C of 0.21‰). Pooled SPOM, SOM, and drift kelp were potential sources to the planktivore, detritivore, and herbivore trophic guilds. SPOM, planktivore, and SOM groups were potential sources to the zooplanktivore guild. Zooplanktivore, detritivore, and the herbivore guilds were potential sources to the two carnivore trophic guilds

Both scenarios used the same Trophic Enrichment Factors (TEFs) for secondary consumers, therefore the scenarios had the same contributions of sources to the zooplanktivore guild and of consumer sources to the carnivore groups (Fig. 2). Zooplanktivore diet was composed of mixed contributions from the planktivore (41.0% ± 22.9), SPOM (34.4% ± 23.2), and SOM sources (24.7% ± 17.4). Carnivore group diets differed with group 1 having the highest contribution from zooplanktivorous prey (88.4% ± 4.2) while group 2 had more similar contributions from zooplanktivorous prey (52.7% ± 10.5) and herbivorous prey (38.8% ± 8.7).

The differences in the potential contribution of SPOM, SOM, and drift kelp to primary consumer diets impacts the relative importance of basal resources as they propagate through the food web (Fig. 3, Fig. S1). In scenario 1, SPOM contributes to a much greater proportion of primary consumer diets (planktivore, detritivore, herbivore) with less contribution from drift kelp and SOM, suggesting a mainly phytoplankton-based food web (Fig. 3, Fig. S1). In scenario 2, SPOM contributes most to planktivore diet, SOM contributed most to detritivore diet, and drift kelp contributed most to herbivore diet with those differences propagating to the carnivore (1) and carnivore (2) groups. In scenario 2, SPOM, and SOM were overall more important for consumer diets, suggesting a mainly phytoplankton and detrital-based food web (Fig. 3, Fig. S1).
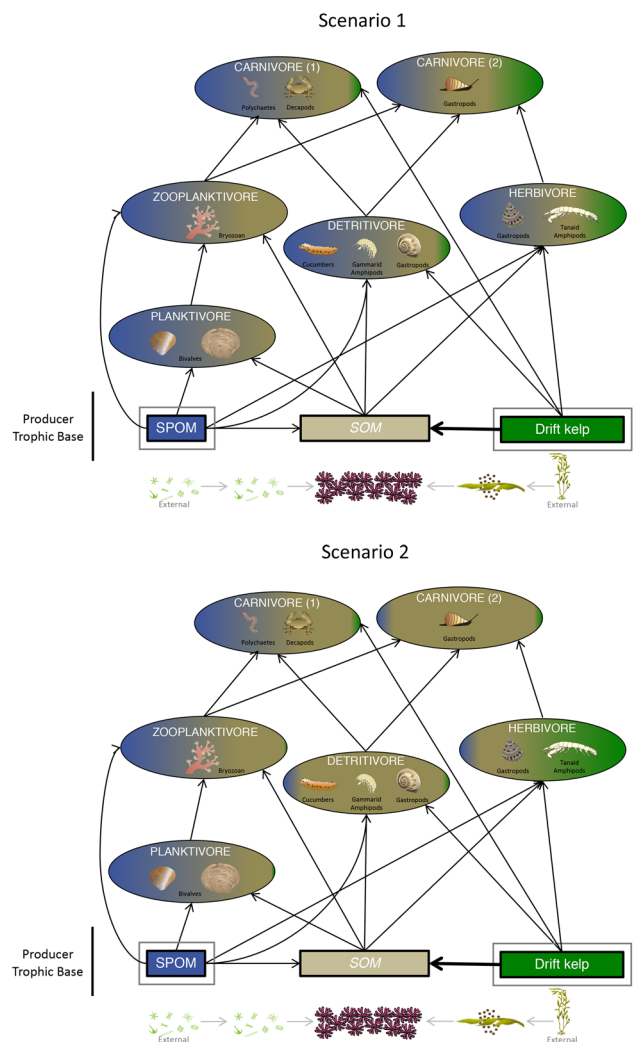
Fig. 3 Generalized Isthmus Cove rhodolith bed food web model based on δ^{13}C and δ^{15}N data, incorporating pooled food sources and consumers across sampling times. Flow of carbon and nitrogen follows the same orientation as the isotope biplot from Fig. 1. Food sources: externally produced Suspended Particulate Organic Matter (SPOM, blue) and drift kelp subsidies from kelp forests (green). These producers directly contribute to consumer diet and indirectly contribute via Sediment Organic Matter (SOM), which collects within rhodolith thalli (light brown). Arrows to SOM are scaled to match percent contribution of SPOM and drift kelp. Ellipse color denotes estimated proportion of each of the primary sources to a consumer from the MixSIAR mixing model and how this propagates through the food web. This was conducted under two scenarios with different Trophic Enrichment Factors (TEFs) for primary consumers (see the Conceptual model of the rhodolith bed food web section within the methods for details). The scenarios reveal differences in the estimated importance of primary sources as they propagate through the food web. (Images: ian.umces.edu/imagelibrary/)

Conceptual model of the rhodolith bed food web

Incorporating pooled isotope values from food sources and consumers yielded a generalized food web model for both
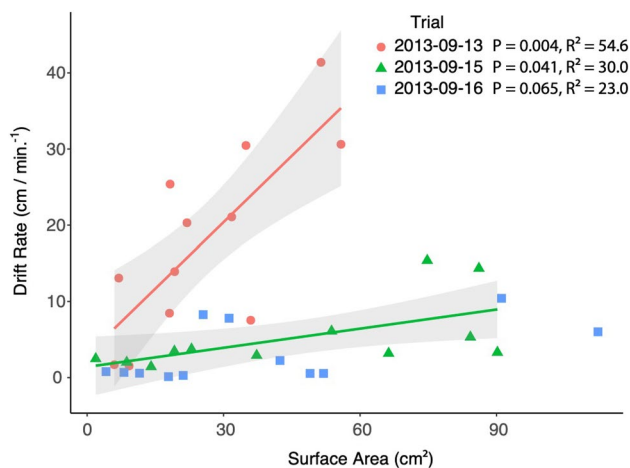
Fig. 4 Relationship between giant kelp *Macrocystis pyrifera* blade surface area (cm^2) and drift rate (cm min^{-1}). Three trials were conducted on different days within the Isthmus Cove rhodolith bed

Table 3 Results of ANCOVA testing for the effect of surface area (SA) on the drift rate of giant kelp pieces and whether this relationship varied by experimental trial (Date)

Source	df	SS	MS	F	P
Surface Area	1	101.2	101.20	3.127	0.087
Trial	1	1876.5	938.30	28.994	**< 0.001**
SA × trial	2	686.1	343.00	10.600	**< 0.001**
Residuals	30	970.8	32.40		

Bold indicates significance at $P < 0.05$

scenarios (Fig. 3). The food web sources representing major pathways of carbon and nitrogen (SPOM, SOM, and drift kelp) contributed differentially to primary and secondary consumers. The coloring of trophic group ellipses of primary consumers summarizes the degree of contribution of the different sources from MixSIAR. The percent contribution of basal sources to secondary consumers were estimated using the percent source contributions to primary consumers and the MixSIAR results (Fig. 3).

Drift kelp retention experiment

Increasing surface area of giant kelp pieces increased drift rate and decreased retention in the rhodolith bed, though the relationship varied by experimental trial day (Fig. 4, Table 3). The tidal periods for each day were between the lower high water and higher low water tides. The wind direction, wind speed, wave height, and wave direction (NOAA buoy station 46025) during the release and hours previous to the trials did not appear to correspond with drift rates. Much of the variation in the relationship between surface area and drift rate could be explained by fitted lines for each

trial (Fig. 4). Regardless of the trial day, drift kelp pieces with small surface areas (~ < 10 cm) had lower drift rates and therefore movement (Fig. 4). Larger drift kelp pieces had greater variability in export rates among days relative to smaller particulates (Fig. 4).

Discussion

Although rhodolith beds are globally distributed habitats (Foster 2001) and recognized as supporting benthic macroalgal, invertebrate, and vertebrate abundance and biodiversity (Foster 2001; Steller et al. 2003; Kamenos et al. 2004; Gagnon et al. 2012; Gabara et al. 2018), little work has been done to characterize rhodolith bed food webs (Grall et al. 2006) and the role of external subsidies in potentially supporting them. The isotope data in the present study suggests the importance of phytoplankton phytodetritus and macroalgal drift or detrital matter to rhodolith bed consumers. The conclusions drawn from these data are consistent with trophic dynamics in an Atlantic rhodolith bed (Grall et al. 2006) and similar to what has been found in other communities such as seagrass beds (Moncreiff and Sullivan 2001), mangrove habitats (Bouillon et al. 2008), and kelp holdfast communities (Schaal et al. 2012).

In the present study, isotopic results support the hypothesis that rhodolith bed communities receive carbon and nitrogen subsidies from adjacent systems including the water column and potentially from giant kelp forests. The dominant source of primary production for detritivores, herbivores, and predators in the Isthmus Cove rhodolith food web appeared to be POM that originated from the water column in scenario 1 and SPOM, SOM, and drift kelp, in scenario 2. Consumers within an Atlantic rhodolith bed were hypothesized to be supported by detrital phytoplankton (Grall et al. 2006). The present study also supports this notion, while indicating that macroalgae can contribute to over 30% of herbivore diets.

SOM within rhodoliths, drifting kelp tissue within the rhodolith bed, and fresh attached kelp from nearby kelp forests had similar isotope values, suggesting rhodolith communities may receive organic matter from adjacent kelp forests. The isotopic values for SOM plotted between phytoplankton and drift kelp, and the MixSIAR mixing model suggested contributions of ~ 30% and ~ 70% of SPOM and drift kelp to SOM, respectively. This suggests both of these sources may contribute to SOM within rhodoliths. However, other benthic algae like diatoms may have similar isotopic signatures to benthic macroalgae. An isotopic value for diatoms has not been identified and therefore their potential influence cannot be estimated (Grall et al. 2006). Similarly, in this study, it was difficult to separate biofilm and diatoms from rhodoliths and diatom collections from rhodolith surfaces

did not yield sufficient sample mass for an isotope measurement (Grall et al. 2006). The importance of the microphytobenthos, mostly microalgae and bacteria, to consumer diets is still unknown and warrants further investigation as a potential food resource (Grall et al. 2006). Future work should consider techniques that could increase resolution in identifying and distinguishing potential food sources such as using fatty acids or essential and non-essential amino acids which create multiple tracers relative to the two (carbon and nitrogen isotope ratios) used here (Boecklen et al. 2011; Galloway et al. 2015).

The relationship between surface area of drift kelp pieces and their export rate suggests large drift kelp particulates have low retention during periods of increased water motion relative to smaller particulates. A MixSIAR mixing model revealed that the particulate matter within rhodoliths was 70% detrital kelp, which supports the idea that kelp particulates may be retained within rhodolith thalli. Temporal variability in the relationship between drift kelp surface area and export rate across trials suggests export or retention of drift kelp may differ through time spanning different wave, wind, and tidal conditions. More work is needed to understand temporal variability of drift kelp detritus production and its export or retention, both within seasons, and among them. The ability of rhodoliths to trap organic matter within the interstitial spaces among branches and among rhodolith individuals remains unexplored. Rhodolith structural complexity may be an important determinant for the aggregation of particulate organic matter from the water column. This aggregation may provide a food resource to the associated community and thus contribute to the role of rhodoliths as a foundation species.

Despite relatively high export rates of larger kelp pieces, stable isotopes suggested kelp tissue contributed at least 30% to the diet of the herbivores examined in this study regardless of the scenario. The pooled isotopic signatures of the gastropod *Lirularia* spp. and tanaid crustaceans were most similar to drift kelp and close to the values of the Norris's top snail (*Norrisia norrisii*), a consumer with a preference for kelp (Wakefield and Murray 1998). This suggests that a large proportion of herbivore diet could be derived from kelp or other benthic micro- or macroalgae not sampled that have a similar isotopic ratios. Tanaids are likely selective deposit feeding omnivores (Blazewicz-Paszkowycz and Ligowski 2002) that consume detritus (Bracken et al. 2007), macroalgae, or epiphytes (Blazewicz-Paszkowycz and Ligowski 2002). The importance of giant kelp to the epibenthic invertebrate gastropods *Lirularia* spp. and *Megastraea undosa* support the observations that individuals were found on drift kelp blades within the bed and hypothesized to be grazing these blades.

Pooled SPOM isotope values were distinctly lower in $\delta^{13}C$ relative to the more enriched values of SOM and drift kelp. Instead, they were similar to those reported from seawater collected in other studies off Southern California (Page et al. 2008; Kurle and McWhorter 2017), similar to SPOM from samples collected offshore, and unlikely to have been influenced by adjacent kelp forests. The isotope mixing model for scenario 1 indicated that SPOM was the dominant carbon source for most rhodolith trophic groups either directly, or indirectly, indicating subsidies from water column-based sources are important and propagate through this food web. Additional long-term sampling of SPOM in the vicinity of rhodolith beds and further offshore could better elucidate the importance of this source (Miller et al. 2013). While pooled isotopic values for SPOM collected from nearshore and offshore seawater were similar, seasonal variation did exist. During summer, the carbon and nitrogen isotopic values in nearshore water became enriched compared to offshore values. Seasonal changes could be due to differential mixing, different growth and species compositions of phytoplankton (Page et al. 2008), or potential isotopic enrichment of seawater by nearshore macroalgal particulates or phytoplankton during summer (Miller et al. 2013). The bivalves sampled had relatively low $\delta^{15}N$ values relative to SPOM and SOM, suggesting the trophic enrichment factor used in scenario 1 may be too large of a correction for these taxa, fractionation of SPOM may occur en route to the sediment, and/or there is a mismatch between consumer tissue turnover and temporal variation of SPOM. Regardless of the trophic enrichment factor for bivalves (scenario 1 or 2), they rely primarily upon SPOM and are thus isotopically distinct from other primary consumers (Grall et al. 2006).

The detritivores in the present study were influenced by benthic production, as they had greater isotopic values relative to the isotopic signatures of planktivorous filter-feeding bivalves. Detritivores were likely suspension or deposit feeders consuming suspended particulates or particulates settled on or within the sediment, similar to infaunal and epibenthic selective deposit feeders found within an Atlantic rhodolith bed (Grall et al. 2006). Macroalgal particles could be utilized by the suspension/deposit feeding sand dollar *Dendraster excentricus* and the deposit feeding sea cucumber *Parastichopus parvimensus* as they are both capable of consuming organic particulates on the sediment surface (Timko 1976; Yingst 1982). *Megastraea undosa* was identified as a detritivore, albeit is known to consume kelp (Cox and Murray 2005). Whether these species consume kelp particulates and detrital algae remains unknown. Further, gammarid amphipods consume decaying algae (Martin 1966) and *Lytechinus pictus* can consume juvenile kelps (Dean et al. 2009). The high degree of isotopic overlap of detritivores in this study suggests that these species have similar food resources and similar feeding strategies with the exception of *Lytechinus pictus*.

Invertebrate predator taxa sampled in the rhodolith bed appeared to mainly consume prey from the zooplanktivore and detritivore groups. Predators do not display isotopic values indicative of large contributions from herbivorous invertebrates but have significant influence from planktivorous and detritivorous prey, suggesting a reliance on the phytoplankton and detrital pathway (Grall et al. 2006; Schaal et al. 2012). Polychaetes and the decapod *Podochela hemphilli* appear to consume mainly zooplanktivorous prey while the gastropod *Californiconus californicus* receives a greater contribution from detritivorous prey, reinforcing the importance of the sources of detritus including pelagic derived food and macroalgae.

All trophic consumer groups sampled (planktivore, zooplanktivore, detritivore, herbivore, and predator) were potential prey for higher-level predators such as fishes, which were observed foraging within the rhodolith beds (Gabara et al 2018). The fishes observed most often within rhodolith beds include Senorita *Oxyjulis californica*, Rock wrasse *Halichoeres semicinctus*, Kelp bass *Paralabrax clathratus*, and Sheephead *Semicossyphus pulcher* (Gabara et al. 2018). Observations and gut content analysis of these fishes at Catalina suggest that they may forage on many of the invertebrates found within the rhodolith beds such as crustaceans, bivalves, gastropods, and ophiuroids (Hobson and Chess 1986, 2001). Incorporating these mobile predators into future food web studies will create a more complete food web depiction and may reveal connections between the food webs of adjacent foundation species.

Stable isotopes may help reveal the dietary niche of an organism (Newsome et al. 2007) and the potential role they serve in an ecosystem (Newsome et al. 2009). Here, limitations in identifying the most representative rhodolith bed food web and the relative importance of basal food sources were (1) characterizing temporal variability in SPOM and SOM within the rhodolith bed and (2) selecting a trophic enrichment factor (TEF) for primary and higher-level consumers. Future work should consider potential food web sources suspended within the water column and those sedimenting on the benthos while including how they may be altered over time. Further, different trophic enrichment factors can substantially alter estimated source contributions from mixing models as observed when comparing outcomes of scenarios 1 and 2 (Bond and Diamond 2011). Trophic enrichment factors are needed for rhodolith bed consumers to better select the model that more accurately reflects carbon and nitrogen flow. Another limitation was that by pooling individuals to meet mass requirements for sample isotope analysis (gammarids, tanaids) and by pooling species within taxonomically large groups (gammarids, tanaids, polychaetes), resolution in identifying species specific stable isotope values and estimating diet contributions to these taxa in this system was reduced. Future work should determine species specific isotope values

that will aid in identifying the functional roles of rhodolith associated species and their potential diet specialization or redundancy (Mouillot et al. 2011).

Stable isotope analysis of a California rhodolith bed revealed a food web reliant on subsides in the form of phytoplankton and detritus supporting planktivores, zooplanktivores, detritivores, herbivores, and carnivores. The interstitial spaces within and among rhodoliths appears important for collecting detrital organic matter from phytoplankton and macroalgae that supports this community. Rhodolith structural complexity is important for supporting epifauna, cryptofauna, and infauna (Steller et al. 2003; Gabara et al. 2018). The ability of rhodoliths to collect organic matter within and under thalli may be an important mechanism contributing to the high abundance, biodiversity, and stability of rhodolith bed habitats (Grall et al. 2006; Millar and Gagnon 2018; Gabara et al. 2018). Future work on rhodolith bed ecology should consider experiments testing the relative importance of habitat and food provision in supporting rhodolith associated biodiversity.

Data availability The datasets analyzed during the current study are summarized in Table 1.

Compliance with ethical standards

Conflict of interest The author declares that they have no conflicts of interest.

Ethical approval All applicable national and/or institutional guidelines for the care and use of animals were followed. I thank the California Department of Fish and Wildlife for permit SCP-10399 to conduct this work.

References

Blazewicz-Paszkowycz M, Ligowski R (2002) Diatoms as food source indicator for some Antarctic Cumacea and Tanaidacea (Crustacea). Antarct Sci 14:11–15

Boecklen WJ, Yarnes CT, Cook BA, James AC (2011) On the use of stable isotopes in trophic ecology. Annu Rev Ecol Syst 42:411–440. https://doi.org/10.1146/annurev-ecolsys-102209-144726

Bond A, Diamond A (2011) Recent bayesian stable-isotope mixing models are highly sensitive to variation in discrimination factors. Ecol Appl 21:1017–1023

Bouillon S, Connolly RM, Lee SY (2008) Organic matter exchange and cycling in mangrove ecosystems: recent insights from stable isotope studies. J Sea Res 59:44–58. https://doi.org/10.1016/j.seares.2007.05.001

Bracken M, Gonzalez-Dorantes C, Stachowicz J (2007) Whole-community mutualism: associated invertebrates facilitate a dominant habitat-forming seaweed. Ecology 88:2211–2219

Brauns M, Brabender M, Gehre M, Rinke K, Weitere M (2019) Organic matter resources fuelling food webs in a human-modified lowland river: importance of habitat and season. Hydrobiologia 841:121–131. https://doi.org/10.1007/s10750-019-04011-4

Britton-Simmons KH, Rhoades AL, Pacunski RE, Galloway AWE, Lowe AT, Sosik EA, Dethier MN, Duggins DO (2012) Habitat and bathymetry influence the landscape-scale distribution and abundance of drift macrophytes and associated invertebrates. Limnol Oceanogr 57:176–184. https://doi.org/10.4319/lo.2012.57.1.0176

Cox TE, Murray SN (2005) Feeding preferences and the relationships between food choice and assimilation efficiency in the herbivorous marine snail *Lithopoma undosum* (Turbinidae). Mar Biol 148:1295–1306. https://doi.org/10.1007/s00227-005-0166-3

Davenport S, Bax N (2002) A trophic study of a marine ecosystem off southeastern Australia using stable isotopes of carbon and nitrogen. Can J Fish Aquat Sci 59:514–530. https://doi.org/10.1139/F02-031

Dean TA, Thies K, Lagos SL (2009) Survival of Juvenile Giant kelp: the effects of demographic factors, competitors, and grazers. Ecology 70:483–495

Duggins DO, Simenstad C, Estes JA (1989) Magnification of secondary production by kelp detritus in coastal marine ecosystems. Sci New Ser 245:170–173

Filbee-Dexter K, Scheibling RE (2016) Spatial patterns and predictors of drift algal subsidy in deep subtidal environments. Estuaries Coasts 39:1724–1734. https://doi.org/10.1007/s12237-016-0101-5

Filbee-Dexter K, Wernberg T, Ramirez-Llodra E, Norderhaug KM, Pedersen MF (2018) Movement of pulsed resource subsidies from shallow kelp forests to deep fjords. Oecologia 187:291–304. https://doi.org/10.1007/s00442-018-4121-7

Foster MS (2001) Rhodoliths: between rocks and soft places. J Phycol 37:659–667

Foster MS, McConnico LM, Lundsten L, Wadsworth T, Kimbal T, Brooks LB, Medina-López M, Riosmena-Rodríguez R, Hernández-Carmona G, Vázquez-Elizondo RM, Johnson S, Steller DL (2007) Diversidad e historia natural de una comunidad de *Lithothamnion muelleri-Sargassum horridum* en el Golfo de California (Diversity and natural history of a Lithothamnion muelleri-Sargassum horridum community in the Gulf of California). Ciencias Mar 33:367–384

Foster MS, Amado Filho GM, Kamenos NA, Riosmena-Rodriguez R, Steller DL (2013) Rhodoliths and rhodolith beds. Smithson Contrib Mar Sci 39:143–155

Fry B (2006) Stable isotope ecology. Springer, New York

Gabara SS (2014) Community structure and energy flow within rhodolith habitats at Santa Catalina Island, CA. In: MSc thesis, San Jose State University, San Jose, CA

Gabara SS, Hamilton SL, Edwards MS, Steller DL (2018) Rhodolith structural loss decreases abundance, diversity, and stability of benthic communities at Santa Catalina Island, CA. Mar Ecol Prog Ser 595:71–88. https://doi.org/10.3354/meps12528

Gagnon P, Matheson K, Stapleton M (2012) Variation in rhodolith morphology and biogenic potential of newly discovered rhodolith beds in Newfoundland and Labrador (Canada). Bot Mar 55:85–99

Galloway AWE, Brett MT, Holtgrieve GW, Ward EJ, Ballantyne AP, Burns CW, Kainz MJ, Müller-Navarra DC, Persson J, Ravet JL, Strandberg U, Taipale SJ, Alhgren G (2015) A fatty acid based bayesian approach for inferring diet in aquatic consumers. PLoS One 10:e0129723. https://doi.org/10.1371/journal.pone.0129723

Gerard V (1976) Some aspects of material dynamics and energy flow in a kelp forest in Monterey Bay, California. Dissertation, University of California Santa Cruz

Gerard V, North W (1984) Measuring growth, production, and yield of the giant kelp *Macrocystis pyrifera*. Hydrobiologia 116(117):321–324

Graham MH (2004) Effects of local deforestation on the diversity and structure of Southern California giant kelp forest food webs. Ecosystems 7:341–357

Grall J, Leloch F, Guyonnet B, Riera P (2006) Community structure and food web based on stable isotopes (δ^{15}N and δ^{13}C) analysis of a North Eastern Atlantic maerl bed. J Exp Mar Bio Ecol 338:1–15. https://doi.org/10.1016/j.jembe.2006.06.013

Harrold C, Reed DC (1985) Food availability, sea urchin grazing, and kelp forest community structure. Ecology 66:1160–1169

Hobson ES, Chess JR (1986) Relationships among fishes and their prey in a nearshore sand community off southern California. Environ Biol Fish 17:201–226. https://doi.org/10.1007/BF00698198

Hobson ES, Chess JR (2001) Influence of trophic relations on form and behavior among fishes and benthic invertebrates in some California marine communities. Environ Biol Fishes 60:411–457

Ince R, Hyndes GA, Lavery PS, Vanderklift MA (2007) Marine macrophytes directly enhance abundances of sandy beach fauna through provision of food and habitat. Estuar Coast Shelf Sci 74:77–86. https://doi.org/10.1016/j.ecss.2007.03.029

Jaschinski S, Brepohl D, Sommer U (2011) Seasonal variation in carbon sources of mesograzers and small predators in an eelgrass community: stable isotope and fatty acid analyses. Mar Ecol Prog Ser 431:69–82. https://doi.org/10.3354/meps09143

Kaehler S, Pakhomov E, Kalin R, Davis S (2006) Trophic importance of kelp-derived suspended particulate matter in a through-flow sub-Antarctic system. Mar Ecol Prog Ser 316:17–22. https://doi.org/10.3354/meps316017

Kamenos NA, Moore P, Hall-spencer JM (2004) Small-scale distribution of juvenile gadoids in shallow inshore waters; what role does maerl play? ICES J. https://doi.org/10.1016/j.icesjms.2004.02.004

Kelly J, Krumhansl KA, Scheibling R (2012) Drift algal subsidies to sea urchins in low-productivity habitats. Mar Ecol Prog Ser 452:145–157. https://doi.org/10.3354/meps09628

Krumhansl KA, Scheibling R (2012a) Production and fate of kelp detritus. Mar Ecol Prog Ser 467:281–302. https://doi.org/10.3354/meps09940

Krumhansl KA, Scheibling RE (2012b) Detrital subsidy from subtidal kelp beds is altered by the invasive green alga *Codium fragile* ssp. *fragile*. Mar Ecol Prog Ser 456:73–85. https://doi.org/10.3354/meps09671

Kurle CM, McWhorter JK (2017) Spatial and temporal variability within marine isoscapes: implications for interpreting stable isotope data from marine systems. Mar Ecol Prog Ser 568:31–45. https://doi.org/10.3354/meps12045

Leclerc J-C, Riera P, Leroux C, Lévêque L, Laurans M, Schaal G, Davoult D (2013) Trophic significance of kelps in kelp communities in Brittany (France) inferred from isotopic comparisons. Mar Biol 160:3249–3258. https://doi.org/10.1007/s00227-013-2306-5

Madigan DJ, Carlisle AB, Dewar H, Snodgrass OE, Litvin SY, Micheli F, Block BA (2012) Stable isotope analysis challenges wasp-waist

food web assumptions in an upwelling pelagic ecosystem. Sci Rep 2:654

Mann KH (1988) Production and use of detritus in various freshwater, estuarine and coastal marine ecosystems. Limnol Oceanogr 33:910–930

Martin A (1966) Feeding and digestion in two intertidal gammarids: *Marinogammarus obtusatus* and *M. pirloti*. J Zool 148:515–525

Mehner T, Rapp T, Monk CT, Beck ME, Trudeau A, Kiljunen M, Hilt S, Arlinghaus R (2019) Feeding aquatic ecosystems: whole-lake experimentaladdition of angler's ground bait strongly affects omnivorous fish despite low contribution to lake carbon budget. Ecosystems 22:346–362. https://doi.org/10.1007/s10021-018-0273-x

Millar KR, Gagnon P (2018) Mechanisms of stability of rhodolith beds: sedimentological aspects. Mar Ecol Prog Ser 594:65–83

Miller RJ, Page HM (2012) Kelp as a trophic resource for marine suspension feeders: a review of isotope-based evidence. Mar Biol 159:1391–1402. https://doi.org/10.1007/s00227-012-1929-2

Miller RJ, Page HM, Brzezinski M (2013) $\delta^{13}C$ and $\delta^{15}N$ of particulate organic matter in the Santa Barbara channel: drivers and implications for trophic inference. Mar Ecol Prog Ser 474:53–66. https://doi.org/10.3354/meps10098

Moncreiff C, Sullivan M (2001) Trophic importance of epiphytic algae in subtropical seagrass beds: evidence from multiple stable isotope analyses. Mar Ecol Prog Ser 215:93–106. https://doi.org/10.3354/meps215093

Mouillot D, Villéger S, Scherer-Lorenzen M, Mason NWH (2011) Functional structure of biological communities predicts ecosystem multifunctionality. PLoS One 6(3):e17476. https://doi.org/10.1371/journal.pone.0017476

Newsome SD, Martinez del Rio C, Bearhop S, Phillips DL (2007) A niche for isotope ecology. Front Ecol Environ 5:429–436. https://doi.org/10.1890/060150.1

Newsome SD, Tinker MT, Monson DH, Oftedal OT, Ralls K, Staedler MM, Fogel ML, Estes JA (2009) Using stable isotopes to investigate individual diet specialization in California sea otters (*Enhydra lutris nereis*). Ecology 90:961–974

Ouisse V, Riera P, Migné A, Leroux C, Davoult D (2012) Food web analysis in intertidal *Zostera marina* and *Zostera noltii* communities in winter and summer. Mar Biol 159:165–175. https://doi.org/10.1007/s00227-011-1796-2

Page HM, Reed D, Brzezinski M, Melack J, Dugan J (2008) Assessing the importance of land and marine sources of organic matter to kelp forest food webs. Mar Ecol Prog Ser 360:47–62. https://doi.org/10.3354/meps07382

Parnell AC, Inger R, Bearhop S, Jackson AL (2010) Source partitioning using stable isotopes: coping with too much variation. PLoS One 5:e9672. https://doi.org/10.1371/journal.pone.0009672

Phillips D (2002) Incorporating concentration dependence in stable isotope mixing models. Oecologia 130:114–125. https://doi.org/10.1007/s004420100786

Polis GA, Holt RD, Menge BA, Winemiller KO (1996) Time, space and life history: influences on food webs. In: Food webs: integration of patterns and dynamics, pp 435–460

Polis G, Anderson W, Holt R (1997) Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. Annu Rev Ecol Syst 28:289–316

Raven JA, Johnston AM, Kubler JE, Korb R, McInroy SG, Handley LL, Scrimgeour CM, Walker DI, Beardall J, Vanderklift M, Fredriksen S, Dunton KH (2002) Mechanistic interpretation of carbon isotope discrimination by marine macroalgae and seagrasses. Funct Plant Biol 29:355–378

Rodríguez SR (2003) Consumption of drift kelp by intertidal populations of the sea urchin *Tetrapygus niger* on the central Chilean coast: possible consequences at different ecological levels. Mar Ecol Prog Ser 251:141–151

Schaal G, Riera P, Leroux CC (2012) Food web structure within kelp holdfasts (Laminaria): a stable isotope study. Mar Ecol 33:370–376. https://doi.org/10.1111/j.1439-0485.2011.00487.x

Semmens BX, Moore JW, Ward EJ (2009) Improving Bayesian isotope mixing models: a response to Jackson et al. (2009). Ecol Lett 12:E6–8. https://doi.org/10.1111/j.1461-0248.2009.01283.x

Steller DL, Riosmena-Rodriguez R, Foster MSM, Roberts CA (2003) Rhodolith bed diversity in the Gulf of California: the importance of rhodolith structure and consequences of disturbance. Aquat Conserv Mar Freshw Ecosyst 13:S5–S20. https://doi.org/10.1002/aqc.564

Stock BC, Jacoson AL, Ward EJ, Parnell AC, Phillips DL, Semmens BX (2018) Analyzing mixing systems using a new generation of Bayesian tracer mixing models. PeerJ Preprints 6:e26884v1. https://doi.org/10.7287/peerj.preprints.26884v1

Timko PL (1976) Sand dollars as suspension feeders: a new description of feeding in Dendraster excentricus. Biol Bull Mar Biol Lab Woods Hole 151:247–259

Tompkins PA (2011) Distribution, growth, and disturbance of Catalina Island rhodoliths. In: Masters Thesis. Moss Landing Marine Laboratories, San Jose State University

Tompkins PA, Steller DL (2016) Living carbonate habitats in temperate California (USA) waters: distribution, growth, and disturbance of Santa Catalina Island rhodoliths. Mar Ecol Prog Ser 560:135–145. https://doi.org/10.3354/meps11919

Vafeiadou A-M, Materatski P, Adão H, De Troch M, Moens T, Troch M, Moens T (2013) Food sources of macrobenthos in an estuarine seagrass habitat (*Zostera noltii*) as revealed by dual stable isotope signatures. Mar Biol 160:2517–2523. https://doi.org/10.1007/s00227-013-2238-0

Vanderklift MA, Ponsard S (2003) Sources of variation in a consumer-diet $d^{15}N$ enrichment: a meta-analysis. Oecologia 136:169–182

Vetter EW (1995) Detritus-based patches of high secondary production in the nearshore benthos. Mar Ecol Prog Ser 120:251–262. https://doi.org/10.3354/meps120251

Vetter EW, Dayton PK (1998) Macrofaunal communities within and adjacent to a detritus-rich submarine canyon system. Deep Sea Res Part II Top Stud Oceanogr 45:25–54. https://doi.org/10.1016/S0967-0645(97)00048-9

Vetter EW, Dayton PK (1999) Organic enrichment by macrophyte detritus, and abundance patterns of megafaunal populations in submarine canyons. Mar Ecol Prog Ser 186:137–148. https://doi.org/10.3354/meps186137

Wakefield RL, Murray SN (1998) Factors influencing food choice by the seaweed-eating marine snail Norrisia norrisi (Trochidae). Mar Biol 130:631–642. https://doi.org/10.1007/s002270050285

Yingst JY (1982) Factors influencing rates of sediment ingestion by *Parastichopus parvimensis* (Clark), an epibenthic deposit-feeding holothurian. Estuar Coast Shelf Sci 14:119–134