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What is the relative importance of phytoplankton and attached macroalgae and epiphytes to food webs on offshore oil platforms?

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Running head: Basal resources on offshore oil platforms

## Abstract

Offshore oil platforms function as artificial reefs but little is known about the food webs that fuel platform-dwelling biota. Carbon and nitrogen isotopes in tissues of biota from two offshore oil platforms were analyzed to determine the potential importance of phytoplankton and platform-associated macroalgae and epiphytic algae to the diets of platform-dwelling consumers. Phytoplankton accounted for an estimated 13-90% and red algae accounted for 5-50% of the basal resource contribution to mobile primary consumers including crabs (*Pseudomedeus agassizii*, *Teleophrys pococki*, *Pachygrapsus transverses*, *Micropanope nuttingi*), stenothoid and melitid amphipods and harpacticoid copepods. Sessile suspension-feeding barnacles and oysters consumed phytoplankton and epiphytic algae, and likely redirected large amounts of pelagic production to small, platform-dwelling consumers. Melitid amphipods and secondary consumers including syllid polychaetes and the blennies *Scartella cristata* and *Hypsoblennius invemar* exhibited a distinct contribution from epiphytic algae although all potential basal resources had large, poorly resolved ranges in contributions. Elemental and isotope analysis of the gut contents of individuals indicated that the nektonic grey triggerfish, *Balistes capriscus*, was omnivorous, directly consuming reef-derived red algae and epiphytes as well as animal tissue. Although reef-derived resources enter benthic and nektonic food webs surrounding platforms, phytoplankton is the dominant basal resource in the platform-dwelling communities we examined. Platform-derived benthic algae may therefore not be integral to food-web function on artificial reefs, and reef function should be similar in areas both favorable to and unfavorable to reef-associated algal growth.

## Introduction

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. Other artificial reefs are formed by objects constructed for other purposes. In the Gulf of Mexico (Gulf) for example, over 4000 standing oil and gas platforms function as artificial reefs. Like other artificial reefs, platforms support abundant fouling communities of 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 (Carney, 2005; Gallaway and Lewbel, 1982; Lewbel et al., 1987). 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). Furthermore, reef-associated nekton is 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).

The role of benthic primary producers in food webs on and near artificial reefs is, in general however, poorly understood. Benthic macroalgae will be incorporated into the food

70 web as a basal resource if grazed and assimilated by reef-dwelling consumers, including by  
71 suspension feeders that filter macroalgal detritus (Kang et al., 2008; Schaal et al., 2010).  
72 Although green algae generally lack chemical or physical defenses and are, therefore,  
73 susceptible to grazing (McConnell et al., 1982), some species of red algae are unpalatable (Kain  
74 and Norton, 1990) and may not contribute to the food web. Benthic microalgae are generally  
75 considered highly nutritious for consumers (Miller et al., 1996), and epiphytic microalgae could  
76 be directly grazed by mobile consumers from surfaces associated with reefs, or consumed by  
77 suspension feeders after entrainment into the water column. Alternatively, phytoplankton may  
78 be consumed by reef-dwelling suspension feeders (e.g., barnacles and bivalves; Gallaway and  
79 Lewbel, 1982), and then redirected to platforms in the form of feces or pseudofeces (Beaver,  
80 2002). Small, mobile grazers may also consume phytoplankton directly after it adheres to  
81 surfaces or is trapped in crevices, or as a by-product of suspension feeding. Taxonomically  
82 similar grazing consumers studied in other environments have been found to be selective in  
83 their choice of resources (Pascal et al., 2009), but the basal resource of choice may change  
84 depending on habitat, environmental factors and resource availability (Galván et al., 2008).  
85 Studies of food webs in hard-bottom ecosystems have described several possible and variable  
86 trophic pathways for phytoplankton and reef-associated algae. For example, algae growing on  
87 hard bottoms have been found to contribute to the diet of nearby consumers (Kang et al.,  
88 2003; Behringer and Butler, 2006; Doi et al., 2008; Fukumori et al., 2008), and phytoplankton or  
89 epiphytes may be important basal resources to consumers inside dense macroalgal beds (Kang  
90 et al., 2008; Gollety 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. High nekton abundance associated with platforms 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 has been shown to affect the community structure of epibiota by reducing macroalgae and altering epifaunal communities (Glasby, 1994); yet current understanding makes it difficult to predict 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 ( $^{13}\text{C}$  and  $^{15}\text{N}$ ) 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 C and N stable isotope analysis was performed on potential basal resources and consumers to test the null hypothesis that endemic primary 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

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 Procedure***

Primary producers and epibenthic consumers residing on platforms were collected in September 2009 and April 2010. These reef-dependent communities were sampled by SCUBA divers on two legs of each platform in September at 0-m, 6-m, 12-m, 18-m, and 30-m depths and in April at 1-m and 5-m depths. At each depth, divers removed barnacles and oysters (and incidentally resident organisms) from the surfaces of the platform legs by hand, placing contents into 250- $\mu$ m 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- $\mu$ m mesh stacked sieves to remove and retain organisms that were attached to barnacles and oysters. Epiphytic microalgae was extracted from the 20- $\mu$ m size 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. Animals from appropriate sieve fractions were extracted and identified to the lowest practical taxon. Amphipods in two families (Stenothoidae and Melitidae), 4 species of crab (*Teleophrys pococki*, *Pseudomedaeus agassizii*, *Pachygrapsus transverses*, and *Micropanope nuttingi*), polychaetes in one family (Syllidae), harpacticoid copepods as a composite taxon, and 2 blenny species (*Scartella cristata* and



*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 one sample. Not all taxa were available on both collection dates. Sample sizes ranged from 2 to 20 (Tables 1 and 3) for platform-dwelling primary producers and mobile fauna on each collection date, and the number of individuals pooled in each sample ranged from 2 to 40 for amphipods, 1 to 4 for all crabs, 20 to 100 for syllid polychaetes, > 400 for harpacticoid copepods and was always 1 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 and the central adductor muscle of oysters were pooled from up to 5 individual barnacles and oysters from each depth for analysis. A total of 10 barnacle- (*Balanus tintinnabulum*) and 10 oyster- (*Chama* cf. *macerophylla* and *Ostrea* sp.) isotope samples were obtained in this fashion in September, representing over 60 individuals; sample sizes from April were smaller for barnacles (n = 4) and oysters (n = 2). The remaining shells of barnacles and oysters were 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.

Water column particulate organic matter (WPOM), including phytoplankton, was sampled during quarterly cruises from 2008-10 around one or both platforms by towing a 30- $\mu$ m mesh plankton net for 2 to 3 5-min intervals at discrete depths ~250 m from platforms. Samples around both platforms were collected in September, 2009; however, collections in April 2010 were subsequently misplaced and were unavailable for analysis. WPOM samples

were immediately frozen and stored at -20 °C. WPOM was filtered to < 125 µm size fraction using a Whatman glass filter. Samples were fumed with HCl to dissolve inorganic carbonates before isotope analysis. A total of 56 WPOM samples for isotope analysis were obtained.

Four specimens of *Balistes capriscus* (grey triggerfish, 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.

### **Data Analysis**

Stable isotope analysis results were determined by the following equation:

$$\delta^{13}\text{C} \text{ or } \delta^{15}\text{N} = [(R_{\text{sample}}/R_{\text{standard}})-1] \times 1000,$$

where  $R_{\text{sample}}$  is the ratio of the heavy to light isotopes in the sample (i.e.  $^{13}\text{C}/^{12}\text{C}$  and  $^{15}\text{N}/^{14}\text{N}$ ) and  $R_{\text{standard}}$  is the ratio of the heavy to light isotopes in PeeDee limestone for carbon values and nitrogen gas in the atmosphere for nitrogen values. Legs from the same platform were considered as subsamples of a platform and were pooled for isotope analysis.

The isotopic composition of carbon and nitrogen of primary producers were compared to each other in separate one-way ANOVAs. To determine if, 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  $\delta^{13}\text{C}$

200 and  $\delta^{15}\text{N}$  bi-plots as well as quantitatively using a Bayesian isotopic mixing model. SIAR (Stable  
201 Isotope Analysis in R; Parnell et al., 2010) incorporates the variability of sources, consumers,  
202 and trophic enrichment factors (TEFs) to produce a 95% confidence interval of the percent  
203 contribution of each source to a consumer.  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values (mean  $\pm$  1SD) of three sources  
204 (red algae, phytoplankton, and epiphytic microalgae) were included in the model for September  
205 2009. Green algae were included as a fourth source in April 2010 but were not included in the  
206 model for September due to its rarity (present in 10% of samples). The isotopic composition of  
207 WPOM (a surrogate for phytoplankton) in the Gulf (apart from spring blooms which occur in the  
208 immediate coastal zone, Grippo et al., 2011), typically shows relatively low levels of variability  
209 (Daigle, unpublished), and the average  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of WPOM collected in quarterly  
210 cruises were used as a surrogate for phytoplankton in April 2010 SIAR models. Observed  $\delta^{15}\text{N}$   
211 values for September 2009 were, however, significantly different from other cruises (see Table  
212 1), and September data were not used to estimate mean WPOM isotope values. Observed  
213 values for September were used in SIAR models for September. September and April  $\delta^{13}\text{C}$  and  
214  $\delta^{15}\text{N}$  values of producers and platform consumers were compared with t-tests, or Mann-  
215 Whitney tests for data that failed normality, in order to determine if temporal isotopic shifts in  
216 producers contributed to shifts in consumer isotopic compositions. TEFs were obtained both  
217 from the literature (Vander Zanden and Rasmussen, 2001) and from empirical comparisons of  
218 stomach and muscle isotopic compositions from nekton (Daigle, 2011). TEFs used for all  
219 invertebrates were  $0.47 (\pm 1.23)$  for carbon and  $2.92 (\pm 1.78)$  for nitrogen for all primary  
220 consumers. TEFs used for all fish were  $1.52 (\pm 1.34)$  for carbon and  $3.36 (\pm 1.95)$  for nitrogen.

Molar carbon:nitrogen ratios were used to support SIAR estimates of the stomach contents of *Balistes capriscus*.

## Results

The most abundant basal resources accessible to consumers residing directly on platforms were phytoplankton, red algae, green algae, 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, suggesting a very low relative abundance. Sufficient red algae was available for 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. WPOM was used as a surrogate for phytoplankton.

Tests for differences in isotopic composition (based on t-tests or Mann-Whitney tests for data that failed normality) were not significant between platforms (EI 325 and EI 346) for most producers and consumers. Therefore, the two platforms were considered replicates and data were pooled in all analyses.

In September, mean phytoplankton isotope composition was -19.71 and 2.42‰ for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , respectively. Averaged across quarterly collections from 2008-10 (excluding September 2009), phytoplankton  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values were -20.78 and 6.33‰ respectively (Table 1). These long-term mean isotope values were used for phytoplankton in April 2010 for all calculations.

Isotope composition varied among primary producer and consumer taxa and between the two sampling times. In September,  $\delta^{13}\text{C}$  ranged from -28.17 to -15.76 and in April, from -

25.86 to -18.73 among primary producers.  $\delta^{15}\text{N}$  ranged from 2.42 to 4.67‰ in September and from 2.30 to 6.34‰ in April among primary producers. In both September and April, red algae were significantly depleted in  $\delta^{13}\text{C}$  relative to phytoplankton (Table 2). Epiphytes were significantly enriched in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  relative to phytoplankton in September, but not in April. Green algae in April were significantly depleted in  $\delta^{15}\text{N}$  relative to phytoplankton, but not in September.  $\delta^{13}\text{C}$  of phytoplankton and epiphytes was lower in April (by 1.07‰ and 2.97, respectively) than September, but this difference was significant only in phytoplankton (Table 1). Mean  $\delta^{15}\text{N}$  of both red and green algae was higher in September than in April (by 1.14 and 0.49 ‰, respectively), but this difference was not statistically significant (Table 1). Phytoplankton and epiphytes were lower in September (by 3.91 and 1.67‰, respectively) than April; this difference was significant for phytoplankton ( $p < 0.001$ ), but not for epiphytes ( $p = 0.096$ ). No differences in  $\delta^{13}\text{C}$  were found between September and April for any consumer (Table 3). However, all mobile consumers had significantly lower  $\delta^{15}\text{N}$  values in September than in April (Table 3). Crabs had the largest change in  $\delta^{15}\text{N}$ , about 3‰ for each species; other taxa were lower in September by 1.25 to 1.88‰. Large, long-lived suspension feeding oysters and barnacles differed less between the two sampling times than small, mobile taxa; the difference in  $\delta^{15}\text{N}$  between September and April was 0.28 and -0.67‰ in oysters and barnacles respectively.

To determine which basal resources were incorporated by the fouling community, isotope composition of primary producers was compared to that of reef-dwelling consumers (Figures 2 and 3). The unadjusted  $\delta^{13}\text{C}$  values of consumers ranged from -22 to -17.6 ‰ in September (Table 3, Figure 2) and from -20.1 to -17.8 ‰ in April (Table 3, Figure 3); both ranges

were similar to phytoplankton. The  $\delta^{15}\text{N}$  values of consumers ranged from 3.7 to 12.1‰ in September (Table 3, Figure 2) and from 5.8 to 9.3 ‰ in April (Table 3, Figure 3).

In September, 95% confidence intervals obtained from the SIAR basal resource model (using red algae, epiphytes and phytoplankton as sources) were generally broad but indicates that most platform consumers utilized more than one basal resource (Table 4). The highest maximum possible contribution for most taxa was from phytoplankton. For the crabs *Pseudomedeus agassizii*, *Pachygrapsus transverses*, *Teleophrys pococki* and *Micropanope nuttingi*, harpacticoid copepods and stentheid and melitid amphipods (all of which appear to feed as primary consumers based on their  $\delta^{15}\text{N}$  values, Table 4), the largest fraction of the diet was estimated to be derived from phytoplankton (confidence intervals ranged from ~13-90%), with a smaller but important fraction of the diet coming 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 ~20-43%, Table 4). Estimated diets of melitid amphipods, syllid polychaetes and fishes (*S. cristata*, *H. inermar* and *B. caprisus*) 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%), indicating either poor resolution or the use of multiple basal resources. Of these, syllid polychaetes and fishes were feeding at the level of secondary consumer or higher based on  $^{15}\text{N}$  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  $^{15}\text{N}$ , suggesting they feed as primary and secondary consumers.

In April, 95% confidence intervals around the percent contribution from the SIAR model of the 4 potential basal resources (red algae, green algae, epiphytes and phytoplankton) for consumers were broad and overlapping, indicating a poor ability to resolve the food web. Most primary producers had lower confidence limits < 5% and upper limits ranged from 23-77% (Table 5). Again, highest possible maximums contribution for most consumers came from phytoplankton. Confidence intervals for the contribution of phytoplankton to the crab *P. transverses* and for barnacles were best defined and ranged from 14-75%, and from 12-77% respectively (Table 5).

Because  $\delta^{13}\text{C}$  values of the stomach contents of *B. capriscus* were highly variable and sometimes different than muscle mean values, individual values were used in the SIAR model for September. Mean muscle values of the 4 fish combined indicate broad 95% confidence intervals around contributions of red algae, phytoplankton, and epiphytic microalgae (Table 4). However, specimens 1 and 2 had confidence intervals around stomach content similar to the muscle mean value, and had molar C:N ratios of 5.31 and 6.26. Specimen 3 suggested significant contributions from red algae (95% confidence intervals for red algal contribution was 36-89%) while confidence intervals 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  $\delta^{13}\text{C}$  value very similar to epiphytic diatoms. The 95% confidence interval around the percent contribution of epiphytic microalgal to specimen 4 was 19-84% (Table 4). The molar C:N ratio of this specimen was 8.56.

## Discussion

Conditions in September 2009 allowed for the delineation of basal resources for several of the platform-dwelling consumers studied. For example, phytoplankton and red algae were separated by large differences in  $\delta^{13}\text{C}$  (-19.1 for phytoplankton and -28.2‰ for red algae), and phytoplankton and epiphytes differed in both  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ . The potential to differentiate basal resources in the diet of consumers in April 2010 was lower, however, because primary producer isotope composition was similar. Significantly, a large temporal isotopic shift occurred between September 2009 and April 2010 and differed in direction among primary producers (i.e.,  $\delta^{15}\text{N}$  increased in epiphytes and phytoplankton across this time but decreased in red and green algae). Such temporal shifts facilitate isotope tracking and can be powerful tools in determining the relative importance of basal resources (McCutchan and Lewis 2002; Perga and Gerdeaux 2005; Grippo et al. 2011).

Our dietary estimates for primary consumers on the platforms are especially well supported. Two lines of evidence suggest that phytoplankton was the most important food resource for a diverse group of mobile consumers that included the crabs *Pseudomedeus agassizii*, *Pachygrapsus transverses*, and *Teleophrys pococki*, harpacticoid copepods, and stenthoid and melitid amphipods. Firstly, the SIAR model indicated that confidence intervals around the estimated contribution of phytoplankton to the diet among these taxa ranged from 34-90%. In addition, the crab *Micropanope nuttingi* was estimated to have a large contribution of phytoplankton in its diet, with confidence intervals ranging from 13-71%. Secondly, the  $\delta^{15}\text{N}$  for these taxa increased significantly with the increase in phytoplankton  $\delta^{15}\text{N}$  from September to April, further supporting the importance of phytoplankton as a basal resource for these small, relatively short-lived primary consumers. For the crabs in particular, the temporal shift in



$\delta^{15}\text{N}$  was large and quantitatively similar to the shift in phytoplankton (both were  $\sim 3\text{‰}$ , Table 3), and suggests the consumption of macroalgae was of little importance even though reef crabs are often considered algal grazers (e.g., Barry and Ehret, 1993). Similarly, Kang et al. (2008) reported that the decorator crab *Hyastenus elongatus* living in a macroalgal bed primarily consumes phytoplankton. Consumers may select for phytoplankton resources over red algae due to increased palatability (Kain and Norton, 1990) because secondary metabolites in red and brown algae can reduce palatability and deter grazers (Vallim et al., 2007). 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 over artificial structures. 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.

The SIAR model estimated that red algae were the second most important basal resource for taxa in this group (except for melitid amphipods), with confidence intervals of contributions ranging from 5-43%. The crab *M. nuttingi* also was found to consume red algae, with confidence intervals that ranged from 20-50%. Epiphytes were of relatively minor importance with confidence interval minimums close to or at 0 for these consumers (again except for melitid amphipods in which epiphytes were the second highest contributor). Reef crabs are likely capable of directly ingesting macroalgae after tearing it, but little is known about assimilation efficiencies of red algae, although some invertebrates are able to assimilate it with high efficiency (e.g., Cox and Murray 2006). Smaller reef-dependent taxa with mouthparts that are unable to tear macroalgae, i.e., amphipods and harpacticoid copepods,

353 also consumed red algae (perhaps decomposing red algae). Although red algae were very  
354 abundant and readily available on the platform at the time of our study, they were not the  
355 dominant basal resource for any consumer, including crabs (that might be expected to consume  
356 large quantities of macroalgae) and suspension feeders that may benefit from drift algae.  
357 Similar findings that the dominant macroalga is not the most common prey item have been  
358 reported for grazers on rocky shores and some artificial reefs (Kang et al., 2008; Gollety et al.,  
359 2010; Shaal et al., 2010).

360         Large, sessile, suspension-feeding epibiota comprise most of the biomass of platform-  
361 dwelling communities (Gallaway and Lewbel, 1982). The long-lived barnacles and oysters  
362 dominant on the platforms showed a distinct dietary importance of epiphytes (confidence  
363 intervals generated by the SIAR model for the contribution from epiphytes ranged from 42-87%  
364 for barnacles and 14-57% for oysters) in September, although the contribution from  
365 phytoplankton could be substantial for both taxa (as high as 49% of the diet in barnacles and  
366 80% in oysters). A significant contribution from macroalgae was not indicated, however, even  
367 though studies in macroalgal beds have shown that a large contribution of macroalgae to the  
368 diet of suspension feeders may occur from consumption of drift or detrital algae (Kang et al.,  
369 2008; Schaal et al., 2010). The SIAR model may be less accurate for slow-growing suspension  
370 feeders because tissue isotope composition represents long-term means for ingested C and N,  
371 and tissue composition was therefore likely not in equilibrium with primary producers at the  
372 time of collection. Furthermore, the observed shifts in phytoplankton and epiphyte isotope  
373 values between September and April were not reflected in barnacle or oyster tissue. It is  
374 therefore possible that phytoplankton is more important to the diet of suspension feeders than

indicated by the model. Barnacles were more enriched in  $^{15}\text{N}$  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; Gollety 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 and/or pseudofeces may be consumed by reef-dependent and reef-associated organisms. Our data also suggest that suspension feeders may make phytoplankton and perhaps epiphytes available to small mobile consumers on platforms.

A group of platform-dwelling, secondary consumers enriched in  $^{15}\text{N}$  (including syllid polychaetes and the blennies *S. cristata* and *H. invemar*) was notable because of the higher diversity of basal contributions and contributions from epiphytic algae could be high. Confidence intervals of the percent contribution from epiphytes ranged from 10-70 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  $\delta^{15}\text{N}$  (1.67‰) was similar to the increase in  $\delta^{15}\text{N}$  (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 sometimes feed on smaller encrusting invertebrates such as hydroids and bryozoans that feed on epiphytes (Shaal 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 on platforms. Mobley and Fleeger (1999) and Mendes et al. (2009) found that *S. cristata* consumes algae and small invertebrates such as amphipods on rocky reefs, and the grey triggerfish, *B. capriscus*, can feed on algae, and soft-bodied and protected (i.e., barnacles and oysters) prey (Vose and Nelson, 1994). 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 the 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 triggerfish as a representative of the surrounding nektonic food web. We examined both the muscle and gut content isotope composition of triggerfish in an effort to better understand how omnivory affects isotope composition. Individual *B. capriscus* stomach contents were highly variable. One of the four fish examined had a high estimated contribution from red algae (with confidence intervals ranging from 36-86%) and one had a high estimated contribution from epiphytes (19-84%). Molar C:N ratios suggest that both individuals consumed plant tissue directly [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]]. Two other individuals

419 had last consumed a meal of animal tissue, based on gut content C:N ratio. The omnivory  
420 observed in the isotopic analysis of *B. capriscus* stomach contents was poorly reflected in the  
421 SIAR analysis of muscle tissue. It is possible that triggerfish assimilate red algae with low  
422 efficiency. Because muscle tissue isotopic composition represents an average of the diet over  
423 several months, evidence of omnivory of *B. capriscus* may be obscured when analyzing only  
424 muscle tissue. It is possible that reef-dependent resources are channeled through omnivorous  
425 fishes to other nekton in the reef-based food web but this transfer may be difficult to detect  
426 with isotopes. We also sampled selected species of non-reef-dwelling, benthic-feeding fish and  
427 bottom-dwelling scallops in the vicinity of these platforms (data reported in Daigle, 2011).  
428 Isotope composition was nearly identical in all samples of the same species including those 250  
429 m, 1.5 km and > 6 km distant from platforms, indicating that platform-derived resources  
430 contribute little to food webs surrounding platforms. More food-web research is needed to  
431 determine the importance of reef-dependent primary producers in the larger platform-  
432 associated food web.

433         The general assumption of the production hypothesis to explain the artificial reef effect  
434 is that platforms stimulate novel production by platform-dwelling primary and secondary  
435 producers, which fuels higher growth rates of resident and transient nekton (Bohnsack, 1989).  
436 Increased food resources are often cited as the main contributor to higher densities of  
437 commercially important fish as well as other nekton around platforms (Bull and Kendall, 1994;  
438 Gallaway and Lewbel, 1982; Stanley and Wilson, 1996; Stone et al., 1979). Our work suggests  
439 that phytoplankton and platform-based micro- and macroalgae all contribute to the diets of  
440 platform-dwelling animals. However, dietary contributions from red algae and epiphytes were

generally smaller than contributions from phytoplankton and were significant in specific taxa, not dominant throughout the platform-dwelling assemblage. Some primary consumers utilized smaller amounts of red algae, while others, especially secondary consumers, had a broader mix of basal resources including epiphytes. Given the high flow rates and large volumes of seawater passing through and over platforms (Keenan et al., 2003) and the potential ability of suspension feeders to capture and redirect phytoplankton to platforms, it seems important to ask if platforms serve primarily as sinks, concentrating pelagic primary production, rather than significant producers of organic matter that fuel nektonic food webs. There are several ways to further test the sink vs. source conjecture. 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 (Drake et al., 2009; Galván et al., 2008; Galván et al., 2011). 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), reducing the height of the structures in order to prevent interference with vessels (Macreadie et al., 2011). In deep or highly turbid shallow water, the rigs-to-reef

conversion reduces surface area of or eliminates hard substrates that reach into the photic zone. If communities are highly dependent on platform-based primary production, then this policy would lead to a decrease in artificial reef function. However, in this study we did not find that consumers were highly dependent on reef-dwelling benthic primary production. Instead, we estimated that phytoplankton is the most important basal resource to these communities. Phytoplankton may be grazed by the high biomass of suspension-feeders attached to platforms or may be accessible to mobile consumers as it comes in contact with and adheres to the complex structures of platforms and epibiota. Reef-dependent suspension feeders have high rates of secondary production and egestion that may be passed on to reef-dependent consumers (Beaver, 2002; Cheung et al., 2010). Thus, reef function may not be strongly affected by factors (such as light) that influence platform-associated primary production, and the functional significance of artificial reefs in the aphotic zone might 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 re-evaluation of the trophic pathways that lead to increased fish production is desirable.

482

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684 **Table 1.** Mean (standard deviation)  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of primary producers near or on platforms used in SIAR mixing models.  
685 Note that  $^{15}\text{N}$  values for phytoplankton and epiphytes increased from September 2009 to April, 2010 while  $^{15}\text{N}$  values for red and  
686 green algae decreased. t-test (for normal data) or a Mann-Whitney test (for data that failed normality) results comparing Sept and  
687 April for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  are reported as p values (bold p-values are significant).  
688

Source	Sept.09			April 10			p, $\delta^{13}\text{C}$	p, $\delta^{15}\text{N}$
	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	Sample size	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	Sample size		
Phytoplankton	-19.71 (1.19)	2.42 (0.94)	12	-20.78 (1.31)*	6.33 (0.96)*	44	<b>0.0303</b>	<b>&lt;0.001</b>
Red Algae	-28.17 (3.48)	3.44 (0.65)	12	-25.86 (3.65)	2.30 (2.14)	4	0.2493	0.3665
Epiphytes	-15.76 (3.25)	4.67 (1.41)	20	-18.73 (1.36)	6.34 (1.75)	5	0.0599	0.0960
Green Algae	-19.68 (0.11)	4.15 (0.08)	2	-22.91 (7.42)	3.66 (1.25)	3	0.7728	0.7728

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690  
691 \*Phytoplankton was not collected in April 2010 and values shown are means of a series of quarterly collections (phytoplankton  
692 values from September 2009 were not included).  
693  
694

**Table 2.** Pair-wise comparisons of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of potential sources of primary producers on and near platforms collected in September 2009 and April 2010. Tukey test results are reported as p-values (significant p-values are in bold).

Producer Comparisons	September 2009		April 2010	
	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$
Phytoplankton vs. Red Algae	<b>&lt;0.0001</b>	0.1264	<b>0.0002</b>	<b>&lt;0.0001</b>
Phytoplankton vs. Epiphytes	<b>0.0029</b>	<b>&lt;0.0001</b>	0.1827	1.000
Phytoplankton vs. Green Algae	1.000	0.194	0.3359	<b>0.0016</b>
Red Algae vs. Epiphytes	<b>&lt;0.0001</b>	<b>0.0223</b>	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>
Red Algae vs. Green Algae	<b>0.0022</b>	0.8421	0.272	0.4136
Epiphytes vs. Green Algae	0.2724	0.9219	<b>0.0435</b>	<b>0.0124</b>

**Table 3.** Mean  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  (standard deviation) of consumers from platform communities sampled in September 2009 and April 2010. p-values compare September and April isotopic composition within each taxon. Significant p-values ( $p < 0.05$ ) are in bold.

Fouling Community		Sample Size		$\delta^{13}\text{C}$			$\delta^{15}\text{N}$		
		Sept.	Apr.	Sept.	Apr.	p	Sept.	Apr.	p
Crabs				Mean (SD)	Mean (SD)		Mean (SD)	Mean (SD)	
	<i>Pseudomedeus agassizii</i>	11	3	-21.04 (0.73)	-20.10 (1.07)	0.0919	5.14 (1.13)	8.16 (0.60)	<b>0.0009</b>
	<i>Pachygrapsus transversus</i>	9	3	-19.91 (0.92)	-19.53 (0.14)	0.2609	5.11 (0.96)	8.12 (0.98)	<b>0.0009</b>
	<i>Teleophrys pococki</i>	11	1	-21.49 (1.07)	-20.6	0.4408	3.67 (1.01)	6.63	<b>0.0186</b>
	<i>Micropanope nuttingi</i>	5	--	-21.27 (1.08)	--	--	5.63 (1.03)	--	--
Copepoda									
	Harpacticoida	20	4	-20.63 (0.86)	-20.42 (1.00)	0.6758	3.91 (0.72)	5.79 (0.59)	<b>0.0001</b>
Amphipoda									
	Stenothoidae	11	4	-21.20 (0.85)	-20.97 (0.59)	0.6380	4.58 (0.79)	5.83 (0.27)	<b>0.0099</b>
	Melitidae	13	4	-19.80 (0.69)	-19.39 (0.53)	0.3375	5.68 (0.69)	7.13 (0.42)	<b>0.0013</b>
Polychaeta									
	Syllidae	20	4	-18.74 (0.48)	-18.62 (0.42)	0.6528	8.34 (0.60)	9.44 (0.81)	<b>0.0046</b>
Suspension-Feeders									
	Balanus sp.	10	4	-17.55 (1.91)	-17.99 (0.25)	0.5356	8.65 (1.31)	9.32 (0.75)	0.3613
	Ostrea sp.	10	2	-19.02 (0.49)	-18.31 (0.07)	0.0789	6.93 (1.85)	6.65 (0.24)	0.3544
Blennidae									
	<i>Scartella cristata</i>	11	--	-18.89 (0.27)	--	--	10.94 (0.94)	--	--
	<i>Hypsoblennius invemar</i>	10	--	-18.50 (0.24)	--	--	12.08 (0.69)	--	--
Nekton									
	<i>Balistes capriscus</i> muscle	4	--	-17.83 (0.55)	--	--	10.84 (0.74)	--	--



**Table 4.** September 2009 95% confidence intervals of the % 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	% contribution to diet (95% confidence interval)		
	Red Algae	Epiphytes	Phytoplankton
Crabs:			
<i>Pseudomedeus agassizii</i>	16-39	0-28	36-81
<i>Pachygrapsus transversus</i>	5-31	1-37	36-88
<i>Teleophrys pococki</i>	17-43	0-27	34-82
<i>Micropanope nuttingi</i>	20-50	2-43	13-71
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
Barnacles	0-26	42-87	0-49
Oysters	2-29	14-57	19-80
Fish:			
<i>Scartella cristata</i>	10-37	10-54	13-76
<i>Hypsoblennius invemar</i>	6-36	10-57	13-80
<i>Balistes capriscus</i> muscle	0-35	15-71	2-72
<i>B. capriscus</i> stomach 1	0-50	2-62	2-74
<i>B. capriscus</i> stomach 2	10-64	0-53	1-64
<i>B. capriscus</i> stomach 3	36-86	0-40	0-48
<i>B. capriscus</i> stomach 4	0-37	19-84	0-68

Table 4. April 2010 95% confidence interval of the % contributions of red algae, green algae, phytoplankton, and epiphytic diatoms to the diets of various consumers based on a Bayesian mixing model (SIAR).

Consumers	% contribution to diet (95% C.I.)			
	Red Algae	Green Algae	Epiphytes	Phytoplankton
<i>Pseudomedeus agassizii</i>	0-36	2-56	0-40	4-60
<i>Pachygrapsus transverses</i>	0-23	3-62	0-33	14-75
<i>Teleophrys pococki</i>	1-47	0-48	0-46	0-48
Harpacticoida	0-37	2-55	0-39	3-55
Stenothoidae	2-50	0-48	0-43	0-49
Melitidae	1-39	1-49	0-42	2-57
Syllidae	3-49	0-47	0-43	0-50
<i>Balanus</i> sp.	0-25	2-59	0-37	12-77
<i>Ostrea</i> sp.	0-46	0-47	0-48	0-50

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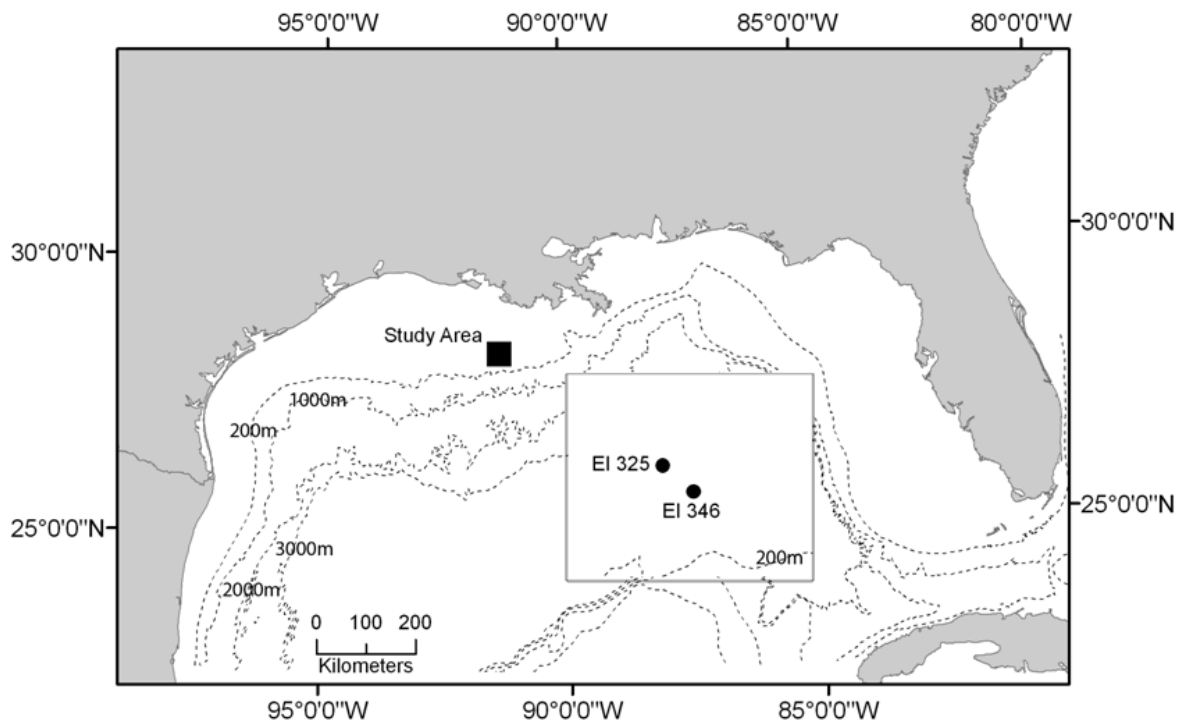
### Figure Legends

720 Figure 1. Location of study area and oil platforms sampled (insert).

721 Figure 2.  $\delta^{13}\text{C}$  vs.  $\delta^{15}\text{N}$  bi-plot of consumers residing on platform legs obtained during the  
722 September 2009 cruise along with primary producers. Primary producers are expressed as  
723 means with error bars ( $\pm 1$  SD). Though error bars are not included on consumers, these data  
724 points represent means of 3-20 samples of pooled individuals; standard deviations are reported  
725 in Table 3.

726 Figure 3.  $\delta^{13}\text{C}$  vs.  $\delta^{15}\text{N}$  bi-plot of consumers residing on platform legs obtained during the April  
727 2010 cruise along with primary producers. Primary producers are expressed as means with  
728 error bars ( $\pm 1$  SD). Though error bars are not included on consumers, these data points  
729 represent means of 1-4 samples of pooled individuals; standard deviations are reported in  
730 Table 3.

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**Figure 1.**

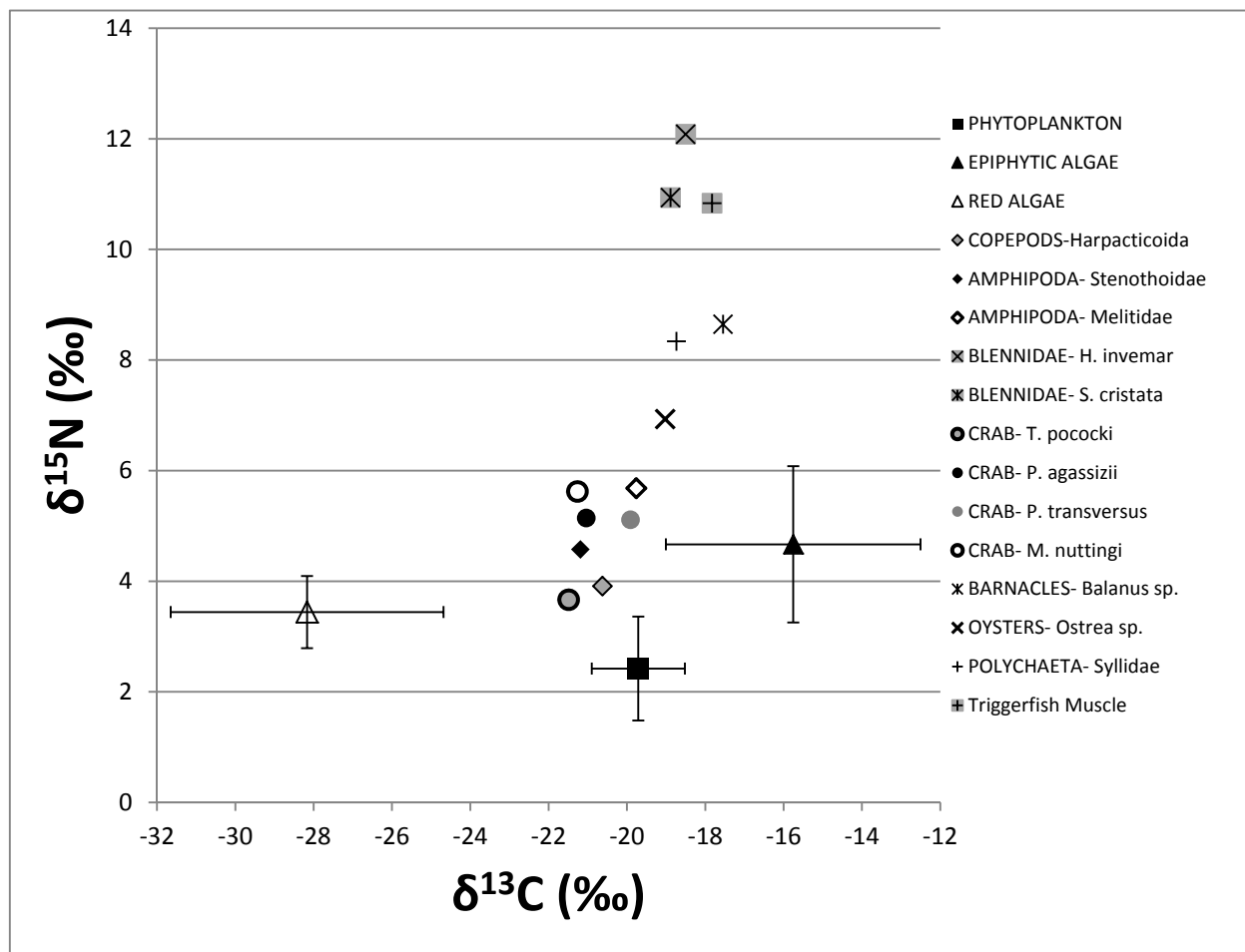
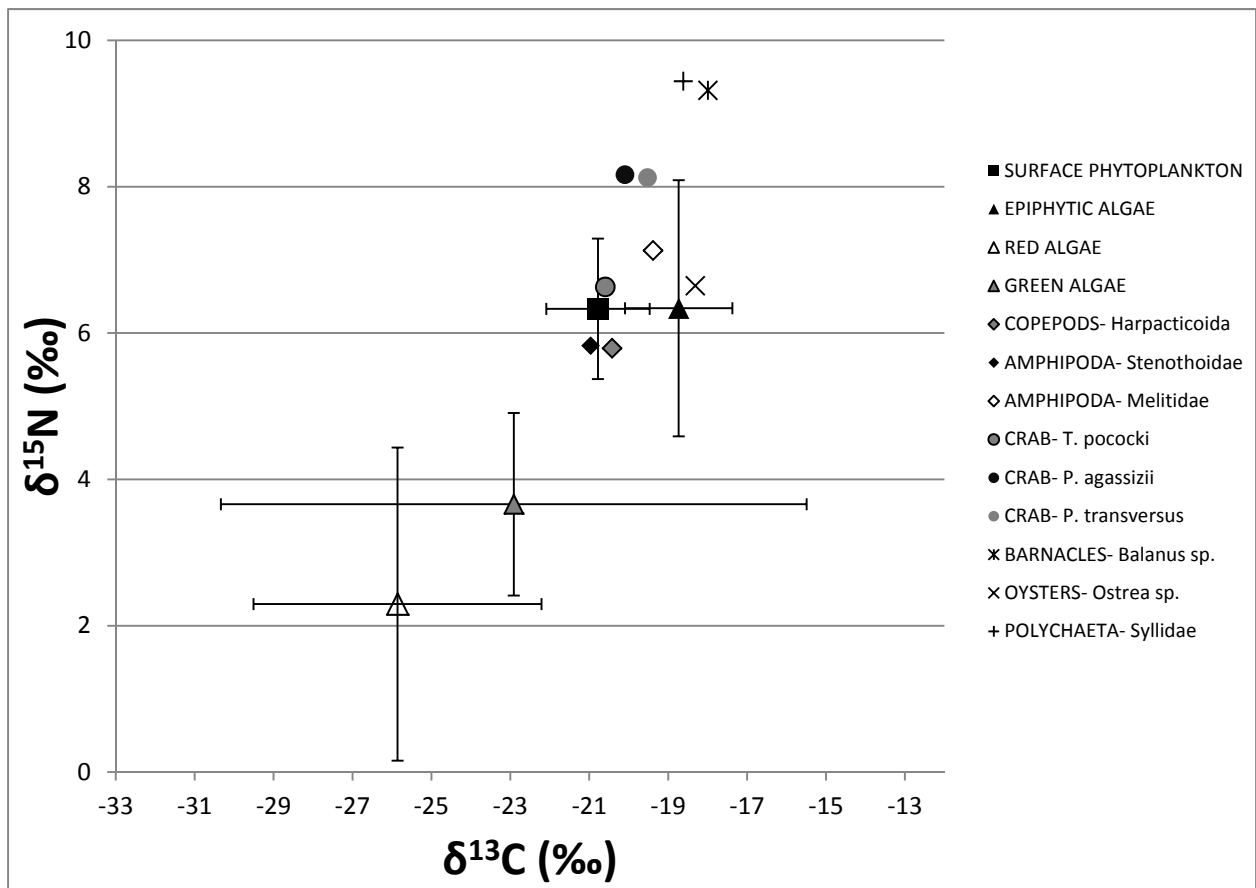


Figure 2.

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**Figure 3.**