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ARTICLE

What Is the Relative Importance of Phytoplankton and Attached Macroalgae and Epiphytes to Food Webs on Offshore Oil Platforms?

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Abstract

Offshore oil platforms function as artificial reefs, but little is known about the food webs that fuel platform-dwelling biota. Here, we use carbon and nitrogen isotopes in tissues of biota from two offshore oil platforms to estimate the importance of phytoplankton and platform-associated macroalgae and epiphytic microalgae to the diets of platform-dwelling consumers. Although the consumption of macroalgae was indicated for small, mobile consumers including crabs, amphipods, and harpacticoid copepods, both a Bayesian mixing model and temporal changes in isotope composition identified phytoplankton as the most important basal resource for these consumers. Sessile suspension-feeding barnacles and oysters consumed phytoplankton and epiphytes, and probably redirected large amounts of pelagic production to other consumers. Secondary consumers including syllid polychaetes and the blennies, Molly Miller *Scartella cristata* and Tessellated Blenny *Hypsoblennius invemar*, exhibited a distinct contribution from epiphytes although large ranges in all potential basal resources were observed. Elemental and isotope analysis of the gut contents of individuals indicated that the nektonic Gray Triggerfish *Balistes capriscus* was omnivorous, directly consuming reef-derived macroalgae and epiphytes as well as animal tissue. Although we found that reef-derived resources entered benthic and nektonic food webs surrounding platforms, phytoplankton was the dominant basal resource fueling platform-dwelling communities at the time of our study, and no consumer studied specialized on a diet of red macroalgae. If these findings are generally representative, platform-derived benthic algae would not be integral to food-web function on artificial reefs, and reef function should be similar in areas both favorable to and unfavorable to in situ algal growth.

The term artificial reef refers to structures constructed or placed in waters for the purpose of enhancing fishery resources and commercial and recreational fishing opportunities. Some artificial reefs are built exclusively for this purpose. Objects constructed for other purposes also act as artificial reefs. In the Gulf of Mexico (Gulf) for example, over 4,000 standing oil and gas platforms function as artificial reefs. Like other artificial reefs, platforms support abundant fouling communities of

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reef-dependent biota. However, platforms differ from most artificial reefs in that they rise to and above the sea surface allowing access to the photic zone for benthic primary producers that inhabit platform surfaces. In the Gulf, reef-associated primary producer communities are dominated by red (e.g., *Polysiphonia* sp.) and green (e.g., *Derbesia* sp.) macroalgae and epiphytic microalgae including diatoms and cyanobacteria (Gallaway and Lewbel 1982; Lewbel et al. 1987; Carney 2005). However, the biomass of epibenthic communities on platforms is typically dominated by large, long-lived, sessile consumers, including barnacles (e.g., *Balanus tintinnabulum*) and bivalves (e.g., *Chama macerophylla* and *Ostrea* spp.), that act as foundation species supporting a high abundance and diversity of small, mobile, reef-dependent organisms including amphipods, tanaids, harpacticoid copepods, polychaetes, crabs, and small reef-dwelling fishes (Gallaway and Lewbel 1982; Lewbel et al. 1987).

However, the role of benthic primary producers in food webs on and near artificial reefs remains poorly understood. Benthic macroalgae will be incorporated into the food web as a basal resource if grazed and assimilated by reef-dwelling consumers, including by suspension feeders that filter macroalgal detritus (Kang et al. 2008; Schaal et al. 2010). Although green algae generally lack chemical or physical defenses and are, therefore, susceptible to grazing (McConnell et al. 1982), some species of red algae are unpalatable (Kain and Norton 1990) and may not contribute to the food web. Benthic microalgae are generally considered highly nutritious for consumers (Miller et al. 1996), and epiphytic microalgae could be directly grazed by mobile consumers from surfaces associated with reefs or consumed by suspension feeders after entrainment into the water column. Alternatively, phytoplankton may be consumed by reef-dwelling suspension feeders (e.g., barnacles and bivalves: Gallaway and Lewbel 1982) and then redirected to platforms in the form of feces or pseudofeces (Beaver 2002; Cheung et al. 2010). Small, mobile grazers may also consume phytoplankton directly after it adheres to surfaces or is trapped in crevices, or as a byproduct of suspension feeding. Taxonomically similar grazing consumers studied in other environments select basal resources (Pascal et al. 2009), but the resource of choice may change depending on habitat, environmental factors, and availability (Galván et al. 2008). Studies of food webs in hard-bottom ecosystems have described several possible and variable trophic pathways for phytoplankton and reef-associated algae. For example, algae growing on hard structures contribute to the diet of nearby nonreef-dwelling consumers (Kang et al. 2003; Behringer and Butler 2006; Doi et al. 2008; Fukumori et al. 2008), and phytoplankton or epiphytes may be important basal resources to consumers inside dense macroalgal beds (Kang et al. 2008; Golléty et al. 2010; Schaal et al. 2010). However, the relative importance of phytoplankton and endemic micro- and macroalgae to platform-based food webs has not been investigated.

Resolution of the role played by benthic algae on platforms may provide insight into the contribution that these structures make in the trophic dynamics in the Gulf and elsewhere. Reef-associated nekton are routinely found in much higher abundances within ~60 m of offshore oil platforms than in open water (Stanley and Wilson 1996; Boswell et al. 2010), and this high abundance may be due to increased reef-based food resources that enhance biomass production (i.e., the production hypothesis for artificial-reef effects). Alternatively, nekton may aggregate to artificial reefs from surrounding areas to seek refuge from predators (i.e., the attraction hypothesis: Bohnsack 1989; Polovina 1989). These hypotheses are not mutually exclusive, and both processes may contribute to the enhancement of secondary production (Pickering and Whitmarsh 1997; Wilson et al. 2001). Organic matter produced by benthic micro- and macroalgae will contribute to and enhance a production-based, artificial-reef effect if benthic algae are incorporated as a basal resource into the diets of organisms living on and around platforms. If so, artificial-reef function may be linked to its endemic algae. However, if benthic algae are unpalatable or are consumed in relatively low amounts, then phytoplankton will serve as the dominant basal resource, and reef function would be less dependent upon reef-associated algae and the factors that control its productivity, composition, and biomass. The conversion of platforms to artificial reefs has been proposed as a way to enhance conservation in the deep sea (Macreadie et al. 2011), and shading in shallow water affects the community structure of epibiota by reducing macroalgae and altering epifaunal communities (Glasby 1999). Still, current understanding makes it difficult to predict artificial reef function under these conditions.

Basal resource determination and trophic interactions can be quantified using natural abundance isotope analysis. The ratios of heavy to light stable isotopes "track" food sources through a food web and determine trophic relationships among members of food webs (Peterson 1999; Fry 2006). Metabolic differences in primary producers, such as phytoplankton and benthic microalgae, contribute to variation in the composition of naturally occurring isotopes. The low velocity of water in the benthic boundary layer partially equalizes uptake of heavy and light isotopes by benthic microalgae, while phytoplankton obtain nutrients from the water column opportunistically (France 1995). As a result, epiphytic microalgae are generally enriched in the heavy isotopes (^{13}C and ^{15}N) while phytoplankton are relatively depleted. Moreover, many species of red algae (Rhodophyta) are depleted in carbon relative to phytoplankton and epiphytic microalgae due to differences in inorganic carbon sources (Raven et al. 1995). When basal resources are sufficiently different from one another, isotope analysis can be useful in determining the contribution of each resource to the diet of consumers.

This study was designed to assess the role of platform-based benthic algae in the food webs of communities residing directly on platforms in the Gulf. Two standing, operational oil platforms were examined. Both support fouling communities that span the entire water column. Dual carbon (C) and nitrogen (N) stable isotope analysis was performed on potential basal resources and consumers to test the null hypothesis that endemic primary

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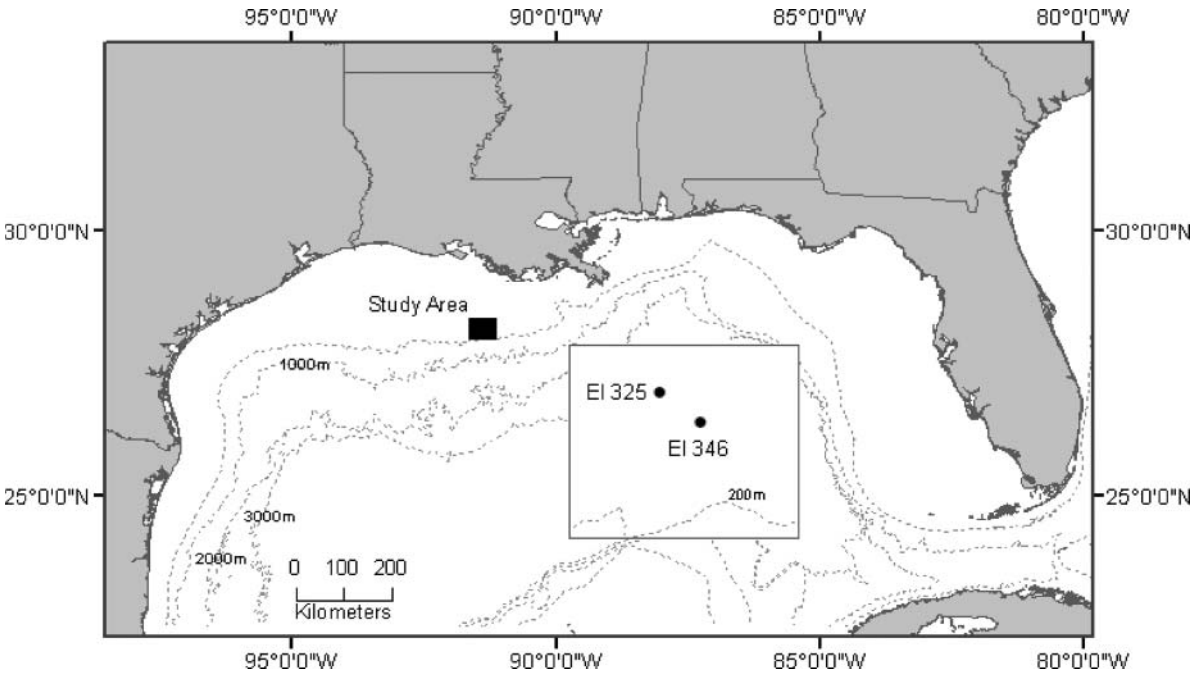


FIGURE 1. Location of study area and oil platforms sampled (insert) in the Gulf of Mexico.

production does not contribute to the diet of reef-dwelling consumers on platforms.

METHODS

The study site was located approximately 130 km off the coast of Louisiana in the Eugene Island (EI) oil field near 28°14′10″N, 91°24′70″W in the northern Gulf (Figure 1). Two representative standing operational oil platforms located on EI blocks 325 and 346 were chosen for study. These platforms began production in 1989 and 1998, respectively, and they are located near the continental shelf edge in water depths of 76 m (EI 325) and 95 m (EI 346).

Sampling procedures.—Water-column particulate organic matter (WPOM) was sampled during quarterly research cruises from the spring of 2009 to the winter of 2010 (i.e., spring 2009, summer 2009, fall 2009, and winter 2010) around one or both platforms. Another collection was made in September 2009 when platform-dwelling biota were collected (see below). The WPOM was obtained with a 30-μm-mesh plankton net, towed for 5-min intervals at discrete depths ~250 m from platforms. Tows were repeated two or three times and collections were then pooled. The samples were immediately frozen and stored at −20°C. Particulate organic matter was filtered to the <125-μm size fraction using a Whatman glass filter. Samples were fumed with HCl to dissolve inorganic carbonates before dual isotope analysis. Recent work in the Gulf indicated that acidification does not affect the stable isotope $\delta^{15}N$ in WPOM (Grippo et al. 2011), and we found identical results in preliminary WPOM collections (S. T. Daigle, unpublished data). The WPOM contained phytoplankton and was used as a surrogate for phytoplankton isotopic composition.

In September, reef-dependent communities were sampled by SCUBA divers on two legs of each platform at 0-, 6-, 12-, 18-, and 30-m depths. At each depth, divers manually removed barnacles and oysters (and incidentally resident organisms) from the surfaces of the platform legs, placing the contents into 250-μm-mesh bags. Contents were frozen immediately and stored at −20°C. In the laboratory, samples were rinsed 2–3 times over 20-, 63-, and 250-μm-mesh stacked sieves to remove and retain organisms attached to barnacles and oysters. Epiphytic microalgae were extracted from the 20-μm fraction using a swirl and decant method following Galván et al. (2011) in which the contents of the sample that settle quickly after disturbance (i.e., heavier sediment and shell fragments) remain in one dish, while the more buoyant contents (i.e., epiphytes) are poured off into another. Epiphytes in the solution were collected on a Whatman glass filter and dried at 75°C for at least 48 h. Samples were fumed with HCl to dissolve inorganic carbonates. The shells of barnacles and oysters were also scraped with forceps to remove attached macroalgae. Using a dissection microscope, samples were cleaned of shell and debris and visually separated into categories of red or green macroalgae. Resident, cryptic consumers were removed from sieves and identified to the lowest practical taxon. Amphipods in two families (Stenothoidae and Melitidae), four species of crab (*Teleophrys pococki*, *Pseudomedaeus agassizii*, *Pachygrapsus transverses*, and *Micropanope nuttingi*), polychaetes in one family (Syllidae), harpacticoid copepods as a composite taxon, and two blenny species (Molly Miller *Scartella cristata*

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and Tessellated Blenny *Hypsoblennius invemar*) were selected for stable isotope analysis. Entire invertebrates and muscle tissue from fishes were used in the analysis. Individuals of the same taxon collected from a particular platform, leg, and depth were pooled into a single sample (see Tables 1 and 3 for sample sizes). The number of individuals pooled in each sample ranged from 2 to 40 for amphipods, one to four for all crabs, 20 to 100 for syllid polychaetes, >400 for harpacticoid copepods, and was always one for blennies. Numbers of individuals depended both on the availability of organisms in a sample and the mass of individuals. Crabs were acidified using HCl to remove carbonates. The depressor muscle of the tergum of barnacles (*Balanus tintinnabulum*) and the central adductor muscle of oysters (*Chama* cf. *macerophylla* and *Ostrea* sp.) were pooled from up to five individual barnacles and oysters from each depth for analysis.

Four specimens of Gray Triggerfish *Balistes capriscus* (a reef-dependent omnivore) were also collected near platforms by spear-fishing and hook and line in September and December 2009 as a representative of the surrounding reef-dependent nekton community. Muscle tissue was extracted from the dorsal posterior region of each fish and stored at −20°C. The stomachs were removed immediately upon capture and stored in liquid nitrogen. In the laboratory, stomach contents of each fish were examined and descriptive records of the contents were taken. All contents of an individual stomach were pooled together into one sample for isotopic analysis.

To permit the examination of temporal trends in isotope composition, a second collection of reef-dwelling biota was taken from one leg of each platform by free divers in April 2010. Platforms were sampled at 1- and 5-m depths, and producer and consumer samples were treated as above. Not all taxa were available in both September and April collections and sample sizes in April were smaller (see Tables 1 and 2).

Data analysis.—Stable isotope analysis results were determined by the following equation:

$$\delta^{13}\text{C or } \delta^{15}\text{N} = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1{,}000,$$

where R_{sample} is the ratio of the heavy to light isotopes in the sample (i.e., $^{13}C/^{12}C$ and $^{15}N/^{14}N$) and R_{standard} is the ratio of the heavy to light isotopes. PeeDee limestone for C and nitrogen gas in the atmosphere for N were used as standards.

Phytoplankton (i.e., WPOM) δ^{13}C and δ^{15}N from quarterly collections and September were compared with one-way ANOVA and Tukey's pairwise comparisons test to determine whether isotope composition varied over time. Isotopes δ^{13}C and δ^{15}N of primary producers were also compared with each other with one-way ANOVA and Tukey's test to determine whether isotopic composition differed among taxa. Primary producers collected in September and April (or for phytoplankton, quarterly samples) were compared in separate tests. We used *t*-tests (or Mann–Whitney *U*-tests for data that failed normality tests) for platform-dwelling producers and consumers to determine whether temporal isotopic shifts in occurred. Comparisons of results between September and April allowed us to determine whether consumer variation corresponded to variation in producer isotopic composition. Bonferroni's correction for multiple testing was used to adjust the alpha level (from 0.05) required to reject the null hypothesis for *t*-tests.

To determine whether, and how pervasively, primary producers present on platforms were incorporated into the food web, isotopic compositions were compared among primary producers and consumers both graphically in unadjusted δ^{13}C and δ^{15}N biplots as well as quantitatively using a Bayesian isotopic mixing model. Stable Isotope Analysis in R (SIAR; Parnell et al. 2010) incorporates the variability of sources, consumers, and trophic enrichment factors (TEFs) to produce a 95% CI of the percent contribution of each source to a consumer. The δ^{13}C and δ^{15}N values (mean ± SD) of three sources (red algae, phytoplankton, and epiphytic microalgae) were included in the model for September. Trophic enrichment factors were obtained both from the literature (Vander Zanden and Rasmussen 2001) and from empirical comparisons of stomach and muscle isotopic compositions from nekton (Daigle 2011). The TEFs used for all invertebrates were 0.47 (±1.23) for C and 2.92 (±1.78) for N for all primary consumers. The TEFs used for all fish were 1.52 (±1.34) for C and 3.36 (±1.95) for N. Molar C:N ratios were used to support SIAR interpretation of the stomach contents of *B. capriscus*.

RESULTS

The most abundant basal resources accessible to consumers residing directly on platforms were phytoplankton, red and green macroalgae, and epiphytic microalgae. Although we did not quantitatively sample macroalgae, relative abundances differed between the two sampling times. In September, green algae were abundant enough for isotope analysis in 2 of 20 samples. Red algae were available for isotope analysis in each sample ($n = 20$) in September, and green and red algae also were available in each sample ($n = 4$) in April. Based on a qualitative assessment, epiphytic microalgae consisted mostly of pennate diatoms. Furthermore, the isotopic composition of platform-dwelling biota on platforms EI 325 and EI 346 did not differ significantly for most producers and consumers, and data from the two platforms were pooled in both collections for all analyses.

Isotope composition for phytoplankton from quarterly collections varied from about −22‰ to −19.5‰ for δ^{13}C and from about 5‰ to 7‰ for δ^{15}N (Figure 2). Phytoplankton isotope means for September 2009 were very different from values from quarterly collections, especially for δ^{15}N. Means of δ^{13}C and δ^{15}N calculated across quarterly samples (excluding September) for phytoplankton were −20.78‰ and 6.33‰ respectively (Table 1). In September, mean phytoplankton isotope composition was −19.71‰ and 2.42‰ for δ^{13}C and δ^{15}N, respectively. Phytoplankton δ^{13}C and δ^{15}N were compared across time (for each quarter and the September collection), and

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TABLE 1. Mean (and SD) $\delta^{13}C$ and $\delta^{15}N$ of primary producers near or on oil platforms examined in the Gulf of Mexico. *t*-test or Mann–Whitney *U*-test results comparing September and April for platform-dwelling producer $\delta^{13}C$ and $\delta^{15}N$ are reported as *P*-values. Results of comparisons between phytoplankton from quarterly collections with ANOVA are provided in the text.

	September 2009			April 2010				
Source	$\delta^{13}C$	$\delta^{15}N$	Sample size	$\delta^{13}C$	$\delta^{15}N$	Sample size	P $\delta^{13}C$	P $\delta^{15}N$
Phytoplankton	−19.71 (1.19)	2.42 (0.94)	12	−20.78 (1.31)[a]	6.33 (0.96)[a]	44		
Red algae	−28.17 (3.48)	3.44 (0.65)	12	−25.86 (3.65)	2.30 (2.14)	4	0.249	0.367
Epiphytes	−15.76 (3.25)	4.67 (1.41)	20	−18.73 (1.36)	6.34 (1.75)	5	0.060	0.096
Green algae	−19.68 (0.11)	4.15 (0.08)	2	−22.91 (7.42)	3.66 (1.25)	3	0.773	0.773

[a]Phytoplankton was not collected in April 2010 and values shown are means of a series of quarterly collections (phytoplankton values from September 2009 were not included).

significant differences among collections were detected for both isotopes (ANOVA: df = 4, $P < 0.001$). Tukey's test results revealed that no $\delta^{13}C$ quarterly means differed from each other but that $\delta^{13}C$ in September differed from two (summer and fall) of the quarterly collections. Quarterly $\delta^{15}N$ means did not differ from each other but the mean in September was significantly lower than all quarterly means (Tukey's test: $P < 0.001$). The δ^{15} N for phytoplankton increased after September into the late fall of 2009 and winter of 2010 to mean values (6.86‰) close to the quarterly average. Isotope composition for epiphytes and green and red algae did not differ between September and April collections (Table 1).

Isotope composition differed among the most abundant primary producers, and this difference was consistent over time for some taxa (Table 2). In September, $\delta^{13}C$ differed between all major primary producers (i.e., red algae were depleted in ^{13}C compared with phytoplankton and epiphytes, and epiphytes were enriched compared with phytoplankton). In April, red algae were also depleted in ^{13}C compared with epiphytes and phytoplankton from quarterly collections. In September, epiphytes were enriched in ^{15}N compared with phytoplankton and red algae. In April, epiphytes and phytoplankton from quarterly collections were enriched in ^{15}N compared with red algae.

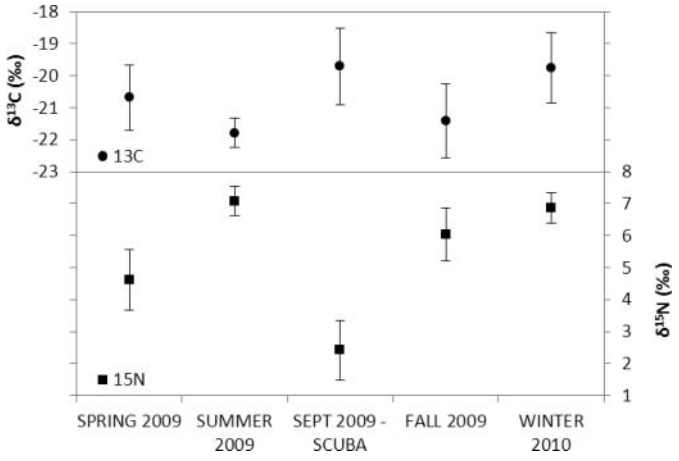


FIGURE 2. Plots of phytoplankton $\delta^{13}C$ (top panel) and $\delta^{15}N$ (bottom panel) from quarterly cruises from 2009 to 2010 and from September 2009. Solid circles are means (±1 SD) of $\delta^{13}C$ and solid squares are means (±1 SD) of $\delta^{15}N$ for each collection.

The isotope composition for several consumer taxa differed between the two sampling times (Table 3). No differences in consumer $\delta^{13}C$ were found between September and April for any taxon. However, all mobile consumers had lower $\delta^{15}N$ values in September than in April, and significant differences (*t*-tests, based on an alpha of 0.002 corrected for multiple comparisons) were found in the crabs, *Pseudomedaeus agassizii* and *Pachygrapsus transverses*, harpacticoid copepods, and melitid amphipods (Table 3). Crabs had the largest change in $\delta^{15}N$, about 3‰ for each species; other taxa were lower in September by 1.25–1.88‰. Differences between September and April for large, long-lived suspension feeders were smaller (0.28‰ and −0.67‰ for oysters and barnacles, respectively) and means did not significantly differ.

To determine which basal resources were incorporated by the fouling community in September, isotope composition of

TABLE 2. Results of Tukey's pairwise test comparisons of $\delta^{13}C$ and $\delta^{15}N$ values of potential sources of primary producers collected on and near platforms in September 2009 and April 2010. Results are reported as *P*-values.

	September 2009		April 2010	
Producer comparisons	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$
Phytoplankton versus red algae	<0.0001	0.126	0.0002[a]	<0.0001[a]
Phytoplankton versus epiphytes	0.003	<0.0001	0.183[a]	1.000[a]
Phytoplankton versus green algae	1.000	0.194	0.336[a]	0.002[a]
Red algae versus epiphytes	<0.0001	0.022	<0.0001	<0.0001
Red algae versus green algae	0.002	0.842	0.272	0.414
Epiphytes versus green algae	0.272	0.922	0.044	0.012

[a]Phytoplankton was not collected in April 2010 and comparisons with phytoplankton are based on quarterly collections (phytoplankton values from September 2009 were not included).

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TABLE 3. Mean $\delta^{13}C$ and $\delta^{15}N$ (and SD) of consumers from platform communities sampled in September 2009 and April 2010. *P*-values compare September and April isotopic composition within each taxon. Sample sizes (*n*) are presented for each collection period.

	n		$\delta^{13}C$			$\delta^{15}N$		
Fouling-community taxon	Sep	Apr	Sep	Apr	*P*	Sep	Apr	*P*
Crabs								
Pseudomedaeus agassizii	11	3	–21.04 (0.73)	–20.10 (1.07)	0.092	5.14 (1.13)	8.16 (0.60)	0.001
Pachygrapsus transversus	9	3	–19.91 (0.92)	–19.53 (0.14)	0.261	5.11 (0.96)	8.12 (0.98)	0.001
Teleophrys pococki	11	1	–21.49 (1.07)	–20.6	0.441	3.67 (1.01)	6.63	0.019
Micropanope nuttingi	5		–21.27 (1.08)			5.63 (1.03)		
Copepoda								
Harpacticoida	20	4	–20.63 (0.86)	–20.42 (1.00)	0.676	3.91 (0.72)	5.79 (0.59)	0.0001
Amphipoda								
Stenothoidae	11	4	–21.20 (0.85)	–20.97 (0.59)	0.638	4.58 (0.79)	5.83 (0.27)	0.010
Melitidae	13	4	–19.80 (0.69)	–19.39 (0.53)	0.338	5.68 (0.69)	7.13 (0.42)	0.001
Polychaeta								
Syllidae	20	4	–18.74 (0.48)	–18.62 (0.42)	0.653	8.34 (0.60)	9.44 (0.81)	0.005
Suspension feeders								
Barnacles	10	4	–17.55 (1.91)	–17.99 (0.25)	0.536	8.65 (1.31)	9.32 (0.75)	0.361
Oysters	10	2	–19.02 (0.49)	–18.31 (0.07)	0.079	6.93 (1.85)	6.65 (0.24)	0.354
Blennidae								
Scartella cristata	11		–18.89 (0.27)			10.94 (0.94)		
Hypsoblennius invemar	10		–18.50 (0.24)			12.08 (0.69)		
Nekton								
Balistes capriscus muscle	4		–17.83 (0.55)			10.84 (0.74)		

primary producers was compared with that of reef-dwelling consumers (Figure 3). The unadjusted $\delta^{13}C$ values of consumers ranged from −22‰ to −17.6‰ (Table 3; Figure 3); ranges were similar to that of phytoplankton. The $\delta^{15}N$ values of consumers ranged from 3.7‰ to 12.1‰ (Table 3; Figure 3).

In September, 95% CIs obtained from the SIAR basal resource model (using red algae, epiphytes, and phytoplankton as sources) indicated that most platform consumers utilized more than one basal resource (Table 4). The highest maximum possible contribution for most taxa was from phytoplankton. For primary consumers or omnivores (based on their $\delta^{15}N$ values, Table 3, and including the crabs, *Pseudomedaeus agassizii*, *Pachygrapsus transverses*, *Teleophrys pococki*, and *Micropanope nuttingi*, harpacticoid copepods, and stenthoid and melitid amphipods), CIs for the consumption of phytoplankton-based resources ranged from ∼13% to 90%, and a smaller fraction of the diet was derived from red algae (CI = ∼10–50%). Epiphyte minimums were near 0% for these taxa (except for melitid amphipods) although possible epiphyte maxima ranged widely (from ∼20% to 43%, Table 4). Estimated diets of melitid amphipods, syllid polychaetes, and fishes (*S. cristata*, *H. invermar*, and *B. capriscus*) had higher minimum contributions from epiphytes (at least 10%, and for syllid polychaetes, 30%), and maximum contributions from all sources were potentially large (35–80%). Of these, syllid polychaetes and fishes were feeding at the level of secondary consumer or higher based on ^{15}N values (Table 4). Long-lived suspension feeders, i.e., barnacles and oysters, indicated high potential contributions from epiphytes and phytoplankton while minimums from red algae were near zero (Table 4). Minimums for epiphytes were 42% and 14% for barnacles and oysters, respectively. Barnacles were enriched in ^{15}N, suggesting they feed as primary and secondary consumers.

Because $\delta^{13}C$ values of the stomach contents of *B. capriscus* were highly variable and sometimes different than mean values of muscle, individual values were used in the SIAR model for September. Mean muscle values of the four individuals combined indicate broad 95% CIs around contributions of red algae, phytoplankton, and epiphytic microalgae (Table 4). However, specimens 1 and 2 had CIs around stomach contents similar to the mean value for muscle, and had molar C:N ratios of 5.31 and 6.26, respectively. Confidence intervals for the consumption of red algae in specimen 3 ranged from 36% to 89% while CIs for phytoplankton and epiphytes were broad and included 0% (Table 4). The molar C:N ratio of the gut contents of specimen 3 was 10.81. Specimen 4 had a $\delta^{13}C$ value very similar to epiphytic diatoms. The 95% CI around the contribution of epiphytic microalgae to specimen 4 was 19–84% (Table 4). The molar C:N ratio of this specimen was 8.56.

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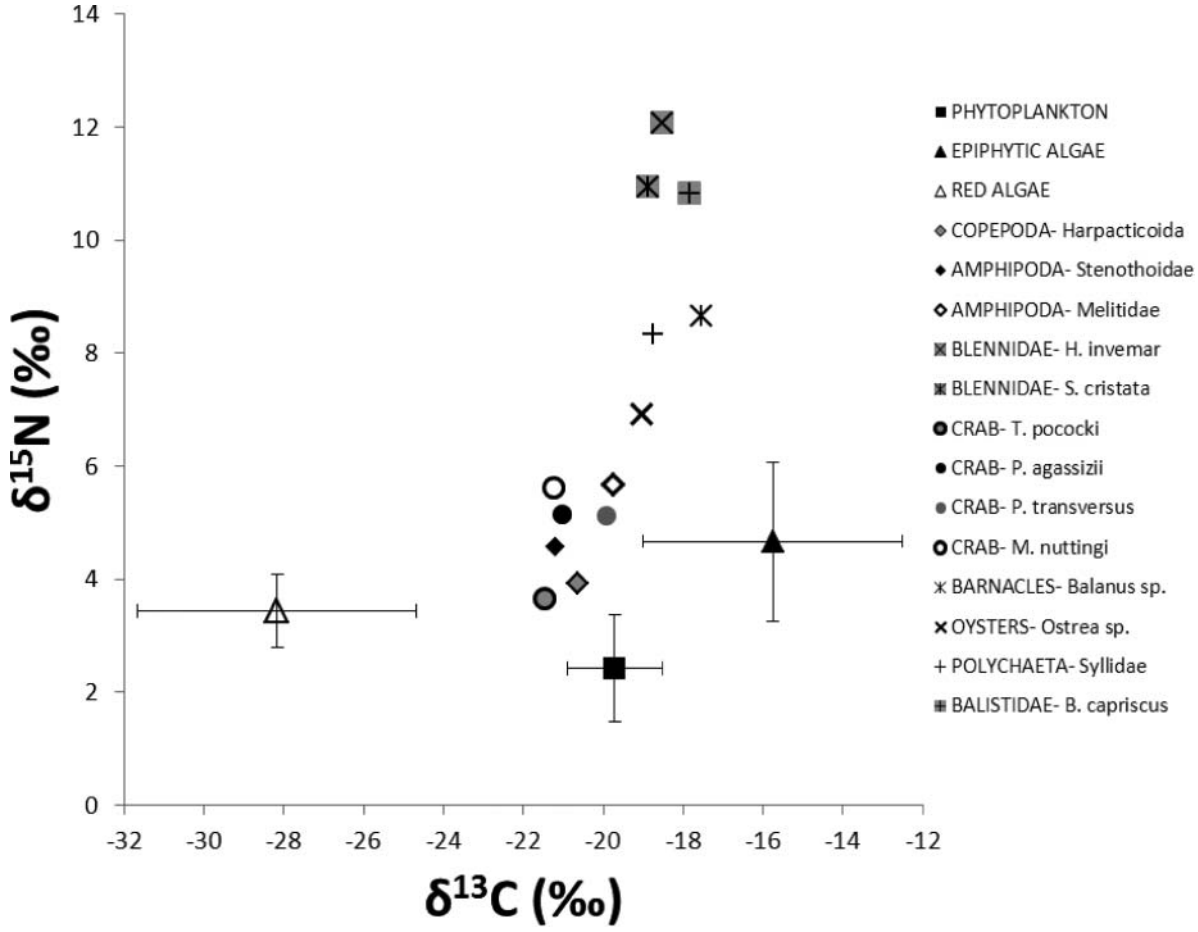


FIGURE 3. Values for $\delta^{13}C$ and $\delta^{15}N$ of consumers residing on platforms and obtained in September 2009 along with primary producers. Primary producers are expressed as means with error bars (±1 SD). Though error bars are not included for consumers, these data points represent means of 3–20 samples of pooled individuals; SD values are reported in Table 3.

DISCUSSION

The isotope composition of primary producers collected in September 2009 varied in ways that enhanced our ability to resolve producer dietary contributions to consumers. For example, $\delta^{13}C$ of phytoplankton and red algae differed by a relatively large and statistically significant amount, and phytoplankton and epiphytes differed significantly in both $\delta^{15}N$ and $\delta^{13}C$. In addition, temporal changes in isotopic composition were detected, and September $\delta^{15}N$ values for some producers and consumers differed from those observed in other collections. Temporal shifts facilitate isotope tracking and can be powerful tools in resolving the relative importance of basal resources (McCutchan and Lewis 2002; Perga and Gerdeaux 2005; Grippo et al. 2011) even when mixing models indicate high levels of overlap or when gut content data are rare (as is the case for many taxa here such as amphipods, copepods, and crabs). Here we use both lines of evidence to support the contention that phytoplankton rather than platform in situ primary production was the most important resource for platform-dwelling consumers both at the time of our September collection and over the succeeding 7 months.

Our δ^{15} N results indicate that small, relatively short-lived mobile species on the platforms feed as primary consumers or omnivores (Table 3). The group included harpacticoid copepods, stenthoid and melitid amphipods, and the crabs *P. agassizii*, *P. transverses*, *M. nuttingi*, and *T. pococki*. The SIAR model indicated that CIs around the estimated contribution of phytoplankton-derived resources to the diet of these consumers (excluding *M. nuttingi*) ranged from 34% to 90%. *Micropanope nuttingi* was also estimated to have a potentially large basal contribution of phytoplankton in its diet, with CIs ranging from 13% to 71%. In addition, temporal changes in isotope composition in these consumers occurred after September, and changes more closely tracked isotopic variation in phytoplankton than macroalgae or epiphytes. Specifically, $\delta^{15}N$ for all mobile consumers increased from September to April (significantly so for harpacticoids, melitid amphipods, and two crab species), and phytoplankton $\delta^{15}N$ in September (which was lower than all other quarterly samples) increased by the late fall and remained high in the winter. The $\delta^{15}N$ values for macroalgae, however, decreased from September to April. For the crabs in particular, the

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TABLE 4. September 95% CIs (%) of the percentage contributions of red algae, epiphytic diatoms, and phytoplankton to the diets of various taxa based on a Bayesian mixing model (SIAR) for isotopes of carbon and nitrogen.

Consumers	Red algae	Epiphytes	Phytoplankton
Crabs			
Pseudomedaeus agassizii	16–39	0–28	36–81
Pachygrapsus transversus	5–31	1–37	36–88
Teleophrys pococki	17–43	0–27	34–82
Micropanope nuttingi	20–50	2–43	13–71
Harpacticoids			
All harpacticoids	9–25	0–14	63–90
Amphipods			
Stenothoidae	15–37	0–21	45–84
Melitidae	9–29	10–39	35–77
Polychaetes			
Syllidae	7–31	30–70	2–59
Suspension feeders			
Barnacles	0–26	42–87	0–49
Oysters	2–29	14–57	19–80
Fish			
Scartella cristata	10–37	10–54	13–76
Hypsoblennius invemar	6–36	10–57	13–80
Balistes capriscus muscle	0–35	15–71	2–72
B. capriscus stomach 1	0–50	2–62	2–74
B. capriscus stomach 2	10–64	0–53	1–64
B. capriscus stomach 3	36–86	0–40	0–48
B. capriscus stomach 4	0–37	19–84	0–68

temporal shift in $\delta^{15}N$ was large and quantitatively similar to the shift in phytoplankton (both increased by ~3‰, Table 3). These observations suggest the consumption of phytoplankton-based resources by mobile consumers might have been of greater importance than indicated by the mixing model in September and that the most important basal resource remained phytoplankton over the succeeding months.

The SIAR model estimated that platform-dwelling red algae were also consumed and constituted the second most important basal resource for these small mobile consumers (except for melitid amphipods). Confidence intervals of contributions of red algae ranged from 5% to 43%. The crab *M. nuttingi* also consumed red algae, and CIs ranged from 20% to 50%. Although amphipods and harpacticoid copepods lack mouthparts capable of tearing macroalgae, they also consumed red algae (perhaps decomposing red algae). Many reef crabs are considered algal grazers (e.g., Barry and Ehret 1993), although Kang et al. (2008) reported that the decorator crab *Hyastenus elongatius* living in a macroalgal bed primarily consumed phytoplankton-based resources. Some algae may be unpalatable due to the production of secondary metabolites that deter grazers (Kain and Norton 1990; Vallim et al. 2007). Furthermore, little is known about assimilation efficiencies of red algae, although some invertebrates are able to assimilate red algae with high efficiency (e.g., Cox and Murray 2006). Although red algae were very abundant and readily available on the platforms, they were not the dominant basal resource for any consumer, including suspension feeders, which may benefit from drift algae (see below). Similarly, Kang et al. (2008), Golléty et al. (2010), and Schaal et al. (2010) reported that dominant macroalgae were not the most common basal resource for grazers on rocky shores and some artificial reefs. In addition, the biomass and production of platform-associated algae may be overshadowed by the quantity of phytoplankton made available to consumers in seawater flowing around platforms. Beaver (2002) estimated that carbon fixation of benthic algae on platforms accounts for 1% of the gross primary production and that the majority of the carbon on platforms is derived from pelagic phytoplankton.

Isotope results can lead to erroneous conclusions about diet when broad overlapping ranges in basal resource use occur (Galván et al. 2011) or if a significant source is not reflected in mixing models. Green algae in September were rare on platforms and were not included in mixing-model calculations. The low density of green algae in September might have been due to environmental factors or competitive interactions with red algae. Seasonal differences in reef macroalgal composition are known to occur in the Gulf (Britton and Morton 1989). Alternatively, many reef crabs are considered algal grazers or omnivores (Christofoletti et al. 2010), and it is possible that crabs consumed significant amounts of green algae contributing to their low density. If so, the similarity in $\delta^{13}C$ between phytoplankton and green algae would preclude an accurate assessment of the basal resource and would misleadingly implicate phytoplankton as the principal basal resource. Recent work by Christofoletti et al. (2010) in an intertidal environment found that the reef-dwelling crab *Pachygrapsus transverses* is omnivorous but prefers small phytoplankton-feeding animals such as sponges and ascidians, and it does not directly control the abundance of macroalgae by grazing. If other platform-dwelling crabs display similar trophic function, they may not consume large amounts of green algae implying our results from September accurately reflect consumer diet. However, green algae were more abundant at other times of the year (e.g., April). It is possible that grazing of green algae is seasonally important although temporal changes in isotope composition suggest that phytoplankton remained most important after September. However, adequate resolution of diet with the use of natural abundance isotopes would be more difficult to achieve if green algae is an important food resource. Finally, inaccuracies in TEF values used in the SIAR model could also contribute to misinterpretations. The crabs in this study are probably omnivorous but their $\delta^{15}N$ values were consistent with those of primary consumers, suggesting crab TEF values are lower than for other invertebrates. Values for TEF have not been determined in these species, and the use of inaccurate TEFs could lead to an underestimate of the importance of phytoplankton in the diet of platform crabs.

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Large, sessile, suspension-feeding epibiota comprise most of the biomass of platform-dwelling communities (Gallaway and Lewbel 1982). The long-lived barnacles and oysters dominant on the platforms showed a distinct dietary importance of epiphytes based on the SIAR model as CIs ranged from 42% to 87% for barnacles and from 14% to 57% for oysters. The contribution from phytoplankton could also be substantial for both taxa (as high as 49% of the diet in barnacles and 80% in oysters). A significant contribution from macroalgae was not indicated, however, even though studies in macroalgal beds have shown that a large contribution of macroalgae to the diet of suspension feeders may occur from consumption of drift or detrital algae (Kang et al. 2008; Schaal et al. 2010). High seawater flow around platforms (Keenan et al. 2003) probably advects macroalgal detritus away from platforms, making it largely unavailable to suspension feeders. The SIAR model estimates may be misleading for slow-growing suspension feeders because tissue isotope composition represents long-term means for ingested C and N, and tissue composition was therefore probably not in equilibrium with primary producers at the time of the September collection. Furthermore, the observed temporal shifts in phytoplankton and epiphyte isotope values were not reflected in barnacle or oyster tissue. It is likely that phytoplankton was more important to the diet of suspension feeders than indicated by the mixing model. Many isotope and gut content studies (e.g., Page and Lastra 2003; Leal et al. 2008; Quan et al. 2012) conclude that oysters consume phytoplankton and suspended benthic algae, although the study by Fukumori et al. (2008) shows that cultured oysters consume epiphytes growing on the reef itself. Platform-dwelling barnacles were more enriched in ^{15}N than oysters suggesting they feed on a mix of primary producers and primary consumers, as do some other suspension feeders (Dupuy et al. 2000; Lonsdale et al. 2009; Golléty et al. 2010). Barnacles may consume entrained single-celled consumers and microzooplankton from the platforms that ingest epiphytes. Beaver (2002) measured energy flow and production rates on two platforms in the northern Gulf and suggested that suspension feeders assimilate carbon (and therefore obtain energy) from the water column and redirect it to reef-dependent and reef-associated consumers. Their resulting secondary production, feces, or pseudofeces may be consumed by reef-dependent and reef-associated organisms. Our data also suggest that suspension feeders make phytoplankton and perhaps epiphytes available to small mobile consumers on platforms.

Platform-dwelling secondary consumers enriched in ^{15}N included sylllid polychaetes and the blennies *S. cristata* and *H. invemar.* Their diets were notable because possible contributions from epiphytic algae were high. Confidence intervals of the percent contribution from epiphytes ranged from 10% to 70% for these taxa, and epiphytes had the highest minimum dietary contribution in syllids. Syllid polychaetes were present in both collections, and the increase in epiphyte $\delta^{15}N$ (1.67‰) was similar to the increase in $\delta^{15}N$ (1.10‰) in syllid tissue from September to April. Other possible basal resources had large ranges among these consumers suggesting either a diverse range of resources were used or that the SIAR model was poorly resolved. Fauchald and Jumars (1979) reported that syllid polychaetes feed on small encrusting invertebrates such as hydroids and bryozoans that feed on epiphytes (Schaal et al. 2010). The dietary importance of epiphytic algae to shallow-water consumers may be great (e.g., Galván et al. 2008), but little comparative research has been conducted on the functional role of epiphytes on open-water reefs.

The fishes we studied are known to be omnivorous. Mobley and Fleeger (1999) and Mendes et al. (2009) found that *S. cristata* consumes algae and small invertebrates such as amphipods on rocky reefs. *B. capriscus* feeds on algae and soft-bodied and protected prey such as barnacles and oysters (Vose and Nelson 1998). Isotope composition of all three fishes was very similar, suggesting the use of similar food resources. A diverse use of food-web resources by these consumers may also explain isotope composition for these secondary consumers. In a recent review, McCann and Rooney (2009) concluded that most secondary consumers feed on herbivores utilizing all extreme primary producer end members of food webs, increasing the diversity of basal food sources.

Although our study was focused on the platform-dwelling community, we sought evidence for a platform-based isotopic signal in *B. capriscus* as a representative of the surrounding nektonic food web. We examined both muscle and gut content isotope composition of *B. capriscus* to better understand how omnivory affects isotope composition. Individual stomach contents were highly variable. One of the four fish examined had a high estimated contribution from red algae (with confidence intervals ranging from 36 to 86%) and one had a high estimated contribution from epiphytes (19–84%). Animal tissue typically has a molar C:N ratio of approximately 3–5 (McConnaughey and McRoy 1979), while benthic plant tissue typically has a ratio >10 (Atkinson and Smith 1983). *Balistes capriscus* molar C:N ratios indicated that these two individuals directly consumed plant tissue. Two other individuals had consumed a meal of animal tissue, based on gut content C:N ratio. The broad diet observed in the isotopic analysis of *B. capriscus* stomach contents was poorly reflected in the SIAR analysis of muscle tissue. It is possible that this species assimilates red algae with low efficiency. Because muscle tissue isotopic composition represents an average of the diet over several months, evidence of omnivory may be obscured when analyzing only muscle tissue. It is possible that reef-dependent resources are channeled through omnivorous fishes to other nekton in the reef-based food web, but this transfer may be difficult to detect with isotopes. To examine the broader food web, we also sampled nonreef-dwelling, benthic-feeding fish and bottom-dwelling scallops around platforms (data reported in Daigle 2011). Isotope composition was identical at 250 m, 1.5 km and >6 km distant from platforms in all species collected, providing no evidence that platform-derived resources contribute to food webs surrounding platforms. More food-web research is needed to

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determine the importance of endemic primary producers in the larger platform-associated food web.

The production hypothesis postulates that the artificial reef effect occurs because platforms stimulate novel production by platform-dwelling primary and secondary producers, which in turn fuels higher growth rates of resident and transient nekton (Bohnsack 1989). Increased in situ food resources are often cited as the main contributor to higher densities of commercially important fish as well as other nekton around platforms (Stone et al. 1979; Gallaway and Lewbel 1982; Scarborough Bull and Kendall 1994; Stanley and Wilson 1996). However, it is possible that platforms serve primarily as sinks, concentrating pelagic primary production, rather than significant producers of organic matter that fuel nektonic food webs. High flow rates and large volumes of seawater pass through and over platforms (Keenan et al. 2003), and suspension feeders may capture and redirect phytoplankton to platforms providing pathways by which significant amounts of pelagic production may reach platforms. There are several ways to test this conjecture of sink versus source for platforms. The use of highly enriched isotopes to label the benthic algae accessible to platform consumers may yield more definitive conclusions on the contribution of epiphytes and macroalgae to consumers including suspension feeders (Galván et al. 2008, 2011; Drake et al. 2009). Fatty acid composition can also be used to determine the contribution of food resources to nektonic consumers (Kharlamenko et al. 2008; Cheung et al. 2010). Energy flow estimations can be used to compare the rate of macroalgae and epiphyte production with the grazing rate or capacity of suspension feeders as well as other consumers (see Beaver 2002).

Decommissioned platforms are on occasion converted into permanent artificial reefs as part of rigs-to-reefs programs to preserve ecosystem function that develops on the structures during production (Dauterive 2000; Kaiser 2006; Macreadie et al. 2011). Decommissioned platforms are either toppled or partially removed (the top portion is removed and placed adjacent to the base), which reduces the height of the structures in order to prevent interference with vessels (Macreadie et al. 2011). In deep or turbid shallow water, the rigs-to-reef conversion reduces surface area of or eliminates hard substrates that reach into the photic zone or mixed layer where phytoplankton density is highest. If reef-associated communities are highly dependent on platform-based primary production, then this policy would lead to a decrease in artificial reef function. However, if consumers are generally not highly dependent on reef-dwelling benthic primary production as our study suggests, reef function may not be strongly affected by factors (such as light) that influence platform-associated primary production. Therefore, the functional significance of artificial reefs in the aphotic zone may be expected to be equivalent to those in the photic zone. If so, rigs-to-reefs programs may be successful in the deep sea and artificial reefs in shaded areas or the aphotic zone should function as expected. Fisheries resource policies often manage resources at platforms by assuming they increase fish production. Our research does not invalidate this premise, but suggests a reevaluation of the trophic pathways that lead to increased fish production is desirable.

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