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Living kelp versus plankton as food sources for suspension feeders

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ABSTRACT: Large amounts of primary production are routed into detrital food webs, but the importance of detritus is poorly understood in many ecosystems. As one of the most conspicuous primary producers in temperate coastal ecosystems, kelps have long been hypothesized to provide detrital food to benthic suspension feeders through sloughing of canopy laminar tissue. Evidence for this phenomenon has largely rested on interpretation of carbon stable isotope values, and most direct evidence shows that phytoplankton, and to some extent zooplankton and bacteria, are the major sources of nutrition for marine suspension feeders. In this study, we experimentally tested the effects of kelp and naturally occurring phytoplankton on growth and survival of benthic suspension feeders in 2 kelp forest systems, southern California and New Zealand. To do so, we maintained suspension feeders in flow-through tanks with presence or absence of phytoplankton via raw and filtered seawater and presence or absence of mechanically agitated kelp laminae. Suspension feeder growth was significantly increased by phytoplankton but not kelp availability. Large amounts of kelp added to tanks, moreover, did not significantly contribute to the particulate organic matter (POM) pool, suggesting that sloughing from the eroding margins of kelp tissue is not a meaningful mechanism for small detrital particle production. Kelp forests are diverse and important ecosystems, but our results do not support the idea that kelps themselves trophically support subtidal and intertidal suspension feeders through detrital inputs.

KEY WORDS: Detritus · Phytoplankton · Suspension feeding · Sessile invertebrates · Kelp

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1. INTRODUCTION

Primary production is a basic driver of ecosystem function, and much of this production becomes detritus that fuels the 'brown food web' (Schlesinger 1977, Kaspari et al. 2009, Zou et al. 2016). The amount of primary production entering the detrital pool, and its fate, varies as a function of not only the productivity of the ecosystem, but also of the nutritional quality, or palatability, of the plant material produced (Bardgett & Wardle 2003, Wardle et al. 2003, 2005, Harrault et al. 2012, Danger et al. 2012). This quality is shaped by selective pressure on living plants and algae through grazing and other interactions (Ehrlich & Raven 1964, Mello & Silva-Filho 2002) as well as physiological and life history requirements (Lodge 1991) and environmental conditions (Gartner & Cardon 2004). As a result, plant tissues vary widely in palatability, as indicated by characteristics like C:N ratios, nutrient content, toughness, and levels of anti-grazing compounds (Beck 1965, Duggins & Eckman 1997, Pennings et al. 2001, Norderhaug et al. 2003, Gartner & Cardon 2004), in turn influencing the fate and bioavailability of the resulting detritus (Cebrian 1999, Cebrian & Lartigue 2004). In general, terrestrial detritus is considered more refractory than marine detritus (Blair & Aller 2012), and macroalgal detritus, such as kelp, is considered particularly labile (Duarte & Cebrián 1996).

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In temperate coastal waters, the large brown macroalgae known as kelps are regarded as foundation species (Dayton 1972) because they create much of the physical structure in kelp forest ecosystems (Foster & Schiel 1985, Graham et al. 2007). Kelp has physical ecosystem engineering effects through mechanisms such as shading and current dampening (Gaylord et al. 2007, Arkema et al. 2009) and trophic effects (Babcock et al. 1999, Schiel & Foster 2015, Koenigs et al. 2015) on reef ecosystems, but most kelp productivity enters the detrital pool (reviewed by Krumhansl & Scheibling 2012). Kelp forests harbor a diverse community of benthic invertebrates dominated by sessile suspension feeders (Ricciardi & Bourget 1999, Shears & Babcock 2007, Reed et al. 2016), which can be released from competition with understory macroalgae that are shaded out by kelp canopies (Miller et al. 2018).

Kelp forest suspension feeders have long been posited to rely heavily on kelp detritus for food (reviewed by Miller & Page 2012). Proximity to living kelp has been considered a predictor of trophic reliance on kelp (Duggins et al. 1989, Kaehler et al. 2006, Salomon et al. 2008) via shedding of detritus and dissolved organic matter (DOM) consumed by suspension feeders living on the reef below (Duggins & Eckman 1994, Schaal et al. 2009, Feehan et al. 2018), even when residence time of water within a small kelp forest is short (Duggins & Eckman 1994). Kelp have been shown to produce small particulate detritus and release DOM, which has been estimated to make up more than half of exported kelp-derived net primary production (Khailov & Burlakova 1969, Mann 1982, Wada et al. 2007, Krumhansl & Scheibling 2012, de Bettignies et al. 2013, Reed et al. 2015). Scaling up direct measurements of particulate detrital shedding rates of giant kelp using field-measured kelp biomass, however, suggested that kelp detritus comprised <1% of nearshore particulate organic carbon (POC) on a reef off Santa Barbara (Yorke et al. 2013).

Two general approaches have been used to evaluate the hypothesis that kelps are an important trophic resource to suspension feeders through detrital production. First, and most commonly, carbon stable isotope data have been used to infer kelp use. Due to the difficulty of direct observation of trophic interactions and interpreting gut content analysis, isotope data are a valuable tool for exploration of marine food webs, and are particularly attractive for analysis of the trophic role of suspension feeders, since these animals filter tiny particles from the water, making gut content analyses difficult. These studies have typically used mixing models, with $\delta^{13}C$ values of (1) fresh kelp and (2) offshore or cultured phytoplankton, or phytoplankton values from the literature as the 2 endmembers contributing to particulate organic matter (POM) and suspension feeder tissue $\delta^{13}C$ (reviewed by Miller & Page 2012). A major problem with this framework has been that the isotope value of the phytoplankton source, and variability in that value, has not been well constrained, and this can result in systematic overestimation of kelp contributions to POM and suspension feeder diet (Miller & Page 2012, Miller et al. 2013).

Second, some studies have experimentally examined the potential contribution of kelp detritus to suspension feeder nutrition and growth in laboratory experiments using homogenized (and often aged) kelp as a food source. Although this approach is more direct than the isotope studies, it assumes that homogenized kelp resembles naturally produced detritus in quality, size, and, perhaps most importantly, concentration and availability (reviewed by Miller & Page 2012).

In this study, we took a different approach to addressing the question of whether living kelp in close proximity to suspension feeders represents a food source. Instead of grinding up kelp and presenting it to suspension feeders, we manipulated the presence of kelp and phytoplankton in flow-through laboratory seawater systems to examine the extent to which living kelp acts as a resource for suspension feeders from kelp forests of southern California (CA) and New Zealand (NZ). Our approach did not assume that the kelp produced POM or DOM, although that is the hypothesized mechanism through which kelp can affect the nutrition of suspension feeders. Our broad hypothesis, based on the previous body of research described above, was that an ecologically relevant supply of living kelp would augment POM and DOM resources, which would benefit suspension feeders in close proximity. We tested this hypothesis using a diverse range of benthic suspension feeders and the dominant kelp species in each region: *Macrocystis pyrifera* in CA and *Ecklonia radiata* in NZ. Based on our previous results, we predicted that availability of living kelp tissue would not positively contribute to the growth and survival of suspension feeders, even during periods of low phytoplankton concentration.

2. MATERIALS AND METHODS

2.1. Study sites

This work was conducted at the Marine Laboratory, University of California Santa Barbara, USA and

at Leigh Marine Laboratory, University of Auckland, Leigh, New Zealand. The Santa Barbara Channel (SBC) sits at the northern margin of Southern California, where it is relatively protected from wave exposure by Point Conception to the north and by the northern Channel Islands, about 20 miles (~32 km) offshore. The region is dynamic, with periods of low productivity along with seasonal upwelling events that support large and diverse phytoplankton blooms (Brzezinski & Washburn 2011). The surface-canopy-forming giant kelp *Macrocystis pyrifera* dominates nearshore reefs in the SBC. *M. pyrifera* biomass varies seasonally and interannually, with high growth rates and recruitment from spring to early summer and senescence and removal by storm disturbance from fall to early winter (Graham et al. 2007, Reed et al. 2008).

Cape Rodney-Okakari Point Marine Reserve in northeastern New Zealand sits at the northern extent of the Hauraki Gulf, which, similar to the SBC, is relatively protected from the open Pacific by Great Barrier Island and Little Barrier Island to the northeast, and by the Coromandel Peninsula to the east. Seasonal wind-driven upwelling and relaxation events support large offshore phytoplankton blooms in the winter and spring (Chang et al. 2003). Low-nutrient and low-chlorophyll subtropical water dominates the Hauraki Gulf during late summer and fall due to seasonal changes in the East Auckland Current and water column stratification (Zeldis et al. 2004). The stipitate kelp *Ecklonia radiata* is the dominant macroalga on rocky reefs in the region, where it forms mono-specific forests with dense subsurface canopies. Seasonal and interannual biomass variability in *E. radiata* occurs primarily through erosion of lamina (de Bettignies et al. 2013) driven by changes in temperature, nutrients, and exposure to waves (Mabin et al. 2013, Hann 2014). Experiments at both locations were planned to coincide with seasonal kelp sloughing in late summer and fall to maximize the possible kelp treatment effect.

2.2. Experimental design

Three common and abundant species of suspension feeders were chosen at each study location. In California, we used the tunicate *Styela montereyensis* (stalked tunicate), and the bivalves *Crassadoma gigantea* (rock scallop) and *Mytilus californianus* (mussel). In New Zealand, we used the sponge *Tethya burtoni* (golf ball sponge) and the bivalves *Perna canaliculus* (green-lipped mussel) and *Crassostrea gigas* (Pacific oyster). We collected *S. montereyensis* from Sterns Wharf in Santa Barbara, California at <5 m depth. *M. californianus* and *C. gigantea* were collected from the UC Santa Barbara seawater filtration system. *P. canaliculus* were gathered from intertidal rocks at Pakiri Beach, New Zealand. *C. gigas* were obtained from marine farms (Matakana Oyster Farm and Biomarine). *T. burtoni* were collected from subtidal reefs at Leigh.

Experiments were conducted in flow-through seawater tanks with tipping buckets that flushed water into each tank; CA tanks were 50 l in volume with 5 l flushes every 2 min (residence time = 20 min), and NZ tanks were 35 l volume with 5 l flushes every 2.5 min (residence time = 17.5 min). Food source and availability were manipulated in a factorial design with 3 replicates per treatment combination. Treatments were phytoplankton (2 levels: presence or absence) and kelp (2 levels: presence or absence; total n = 12 location^{-1}). Phytoplankton were excluded through the use of filtered seawater (CA: sand filtered; NZ: filtered to 10 µm with Arkal discs) versus raw seawater in the phytoplankton-present treatments. In the kelp-present tanks, we placed kelp (CA: 2 m *M. pyrifera* frond lengths; NZ: 2 whole *E. radiata* laminae) directly below the tipping buckets. The tipping buckets mechanically agitated the kelp, which was separated from the suspension feeders by a 1 cm^2 mesh to allow detached kelp particles to be flushed through the mesh and delivered to the suspension feeders. Kelp was replaced weekly for the duration of the experiments. In the CA experiment, surface canopy kelp fronds were collected weekly by boat from nearby reefs, held in water-filled 100 l plastic bins, and transferred within 1 h to a shaded flow-through seawater tank with a subsurface grate to maintain full submersion of the floating kelp. Portions of fronds were then moved from the holding tank to the experimental tanks within 24 h. In the NZ experiments, *Ecklonia* sp. were collected by snorkelers, kept in bags, and transferred to experimental tanks within 1 h. Average (±SE) weekly kelp biomass replaced in mesocosms was much higher than in adjacent natural kelp forests: 610 ± 19 g in CA and 516.6 ± 53.6 g in NZ. Kelp in the CA experiment was weighed after each removal to estimate lamina erosion rates. A single large experiment was conducted in CA from 19 July to 4 October 2013, while the NZ experiments were conducted in 4 separate trials from August to October (26 August–28 October, 11 October–2 December, and 4 November–20 December 2013, and 29 January–17 March 2014).

Each seawater tank contained multiple individuals of each suspension feeding species (CA: 30 *S. montereyensis*, 29 *C. gigantea*, and 30 *M. californianus* $tank^{-1}$; NZ: average of 7 [range 3–10] *C. gigas*, 8.6 *P. canaliculus* [range 8–10], and 2.7 *Tethya burtoni* [range 2–3] $tank^{-1}$ $trial^{-1}$). In the CA experiment, the shell free dry mass (SFDM) of suspension feeders relative to kelp canopy biomass in the mesocosms was within the range of that measured in the SBC (4.26–53.88 g SFDM kg^{-1} kelp canopy vs. 26.94 [±0.53 SE] g SFDM kg^{-1} kelp in mesocosms). Benthic suspension feeder biomass data was not available for NZ reefs. Bivalves were allowed to attach freely, *T. burtoni* were tied to raised mesh with nylon thread, and *S. montereyensis* were attached to ceramic tiles with cyanoacrylate glue. We attached numbered plastic tags to the bivalves (Coyer et al. 1999) to facilitate repeated size measurements. We measured growth of each organism (CA: length to nearest mm weekly; NZ: length and wet weight to nearest mg before and after each trial). To examine whether possible treatment differences were accompanied by changes in the isotope values of suspension feeder tissues, we collected samples of muscle tissue from 5 individuals of each species for $\delta^{13}C$ and $\delta^{15}N$ analysis at the beginning of the experiments and for each treatment at the end of each experiment. In the CA experiment, monthly water samples were collected from each tank to monitor chlorophyll *a* (chl *a*), POC, particulate organic nitrogen (PON), and $\delta^{13}C$ and $\delta^{15}N$ of POM. In the NZ experiments, chl *a* samples were collected once during each trial from 1 $tank\ treatment^{-1}$. POC, PON, $\delta^{13}C$ and $\delta^{15}N$ in the NZ experiments were sampled from 1 $tank\ treatment^{-1}$ on 2 October 2013 and 14 February 2014.

2.3. Sample preparation

Water samples were collected in clean polyethylene bottles. For POM and isotopic analyses, water samples were vacuum-filtered onto precombusted (450°C for 1 h) 25 mm glass fiber filters, dried at 60°C for at least 48 h, and acidified with 2 drops of 10% HCl to remove carbonates. For chl *a* analysis, we filtered water samples onto 0.45 µm pore size 47 mm diameter HAWP Millipore filters. Filters were kept frozen (CA: −20°C; NZ: −80°C) for up to 1 mo. Just prior to analysis, the filters were extracted in 90% acetone for 24 h at −20°C. The fluorescence of each extract was measured with and without acidification to determine chl *a* concentrations on a Turner Designs 10AU digital fluorometer that had been calibrated with pure chl *a* (SIGMA Chemical). In NZ, filters were extracted in 3:1 90% acetone:dimethylsulphoxide for 24 h at 4°C (Shoaf & Lium 1976). Concentration of chl *a* was determined spectrophotometrically, using the equations of Jeffrey & Humphrey (1975). Muscle tissues for isotopic analysis were dissected from organisms, rinsed in deionized water, dried for at least 72 h at 60°C, ground into a fine powder, and stored in glass scintillation vials until analysis (CA: Thermo-Finnigan Delta-Plus Advantage mass spectrometer in the Marine Science Institute Analytical Lab at the University of California Santa Barbara; NZ: Europa 20–20 update stable isotope mass spectrometer interfaced to a NA1500 Carlo Erba elemental analyzer by Isotrace Research at the University of Otago).

2.4. Data analysis

We calculated a growth rate for each individual organism as the slope of length versus time using least-squares linear regression. For each species we used ANOVA analyses to test for significant differences in growth rate, $\delta^{13}C$, and $\delta^{15}N$ across the full factorial cross of treatments: phytoplankton (fixed: presence or absence) and kelp (fixed: presence or absence) with tank, and in the NZ experiments trial, as nested random factors. Given $(1 - \beta) = 0.95$ and $\alpha = 0.05$, we had statistical power to detect moderate effect sizes (power ref) of $f = 0.29$ for the CA experiment and $f = 0.37$ for the NZ experiments. ANOVAs were also used to assess mortality among tank replicates and water parameters with sampling dates as a nested random factor for the CA data. Data were tested for assumptions of normality using the Shapiro-Wilks test and for homogeneity of variance using Levene's test. Results are presented as means ± SE unless otherwise stated.

3. RESULTS

3.1. Treatment effects on phytoplankton and POM

3.1.1. California

Temperature in the CA experimental tanks averaged 14.5 ± 0.01°C (range: 11.72–18.43°C). Chl *a* levels in the +phytoplankton tanks were typical of those found in the SBC (Brzezinski & Washburn 2011), averaging 2.9 ± 0.6 µg l^{-1} (range: 1.0–8.4 µg l^{-1}). As expected, the −phytoplankton treatments had

very low chlorophyll concentrations, averaging 0.0 ± 0.2 µg l^{-1} (range: −1.8 to 0.4 µg l^{-1}, n = 24; Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m614p021_supp.pdf), that were significantly lower than +phytoplankton seawater ($F_{1,36}$ = 76.19, p = 0.0001). The addition of kelp did not significantly affect chlorophyll levels ($F_{1,36}$ = 0.06, p = 0.82; Table S1).

POC and PON patterns paralleled those of chl *a* (Fig. S1). POC concentrations averaged 416 ± 35 µg l^{-1} (range: 167–730 µg l^{-1}, n = 24) in the +phytoplankton treatments, >5× higher than the −phytoplankton treatments (mean: 79 ± 6 µg l^{-1}; range: 32–176 µg l^{-1}, n = 24, $F_{1,36}$ = 289.78, p <0.0001). PON showed the same pattern, averaging 69 ± 6 µg l^{-1} (range: 26.4–123.0 µg l^{-1}, n = 24) in the +phytoplankton treatments and 12 ± 1 µg l^{-1} (range: 4–33 µg l^{-1}) in the −phytoplankton treatments ($F_{1,36}$ = 318.78, p < 0.0001). The presence of kelp did not significantly affect either POC or PON concentrations (POC: $F_{1,36}$ = 0.08, p = 0.78; PON: $F_{1,36}$ = 0.14, p = 0.72; Table S1).

The presence of kelp had no discernable effect on the isotope values of POM (δ^{13}C: $F_{1,36}$ = 2.86, p = 0.13; δ^{15}N: $F_{1,36}$ = 2.48, p = 0.15; Table S1, Fig. S1). POM ^{13}C and ^{15}N were both significantly enriched in the +phytoplankton treatments (δ^{13}C: −21.3 ± 0.2‰, $F_{1,36}$ = 351.56, p < 0.0001; δ^{15}N: 8.1 ± 0.3‰, $F_{1,36}$ = 95.83, p < 0.0001) compared to the −phytoplankton treatments (δ^{13}C: −24.3 ± 0.5‰; δ^{15}N: 4.5 ± 0.6‰). Although shed particles were not detectable in suspension via any of the measured POM components, kelp eroded during the experiment at a mean rate of 11 ± 3 g wet mass d^{-1}.

3.1.2. New Zealand

Chl *a* levels in NZ were much lower than the CA values across all treatments, and treatments did not differ significantly ($F_{3,8}$ = 0.40, p = 0.76; Table S2), averaging 0.48 ± 0.1 µg l^{-1} (n = 6) in the +phytoplankton treatments and 0.39 ± 0.0 µg l^{-1} (n = 6) in the −phytoplankton treatments (Fig. S2). Tank temperatures averaged 18.29 ± 0.21°C (range: 14.9–22°C).

POC and PON concentrations in the NZ experiments were low across all treatments and there were no statistically significant differences among treatments (POC: $F_{3,4}$ = 0.33, p = 0.81; PON: $F_{3,4}$ = 0.19, p = 0.90; Table S2). POC averaged 159 ± 13 µg l^{-1} in the +phytoplankton/+kelp treatment, 198 ± 22 µg l^{-1} in the +phytoplankton/−kelp treatment, 209 ± 43 µg l^{-1} in the −phytoplankton/+kelp treatment, and 185 ± 14 µg l^{-1} in the −phytoplankton/−kelp treatment. PON averaged 25.4 ± 5.3 µg l^{-1} in the +phytoplankton/+kelp treatment, 30.0 ± 5.2 µg l^{-1} in the +phytoplankton/−kelp treatment, 26.1 ± 3.3 µg l^{-1} in the −phytoplankton/+kelp, and 24.1 ± 0.3 µg l^{-1} in the −phytoplankton/−kelp treatment (Fig. S2). No statistically significant differences were detected in δ^{13}C or δ^{15}N POM among treatments in the NZ experiments (δ^{13}C: $F_{3,4}$ = 2.58, p = 0.19; δ^{15}N: $F_{3,4}$ = 1.25, p = 0.40; Table S2). δ^{13}C isotope values averaged −21.1 ± 0.4‰ (n = 4) in the +phytoplankton treatments and −20.4 ± 0.3‰ (n = 4) in the −phytoplankton treatments. δ^{15}N isotope values averaged 6.0 ± 0.6‰ (n = 4) in the +phytoplankton treatments and 7.2 ± 0.3‰ (n = 4) in the −phytoplankton treatments (Fig. S2).

3.2. Growth

Growth data were not normally distributed, and 2 species, *Crassadoma gigantea* and *Mytilus californianus*, departed significantly from homogeneity of variances. Since transformation did not markedly improve this, and ANOVA is robust to deviations from normality (even when sample sizes are small, and to heteroscedasticity with n > 20; Underwood 1997), we ran the analyses with no transformation for ease of interpretation.

In the CA experiment, kelp had no significant effect on growth of any species of suspension feeder (Fig. 1, Table 1). All species grew well when phytoplankton was provided, but growth rates were near zero in the −phytoplankton treatments, regardless of the presence of kelp (Table 1). The differences in growth between +/−phytoplankton treatments were highly significant for each species (Tukey's HSD, p < 0.001 for each species). The water intake in one of the +phytoplankton/+kelp tanks failed and most of the animals died about 1 mo into the experiment, so tank 1 growth rates were only recorded for 1 mo.

Linear growth in the phytoplankton presence treatments was highest for the stalked solitary tunicate *Styela montereyensis*, followed by the rock scallop *C. gigantea*, and the mussel *M. californianus* (Fig. 1). All species experienced growth rates close to 0 mm d^{-1} in the −phytoplankton treatments. In the ANOVA analyses, no significant interactions were found and phytoplankton availability had a significant positive effect on *C. gigantea*, *S. montereyensis*, and *M. californianus* growth rates (Table 1).

In the NZ experiments, none of the species exhibited clear differences in growth across treatments (Fig. 1). The sponge *Tethya burtoni* lost mass in all treatments, but conserved significantly more mass in +kelp treatments with no interactions between treat-

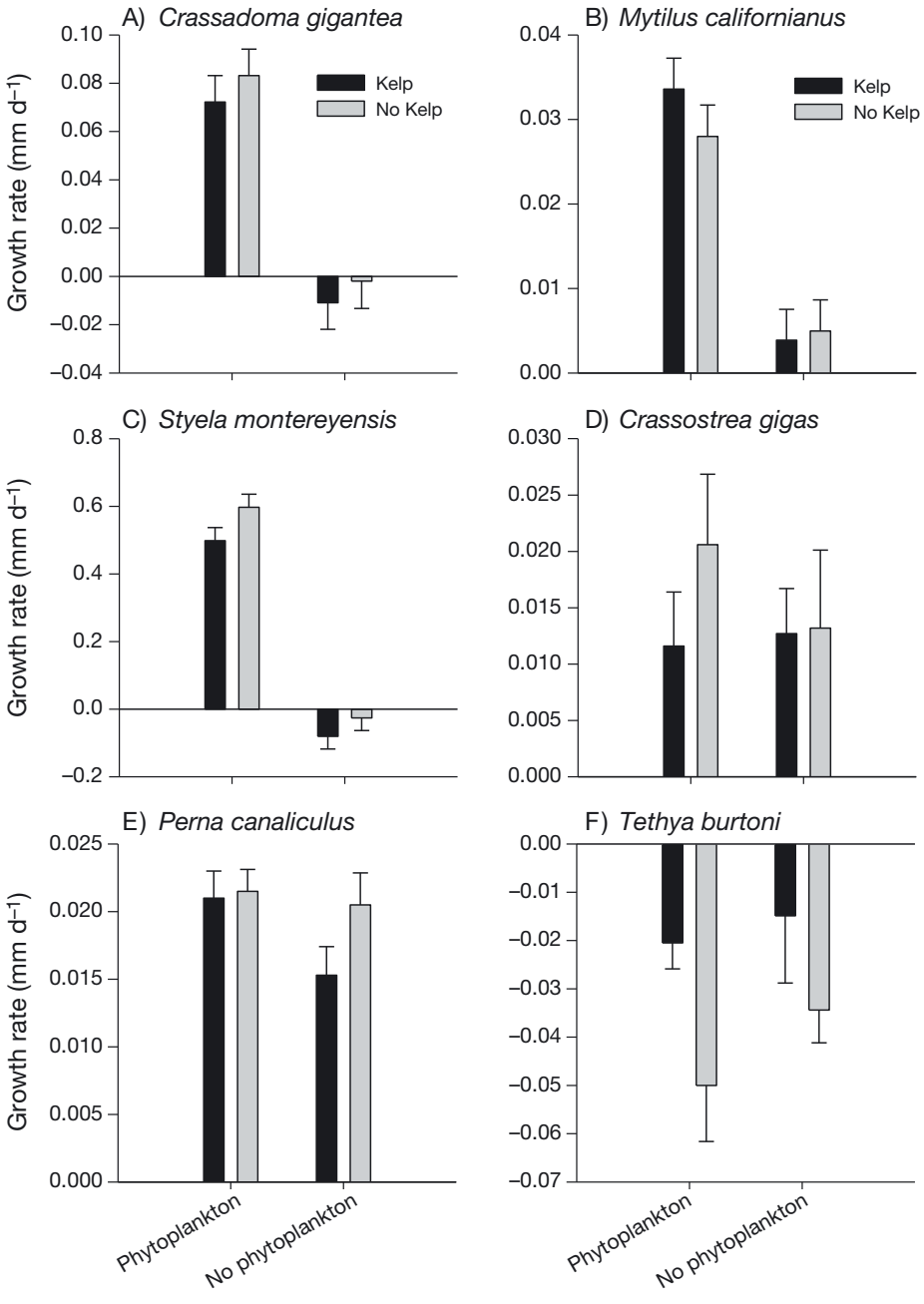

Fig. 1. Mean (±SE) growth rate of California species (A) *Crassadoma gigantea*, (B) *Mytilus californianus*, and (C) *Styela montereyensis*; and New Zealand species (D) *Crassostrea gigas*, (E) *Perna canaliculus*, and (F) *Tethya burtoni* within each treatment. California species' growth rates are averaged from individual lengths (mm) measured weekly over the course of the experiment. New Zealand species' growth rates are averaged from individual lengths (mm) of bivalves and weights (g) of *T. burtoni* measured at the beginning and end of each trial

ments (Table 1). The oyster *Crassostrea gigas* showed a significant interaction between trial number and kelp, but the magnitude of this effect was low and overall growth in all treatments was low for this species.

3.3. Mortality

Mortality was generally low across species and treatments except in the case of *C. gigantea* (CA) and *T. burtoni* (NZ) (Fig. 2). *C. gigantea* mortality was 4.5 ± 2.9% in the +phytoplankton/+kelp treatment, 8.0 ± 6.4% in the +phytoplankton/−kelp treatment, 31.4 ± 7.9% in the −phytoplankton/+kelp treatment, and 13.0 ± 1.7% in the −phytoplankton/−kelp treatment. *C. gigantea* mortality was significantly higher in the −phytoplankton treatments (ANOVA, $F_{1,8}$ = 8.81, p = 0.02; Table S3). Mortality of *T. burtoni* was 28.8 ± 15.6% in the +phytoplankton/+kelp treatment, 44.8 ± 15.7% in the +phytoplankton/−kelp treatment, 21.2 ± 9.4% in the −phytoplankton/+kelp treatment,

Table 1. Analysis of variance comparing the growth of species with fixed factors phytoplankton (presence or absence) and kelp (presence or absence) fully crossed with tank as a nested random factor (4 levels) and trial as a crossed random factor for the New Zealand species

	Crassadoma gigantea				*Mytilus californianus*				*Styela montereyensis*			
Source	df	MS	*F*	p	df	MS	*F*	p	df	MS	*F*	p
Phytoplankton	1	0.56	68.43	<0.0001	1	0.06	52.73	0.0002	1	28.84	307.83	<0.0001
Kelp	1	0.01	1.49	0.26	1	0.00	0.26	0.62	1	0.29	3.08	0.12
Phytoplankton × Kelp	1	0.00	0.03	0.86	1	0.00	0.62	0.46	1	0.01	0.06	0.8
Tank [Phytoplankton, Kelp]	8	0.01	1.07	0.38	7	0.00	1.45	0.18	8	0.09	0.91	0.51
Residual	304	0.01			309	0.00			316	2.75		
	Crassostrea gigas				*Perna canaliculus*				*Tethya burtoni*			
Source	df	MS	*F*	p	df	MS	*F*	p	df	MS	*F*	p
Phytoplankton	1	0.00	0.04	0.85	1	0.00	0.69	0.49	1	0.01	1.67	0.29
Kelp	1	0.00	0.07	0.80	1	0.00	0.89	0.44	1	0.01	20.01	0.02
Phytoplankton × Kelp	1	0.00	1.72	0.20	1	0.00	0.55	0.53	1	0.00	0.73	0.45
Trial	3	0.00	0.69	0.60	2	0.00	0.95	0.53	3	0.01	2.17	0.29
Trial × Phytoplankton	3	0.00	4.56	0.12	2	0.00	1.1	0.47	3	0.00	4.60	0.12
Trial × Kelp	3	0.00	14.84	0.03	2	0.00	2.91	0.26	3	0.00	0.94	0.52
Trial × Phytoplankton × Kelp	3	0.00	0.04	0.99	2	0.00	2.87	0.07	3	0.00	0.31	0.82
Tank [Phytoplankton, Kelp, Trial]	24	0.00	0.14	1.00	24	0.00	0.64	0.90	28	0.00	0.92	0.58
Residual	290	3.17			238	0			75	0		

and 8.1 ± 4.1% in the −phytoplankton/−kelp treatment, with no significant effect of treatment.

3.4. Tissue isotopes

Species with higher relative growth rates within each study site showed slight differences in isotope composition between phytoplankton presence and absence treatments (Figs. S3 & S4). No kelp effect was detected in tissue isotope samples (Tables S4 & S5). The fastest growing CA species, *S. montereyensis*, had depleted $\delta^{13}C$ values (ANOVA; $F_{1,8} = 51.10$, $p < 0.0001$) and enriched $\delta^{15}N$ values (ANOVA; $F_{1,8} = 8.52$, $p = 0.02$) in the −phytoplankton treatments compared to +phytoplankton treatments.

4. DISCUSSION

Our results show that living kelp, even if it is immediately proximal to benthic suspension feeding invertebrates, is not a significant source of food to them, and provide further evidence that plankton, including phytoplankton, is the main source of trophic support for kelp forest invertebrates in these experimental conditions. Kelp had no effect on the growth, mortality, or isotope composition of the suspension feeders that would indicate a trophic effect. Instead, the presence of kelp actually seemed to increase the mortality of some species, possibly due to bioactive compounds that can be produced by kelps (reviewed by Ioannou & Roussis 2009). The exception was the NZ sponge *Tethya burtoni*, which lost less tissue mass in the presence of kelp. This result may reflect an increase of DOC and bacterioplankton in the kelp treatments, since sponges are known to consume both DOM (de Goeij et al. 2013) and bacteria (Hill & Hill 2009). While kelp can have a positive effect on the abundance of suspension feeders on reefs, the mechanisms of this effect are likely not trophic but rather through shading and consequent suppression of understory algae, releasing invertebrates from competition for space (Arkema et al. 2009, Miller et al. 2015, 2018).

Growth of the mussel *Mytilus californianus* and the rock scallop *Crassadoma gigantea* in the +phytoplankton treatments were similar to rates measured in the field (Leighton 1979, MacDonald & Bourne 1989, Blanchette et al. 2007). No previous growth studies were found for *Styela montereyensis*, but the solitary tunicate had the lowest mortality and highest growth rates in the +phytoplankton treatments compared to other species in this study.

In NZ species, growth was low across all treatments, likely as a result of the low phytoplankton abundance as reflected in chl *a* levels in the unfiltered seawater. Growth rates of *Perna canaliculus* were much lower than values reported in growth studies around NZ (Hickman 1979, Ren & Ross 2005), whereas *Crassostrea gigas* growth rates were within the range of expected values for the chlorophyll con-

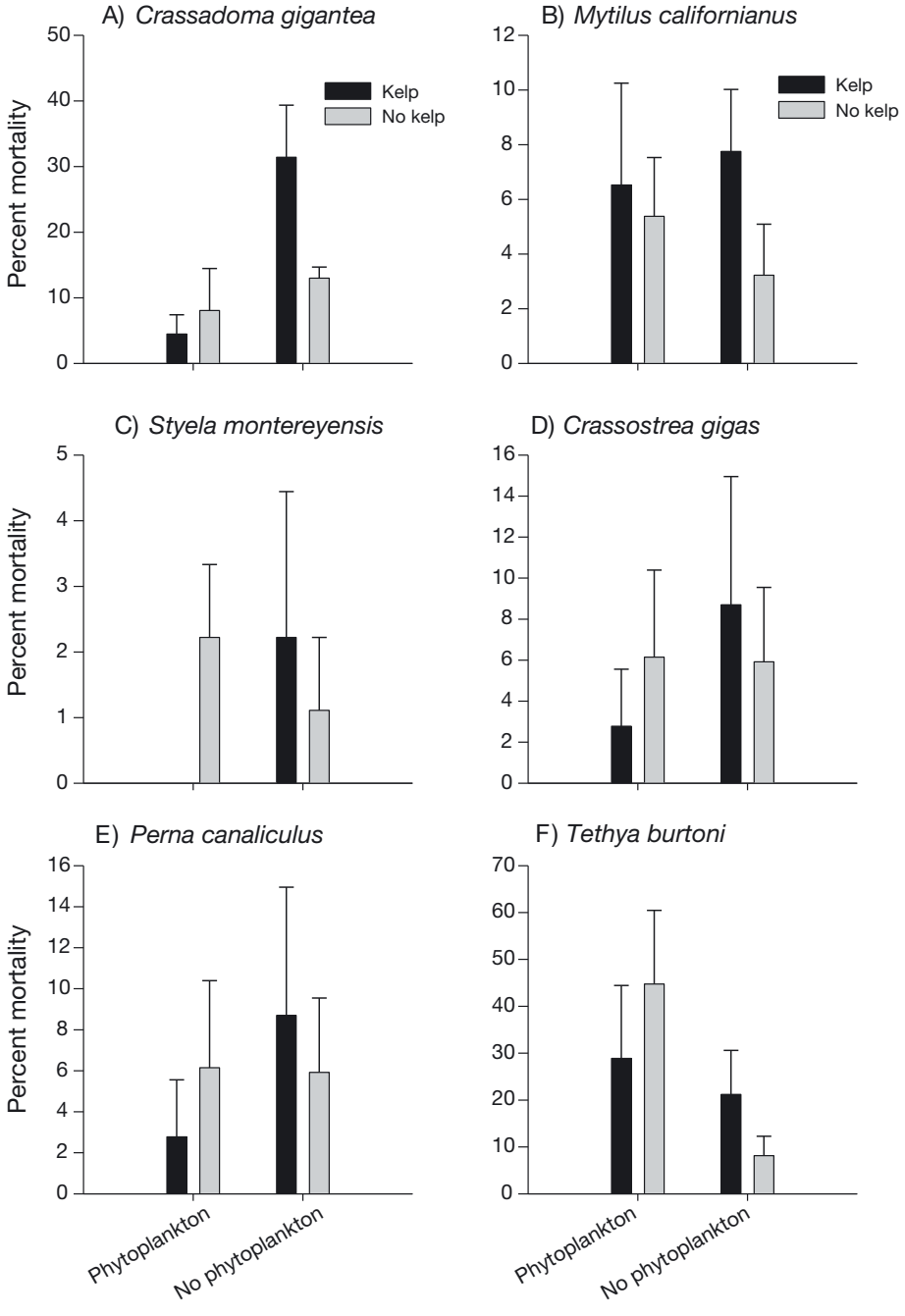

Fig. 2. Mean (±SE) percent mortality of California species (A) *Crassadoma gigantea*, (B) *Mytilus californianus*, and (C) *Styela montereyensis*; and New Zealand species (D) *Crassostrea gigas*, (E) *Perna canaliculus*, and (F) *Tethya burtoni* within each treatment over the course of each experiment. *P. canaliculus* trial 2 mortality data was excluded because of high mortality due to water pump failure

centrations we measured (Brown 1988). No previous growth studies were available for *T. burtoni*. Satellite-derived chlorophyll data from a 25 m^2 pixel near the Goat Island seawater intake showed much higher long-term average chlorophyll levels at 1.26 g m^{-2}, corresponding to ~4.2 µg l^{-1} assuming a 30 m water column (MODIS, sampling period: 4 July 2002–31 October 2015; coordinates: 174.799° N, 36.262° W), suggesting that the experimental period was anomalous in this regard. Water samples collected within this area at 6 m depth on 4 September 2013 showed 0.36 µg l^{-1} chl *a*, further suggesting an anomalously low chlorophyll period during the course of the NZ experiments (N. Shears unpubl. data). Although this limited our ability to assess the effect of phytoplankton on growth of suspension feeders, it has been suggested that macroalgal detritus becomes a more important food source during such low-productivity periods (Marin-Leal et al. 2008, Marchais et al. 2013, Feehan et al. 2018). Our results did not support this.

Kelp did not affect POC or PON concentrations or the C and N isotope values of the POM, despite a much higher kelp biomass per unit area or volume in the experimental tanks relative to kelp forest ecosystems. For example, kelp biomass averaged 6.08 ± 0.36 kg wet weight m^{-2} at Mohawk Reef in the SBC (SBC LTER data 2002–2015; Rassweiler et al. 2008) and 5.5 ± 1.1 kg wet weight m^{-2} at Goat Island, near Leigh Marine Lab (N. Shears unpubl. data 2012–2015). Given the depth of the water column at each site, this translates to ~1 kg kelp m^{-3} seawater. In comparison, the experimental tanks at both locations contained an order of magnitude greater kelp biomass per volume seawater (~10 kg kelp m^{-3}). Moreover, seawater residence time in the experimental tanks was ~20 min, very long considering that seawater residence time for an entire kelp forest off Santa Barbara (~300 × 180 m, 5–9 m deep) averaged 1.1 h (Fram et al. 2008). The total biomass of suspension feeders in our mesocosms were also well within the range of biomasses found on Santa Barbara reefs relative to kelp biomass. While we had no data on kelp degradation rates for the NZ experiments, in the CA experiments kelp biomass degraded at a rate equivalent to ~106 g C m^{-2} yr^{-1}, well within the ranges of detrital production estimated in other studies (reviewed by Krumhansl & Scheibling 2012). Estimated kelp-derived carbon shed from live kelp comprised <1% of the total available POC at Mohawk Reef (Yorke et al. 2013), suggesting that even with high kelp biomass, small kelp-derived particles are not an abundant food source for reef suspension feeders. In a 4 yr study of monthly POM isotope composition across reefs varying greatly in kelp biomass, $\delta^{13}C$ and $\delta^{15}N$ of POM did not track changes in kelp biomass, but were highly correlated with chlorophyll concentrations (Page et al. 2008). At Mohawk reef, POM $\delta^{13}C$ was likewise correlated with chlorophyll concentration and phytoplankton primary production rates (Miller et al. 2013). Collectively, these results lend no support to a significant role of living giant kelp as a source of particulate detritus usable by suspension feeders, in contrast to previous reports (reviewed by Miller & Page 2012).

Kelp, as a highly conspicuous form of primary production, has often been assumed to form the base of the kelp forest food web. Likewise, as the most abundant organisms on many kelp-forested reefs (Newell et al. 1982, Reed et al. 2015), suspension feeders seem well positioned to benefit from kelp-derived carbon that might be shed from the kelp canopy. Our experimental approach to testing this idea circumvents issues pertaining to offering suspension feeders environmentally unrealistic concentrations of artificially produced kelp particles, and concerns about appropriate end-members, isotope routing, and fractionation factors that arise when using isotopes in 2-source mixing models to interpret field-collected consumer natural abundance isotope values (Miller & Page 2012). Our laboratory experiments did not support the commonly hypothesized route of kelp detritus shed from living kelp as a food source for suspension feeders (Duggins et al. 1989, Kaehler et al. 2006, Salomon et al. 2008).

Field experiments in which suspension feeders were grown under transplants of live or artificial kelp showed a similar result: no effect of kelp on their growth (Duggins & Eckman 1994). Duggins & Eckman (1994) postulated that this negative result could have been due to either the small scale of their experiments and influxes of kelp detritus from surrounding kelp stands, or the poor food quality of fresh (recently produced) kelp particles relative to aged particles. Our results also do not exclude the possibility that an accumulated pool of kelp detritus may benefit suspension feeders in the ocean, and this idea has motivated studies offering artificially generated kelp detritus to suspension feeders. For example, Feehan et al. (2018) ground up the bull kelp *Nereocystis luetkeana*, aged the resulting slurries for 1 wk, and fed them to sea urchin larvae at particle densities of 5000 or 3750 particles ml^{-1}, based on recommendations for culturing urchin larvae on phytoplankton. Interestingly, the larvae grew well on the kelp particles, but these results do not suggest that sea urchin larvae obtain a significant fraction of their diet from kelp detritus in the field. Feehan et al. (2018) cited Ramshaw et al. (2017) to assert that kelp detritus makes up 33% of the POM up to 30 km off Vancouver Island in summer. Ramshaw et al. (2017) used isotope data in Bayesian mixing models to conclude that kelp detritus contributions to POM are very high off Vancouver Island, and do not vary much in magnitude with distance away from the kelp forests, which are restricted to a very narrow fringe ($\ll$1 km) around the coast (Druehl 1978). Indeed, kelp contributions to POM in summer were estimated to be ~30% both inside the kelp forest itself and 30 km offshore (Ramshaw et al. 2017, their Fig. 10). This result could be due to a large background pool of accumulated kelp detritus, but the average age of such detritus would presumably be high, and although food value of detritus can initially increase due to microbial colonization, it decreases over the longer term (Tenore et al. 1984). The lack of any kind of relationship, moreover, between the abundance of kelp and

putative kelp detritus abundance makes these results uncertain, and better and more direct estimates and trophic tracers of kelp detritus in POM from the field are needed to contextualize laboratory results such as those in Feehan et al. (2018).

Assessing the relative importance of food sources to suspension feeders has been challenging because the components of POM are difficult to separate, and gut content analyses of suspension feeders is difficult. Carbon stable isotope values have often been used to address the importance of kelp and other macrophytes to coastal food webs, but their interpretation can be problematic if they rely on untested assumptions (reviewed by Miller & Page 2012). Stable isotope data is useful for estimating contributions to coastal food webs, but requires information about source variability in isotope value and ancillary data on source abundance. Direct evidence for suspension feeder utilization of kelp detritus is scarce. Transplanting suspension feeders to plots containing natural or artificial kelps showed no effect of kelp on their growth rate, similar to our results (Duggins & Eckman 1994), while experimental feeding studies suggest that although suspension feeders could efficiently digest powdered kelp (imitating detritus) they fed preferentially on phytoplankton (Cranford & Grant 1990, Levinton et al. 2002). Evidence for the trophic importance of phytoplankton to suspension feeders, in contrast, is fairly abundant (reviewed by Gili & Coma 1998). Phytoplankton, including small photosynthetic prokaryotes, are an important part of the natural diet of suspension feeding sponges, cnidarians, bivalves, polychaetes, and ascidians (reviewed by Bayne & Hawkins 1992, Dame 1996, Gili & Coma 1998, Witman et al. 2004). Heterotrophic bacteria and zooplankton may also be important components of suspension feeder diets (Pile et al. 1996, Gili & Coma 1998).

While macroalgae are generally considered more palatable than terrestrial detritus, mixed phytoplankton assemblages have much higher nutritional content (Duarte 1992). Macroalgae have high C:N ratios relative to phytoplankton and often contain unpalatable compounds such as phlorotannins (Tugwell & Branch 1989, Amsler & Fairhead 2005), that limit or inhibit direct grazing on kelps (Mann 2000). The food value of macroalgae can increase with aging due to bacterial colonization, but results testing this hypothesis are mixed (Dethier et al. 2014). Most kelp tissue, therefore, likely ends up in the detrital pool (Krumhansl & Scheibling 2012), and although we know that kelp detritus is a significant trophic resource for beach (Dugan et al. 2003) and deep-sea (Britton-Simmons et al. 2012, Krumhansl & Scheibling 2011, Filbee-Dexter & Scheibling 2017) food webs, its ultimate fate in the coastal habitats where kelp forests thrive remains poorly known. Given the growing evidence against kelp detritus as a significant food source for reef suspension feeders, we continue to suggest more stringent examination of the assumptions behind stable isotope studies of this topic in the future (Miller & Page 2012), and exploration of alternative pathways of utilization of kelp detritus in subtidal ecosystems.

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