Barnacle settlement and growth at oil and gas platforms in the northern Gulf of Mexico

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ABSTRACT: Nearshore oil and gas platforms (platforms) off Louisiana's coast occupy some of the most productive waters in the United States. Platforms are de facto artificial reefs with diverse fouling and fish communities, but little is known about the spatial dynamics of secondary production at platforms. In 2015 and 2016, we used settlement plates to compare barnacle production along a 43.9 km landward–seaward transect at depths of 2 and 7 m. *Amphibalanus reticulatus* settlement was greater at 2 than at 7 m and decreased with distance from shore at rates of −2.0 to −86.2 ind. m^{-2} d^{-1} km^{-1}, depending on depth and year. *A. reticulatus* growth rates were greater closer to shore, at 2 vs. 7 m, and in 2016 vs. 2015. Height growth ranged from 0.02 to 0.13 mm d^{-1}, but width growth was not associated with any variables. *A. reticulatus* total and tissue weight gains were similar to growth rates and ranged from 0.43–8.17 and 0.13–1.82 mg d^{-1}, respectively. The ratio of tissue to total weight was greater in 2016 than 2015 and was similar for smaller barnacles, regardless of distance. However, distance had a strong negative effect on this ratio for larger barnacles and peaked at ~25 to 30%. Greater barnacle settlement and growth rates in nearshore waters suggest that prolific primary and secondary production translate to increased production of fouling organisms. Moreover, greater barnacle production at 2 than at 7 m depth suggests the vertical dimension of platforms is an important aspect of their ecological value.

KEY WORDS: Secondary production · Artificial reefs · *Amphibalanus reticulatus* · Attraction vs. production · Settlement plates

INTRODUCTION

Nutrient discharge from the Mississippi and Atchafalaya rivers drives prolific primary production off the US Louisiana coast (Turner & Rabalais 1991, Dortch & Whitledge 1992, Rabalais et al. 1996). This region produces >73% of all USA fisheries landings in the Gulf of Mexico (GOM; NMFS 2015) and leads in commercial landings of many reef-associated species (red snapper *Lutjanus campechanus*, lane snapper *Lutjanus synagris*, vermillion snapper *Rhomboplites aurorubens*, Warsaw grouper *Epinephelus nigritus*; NMFS 2015). Naturally occurring hard bottom habitat is rare on the continental shelf off Louisiana (Parker et al. 1983), and shelf edge banks provide the only source of natural hard bottom substrate. However, oil and gas platforms (platforms) are de facto artificial reefs that account for ~12 km[2] of hard bottom substrate on the shelf (Gallaway et al. 1998) and are renowned fishing destinations where reef-associated fishes are commonly landed (Stanley & Wilson 1989). The number of platforms in the GOM peaked at ~4000 in 2008 and has decreased to ~2100 in 2017 (BOEM 2017).

The value of platforms as artificial reef habitat has long been the subject of debate (Polovina 1991,

Grossman et al. 1997, Cowan et al. 2011), but it is critical to resolve this debate since nearshore platforms are rapidly being removed. Questions surrounding the ecological value of platforms fall within the broader attraction vs. production artificial reef debate. The attraction side argues that artificial reefs attract fishes and make them more susceptible to fishing (Stone et al. 1979), while the production side argues that artificial reefs produce additional fish biomass (Samples & Sproul 1985, Bohnsack 1989). The explanation is probably not monothetic, and both processes are likely involved (Bohnsack 1989), while the degree of attraction or production is unquestionably taxon-specific. For example, platforms likely result in the production of sheepshead *Archosargus probatocephalus* but may not result in significant production of red snapper *Lutjanus campechanus* (Cowan & Rose 2016).

Most platform research in the GOM has focused on offshore platforms (≥25 m total depth), but nearshore platforms (5 to 25 m total depth) may be especially important because they occupy the highly productive region influenced by the Atchafalaya and Mississippi rivers. Nearshore platforms represent ~40% of platforms in the GOM (BOEM 2017). These nearshore platforms host diverse assemblages of fishes that are associated with varying degrees of freshwater influence (Reeves 2015, Munnelly 2016). Barnacles are the dominant fouling organisms on nearshore platforms (Gunter & Geyer 1955, Lewbel et al. 1987, Reeves et al. 2017a), and they provide structural habitat (microtopographic relief) for other organisms, such as stone crabs *Menippe* spp. (Reeves et al. 2017a). Barnacles are filter feeders that consume zooplankton and phytoplankton (Barnes 1959), and their growth and settlement is positively associated with productivity (Menge et al. 1997, 2003, Sanford & Menge 2001). Understanding secondary production on artificial reefs is critical to resolving the attraction vs. production debate (Bohnsack 1989), and it has received increased attention in recent years. Recent studies of offshore platforms in the GOM have examined the importance of fouling organisms as prey for fishes (Daigle et al. 2013, Schwartzkopf 2014, Foss 2016) and as amphipod habitat (Beaver et al. 2003). While the importance of filter feeders as prey and ecological engineers is well established for platforms off California's coast (Page et al. 1999, Claisse et al. 2014), platform-dwelling barnacles in the GOM have received little attention.

In this paper, we present a 2 yr study where settlement plates were used to examine how growth and settlement of platform-dwelling barnacles varied with distance from shore and depth. We hypothesized that barnacle growth and settlement is greater closer to shore and at shallower depths due to the higher degree of freshwater influence and eutrophication in this part of the coastal zone (Reeves 2015, Munnelly 2016, Reeves et al. 2017b).

MATERIALS AND METHODS

Settlement plate construction and deployment

Settlement plates were constructed from 6 inch (~15.24 cm) diameter PVC schedule 40 pipe. The pipe was split lengthwise to make 2 pieces with concave and convex outer surfaces that were cut into 10 cm long sections. Individual 10 cm sections were considered settlement plates and were mounted to platforms so that convex surfaces faced outwards. The outer 254 cm^2 surface area was used for all analyses.

A total of 72 settlement plates were deployed at 12 platforms (6 settlement plates platform^{-1}) along a 43.9 km landward-seaward transect starting ~15 km south of the Isles Dernieres, Louisiana, in 2015 and 2016 (Fig. 1, Table 1). Platforms were small (1 to 4 pilings) and located in depths of 7.6 to 33.5 m. Divers affixed 2 sets of 3 settlement plates at depths of 2 and 7 m. However, 2 m plates were lost at the 3 most seaward platforms in both years (18 settlement plates). Settlement plate deployments lasted 92 to 125 d. Plates were retrieved by divers who sealed the plates in plastic bags while underwater to prevent the loss of loose materials. Settlement plates were kept on ice until frozen at ca. −18°C.

In conjunction with settlement plate deployment and retrieval, we collected hydrographic profiles of the upper 8 m with a YSI 6820 V2 Sonde. The sonde was lowered from the vessel at a rate of 0.04 ± 0.004 m s^{-1} (95% CI) and recorded temperature (°C), salinity (PSU), and dissolved oxygen (DO) (mg l^{-1}) in 2 s intervals. The sonde was calibrated before and after each sampling trip using the manufacturer's 2012 specifications (YSI).

Settlement plate processing

We subdivided each settlement plate into 6 equal cells and subsampled 5 barnacles (>2 mm width) from each cell for biometrics (≥30 barnacles per plate). Barnacles were only subsampled if their bases were directly attached to the settlement plate. If empty cells were present, additional barnacles were
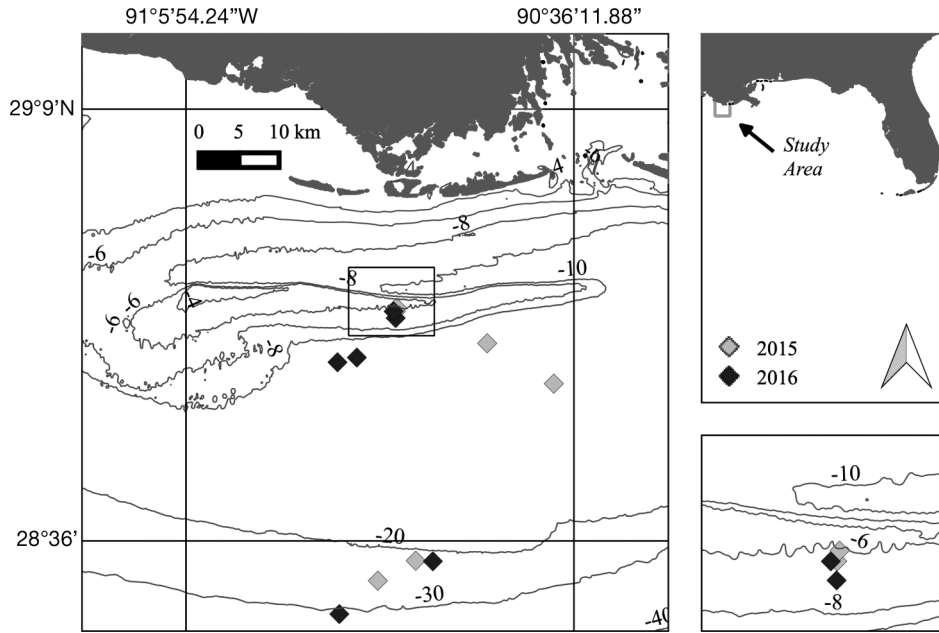
Fig. 1. Locations of platforms where settlement plates were deployed in 2015 and 2016. The panel in the bottom right is an inset for the area demarked by the small rectangle in the main plot. Numbers denote the total depth (m) of contour lines

sampled from adjacent cells so that sample size was as close as possible to 30 barnacles. Barnacle heights and widths were measured to 0.1 mm, total (shell + tissue) and tissue wet weights were measured to 0.001 g, and barnacles were identified to the species level. Settlement plates were then scraped of all fouling material, which was weighed to the nearest 0.1 g. Barnacles were then sorted by species and counted. *Amphibalanus reticulatus* and *A. amphitrite* required dissections to distinguish species, and were thus grouped as *Amphibalanus* spp. for counts. Counted barnacles were categorized as spat (≤2 mm width) or post-spat (>2 mm width). Barnacles used for biometrics were added to estimates of fouling material weight and barnacle counts.

After all settlement plates were sampled, we subsampled an additional 5 *A. reticulatus* from each plate to compare wet vs. dry tissue weights. *A. reticulatus* tissue wet weights were measured, and barnacles were subsequently dried at 110°C for 2 h (Crisp & Patel 1961) and weighed again. We did not include these barnacles in other comparisons of biometrics since this subsampling procedure differed from the original.

Statistical analyses

Barnacle abundances and biometrics were converted to rates by standardizing the following variables by time of deployment: fouling accumulation (g m^{-2} d^{-1}), post-spat and spat *Amphibalanus* spp. abundances (ind. m^{-2} d^{-1}), post-spat and spat *Megabalanus tintinnabulum* abundances (ind. m^{-2} d^{-1}), and *A. reticulatus* height (mm d^{-1}), width (mm d^{-1}), total wet weight (mg d^{-1}), and tissue wet weight (mg d^{-1}). Barnacle abundances were considered settlement rates, and *A. reticulatus* biometrics were considered proxies for growth rates. Since barnacles on an individual plate settled sometime after deployment of plates, growth rates are conservative estimates. It is also likely that barnacles on an individual plate settled at dif-

Table 1. Platform names, distances to shore, settlement plate deployment and recovery dates, and the total time of deployment (d)

Site name	Distance from shore (km)	Total depth (m)	Number of pilings	Deployment date	Recovery date	Deployment time (d)
SS 93-44	15.7	7.6	2	29 Jul 2015	4 Nov 2015	98
SS 93-43	16.2	7.9	1	29 Jul 2015	4 Nov 2015	98
SS 93-61	16.2	7.9	1	19 Aug 2016	21 Nov 2016	94
SS 93-35	17.2	8.2	1	19 Aug 2016	21 Nov 2016	94
PL 21-1	21.4	17.3	1	28 Aug 2015	1 Dec 2015	95
SS 113-52	23.1	14.9	1	21 Aug 2016	21 Nov 2016	92
SS 112-4	23.7	14.6	2	19 Aug 2016	21 Nov 2016	94
ST 72-1	28.7	19.5	1	28 Aug 2015	1 Dec 2015	95
SS 189-C	51.6	22.6	1	29 Jul 2015	1 Dec 2016	125
SS 188-3	51.7	22.3	1	21 Aug 2016	21 Nov 2016	92
SS 209-P	54.6	29.9	4	14 Aug 2015	1 Dec 2015	109
SS 215-C	59.6	33.5	1	21 Aug 2016	21 Nov 2016	92

ferent times, so we interpreted growth rates for the entire plate, not individual barnacles.

Fouling accumulation (g m^{-2} d^{-1}), post-spat and spat *Amphibalanus* spp. abundances (ind. m^{-2} d^{-1}), post-spat and spat *M. tintinnabulum* abundances (ind. m^{-2} d^{-1}), and *A. reticulatus* height (mm d^{-1}), width (mm d^{-1}), tallness (height/width), total wet weight (mg d^{-1}), and tissue wet weight (mg d^{-1}) were compared across distance from shore (km), year (2016 vs. 2017), and depth (2 vs. 7 m) using generalized linear mixed models (GLMMs; Proc Glimmix; SAS 9.4). We also used GLMMs to compare the ratio of tissue:total wet weight (percent tissue) across distance, year, and depth and included height as a covariate to account for size-specific differences. Every feasible combination of variables was considered for the comparisons listed above except for percent tissue. The model of percent tissue was selected using backward elimination because of the high number of possible variable combinations. Akaike's information criterion (AIC) was utilized to select final models. The model with the lowest AIC was selected for comparisons of all feasible models, and backward elimination removed variables that did not reduce the percent tissue model's AIC. Backward elimination began with the full model and was used to remove interactions and main effects in order of complexity (most complex interactions were removed first). When there were models with competing AIC values (ΔAIC <2; Bolker 2008), the model with fewer parameters was selected (Arnold 2010). Indicator variables were used for year (2015 = 1; 2016 = 0) and depth (2 m = 1; 7 m = 0). We also used simple linear regression to compare percent tissue vs. tallness and tissue wet weight vs. dry weight.

All statistical models were fitted with normal or lognormal distributions (identity link function), and assumptions were evaluated using predicted vs. residual plots. Random effects were used to designate individual platforms as the sampling unit for all analyses, and a plate identifier was designated as a cluster for analyses of biometrics to control for the clustered nature of the data (Nelson 2014).

RESULTS

Cross-shelf hydrography

Hydrography varied with distance from shore on plate deployment and retrieval dates (Fig. 2). With the exception of the 2015 deployment, salinity (PSU) generally increased with distance from shore and was higher on retrieval than deployment dates (Δ salinity at 5 m [offshore–nearshore]: −2.2 [2015 deployment]; 3.5 [2015 retrieval]; 1.6 [2016 deployment]; 1.7 [2016 retrieval]). There was strong salinity stratification (low salinity near the surface and high salinity at 7 m) at the platforms nearest to shore during the 2015 deployment. Salinity at 2 m was substantially lower at nearshore vs. offshore, but salinity at 7 m was higher at near-
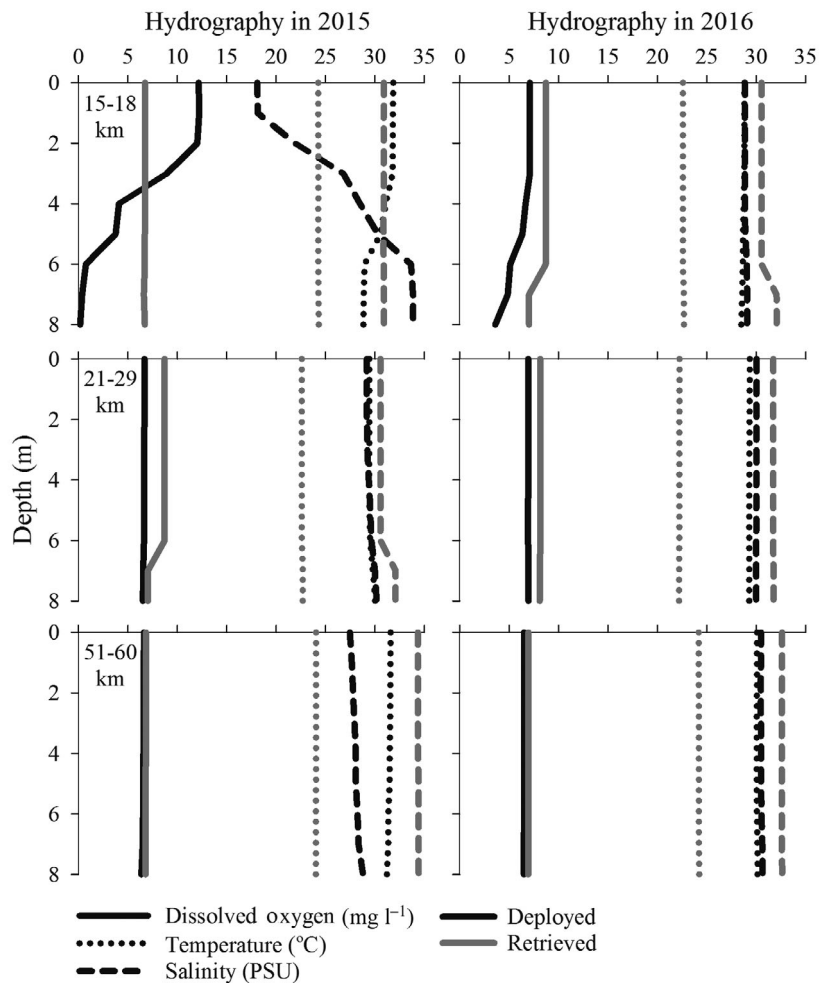

Fig. 2. Depth profiles of DO (mg l^{-1}), temperature (°C), and salinity (PSU) in 2015 and 2016 at platforms on days when settlement plates were deployed and retrieved. For this plot, platforms were grouped into 3 distance from shore categories (15–18, 21–29, 51–60 km). All hydrographic variables are plotted against a single *x*-axis that represents variables and their respective units
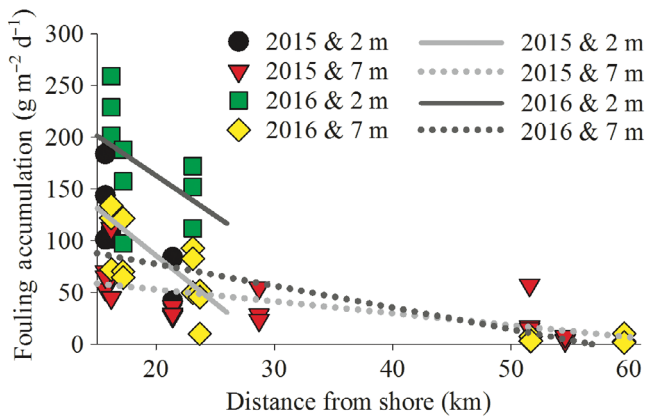
Fig. 3. Patterns of fouling accumulation (g m^{-2} d^{-1}) for each year-by-depth combination of settlement plates (2015 & 2 m, 2015 & 7 m, 2016 & 2 m, 2016 & 7 m) with varying distance from shore. Regression lines were generated by the generalized linear mixed models (GLMM) and were plotted for relationships identified as being important by Akaike's information criterion (AIC) selection

shore vs. offshore platforms. Salinity stratification at these platforms corresponded with high DO (>10 mg l^{-1}) near the surface and extremely low DO (<0.5 mg l^{-1}) at 7 m. With the exception of the 2015 retrieval, temperature (°C) generally increased with distance from shore (Δ temperature at 5 m [offshore−nearshore]: 0.9 [2015 deployment], −0.2 [2015 retrieval], 1.4 [2016 deployment], 2.1 [2016 retrieval]). This trend was not observed during the 2015 retrieval because the settlement plates closest to shore were removed ~4 wk earlier (November 4 vs. December 1) than those further offshore.

Cross-shelf fouling accumulation

Fouling accumulation decreased with increased deployment depth and distance from shore and was higher in 2016 than 2015 (Fig. 3, Table 2; Supplement 1 at www.int-res.com/articles/suppl/m590p131_supp.pdf). Inclusion of the distance-by-depth-by-year interaction indicated that separate regression lines were needed for each year-by-depth combination of plates (2015 & 2 m, 2015 & 7 m, 2016 & 2 m, 2016 & 7 m). Fouling accumulation decreased at a rate of −9.8 g m^{-2} d^{-1} km^{-1} at 2 m in 2015, −1.2 at 7 m in 2015, −7.7 at 2 m in 2016, and −2.1 at 7 m in 2016. It is possible that the steep linear declines for the 2 m plates reflected the beginning of a curvilinear relationships that would have been apparent if 2 m plates further offshore were not lost.

Cross-shelf barnacle abundances

In total, 24 946 post-spat barnacles and 5290 spat were found on the settlement plates. *Amphibalanus* spp. was the most abundant post-spat barnacle counted (~93.2%), but *Megabalanus tintinnabulum* (~6.1%), *Balanus trigonus* (~0.3%), and *A. improvisus* (~0.2%) were also observed. *A. reticulatus* and *A. amphitrite* were pooled as *Amphibalanus* spp. for counts, but *A. reticulatus* represented >99.3% (1328 of 1337) of dissected *Amphibalanus* spp. that were identified to the species level.

Amphibalanus spp. spat and post-spat accumulation rates (ind. m^{-2} d^{-1}) varied across distance from shore, depth, and year; *M. tintinnabulum* post-spat abundance (ind. m^{-2} d^{-1}) varied across year and depth, but no factors were associated with *M. tintinnabulum* spat abundances (Fig. 4, Table 2; Supplement 1). The distance-by-depth-by-year interactions for *Amphibalanus* spp. post-spat (Fig. 4A, Table 2), and spat (Fig. 4B, Table 2) indicated that 4 separate regression lines were needed for each year-by-depth combination of plates. Post-spat accumulation rates (ind. m^{-2} km^{-1} d^{-1}) were −86.2 at 2 m in 2015, −2.0 at 7 m in 2015, −18.2 at 2 m in 2016, and −4.7 at 7 m in 2016. Spat settlement decreased with increased distance from shore by 0.46-fold at 2 m in 2015, 0.97-fold at 7 m in 2015, 0.91-fold at 2 m in 2016, and 0.99-fold at 7 m in 2016. It is possible that the steep linear declines for post-spat on the 2 m plates reflected the beginning of a curvilinear relationships that would have been apparent if 2 m plates further offshore were not lost. *M. tintinnabulum* post-spat accumulation rates were not associated with distance, but there were generally 4.0-fold more post-spat m^{-2} d^{-1} in 2015 vs. 2016 (Fig. 4C, Table 2) and 5.4-fold more post-spat m^{-2} d^{-1} at 2 vs. 7 m (Fig. 4C, Table 2). None of the variables adequately explained *M. tintinnabulum* spat abundances.

Cross-shelf patterns of *A. reticulatus* biometrics

Biometrics were collected for 1468 barnacles representing 5 species; however, analyses were focused on *A. reticulatus* since it represented >90% of barnacles sampled for biometrics. Wet and dry tissue weights were significantly related (Wet = 0.02 + 10.29 × Dry; t_{213} = 31.5, p < 0.01; r^2 = 0.82) and percent tissue vs. tallness (height/width) was not significant (t_{10} = −0.1, p = 0.94).

A. reticulatus heights (mm d^{-1}) and tallness (height/weight) were generally greater closer to shore, at 2 vs. 7 m, and in 2016 vs. 2015, but widths (mm d^{-1})

Table 2. Model intercepts (Int.), degrees of freedom error (df), slopes (β) and their standard errors (SE) in parentheses for variables included in generalized linear mixed models of fouling accumulation, barnacle counts, and barnacle biometrics. Variables were abbreviated as Dist (distance from shore), Dep (depth) Yr (year), and Ht (barnacle height). See 'Statistical analyses' for details on variables and their interactions. NIM: not in model; NT: not tested (denotes that the variable was not evaluated for inclusion in that model). Indicator variables were used for year (2015 = 1; 2016 = 0) and depth (2 m = 1; 7 m = 0)

Response	Int.	df	Dist	Dep	Yr	Dist × Dep	Dist × Yr	Dep × Yr	Dist × Dep × Yr	Ht	Dist × Ht
Fouling accum.	119.510	4	−2.100 (0.5906)	198.030 (88.9595)	−43.580 (30.9306)	−5.631 (4.6047)	0.947 (0.8668)	−4.814 (132.8600)	−2.398 (7.1233)	NT	NT
Amphibalanus spp. settlement											
Post-spat	269.880	4	−4.743 (1.2541)	291.190 (194.8800)	−107.450 (65.6763)	−13.452 (10.0400)	−2.733 (1.8404)	1563.100 (290.9400)	−70.742 (15.5281)	NT	NT
ln[Spat]	1.024	4	−0.008 (0.0150)	0.985 (1.6792)	−4.335 (0.7858)	−0.091 (0.0877)	−0.022 (0.0220)	12.106 (0.2099)	−0.649 (0.1357)	NT	NT
Megabalanus tintinnabulum settlement											
ln[Post-spat]	0.570	9	NIM	1.682 (0.2812)	1.404 (0.2658)	NIM	NIM	NIM	NIM	NT	NT
ln[Spat]	0.006	11	NIM	NIM	NIM	NIM	NIM	NIM	NIM	NT	NT
Amphibalanus reticulatus biometrics											
Height	0.099	7	−0.001 (0.0001)	0.044 (0.0040)	−0.008 (0.0040)	NIM	NIM	−0.035 (0.0052)	NIM	NT	NT
Width	0.092	11	NIM	NIM	NIM	NIM	NIM	NIM	NIM	NT	NT
ln[Tallness (height/width)]	−0.109	7	−0.015 (0.0020)	0.443 (0.0543)	−0.135 (0.0655)	NIM	NIM	−0.356 (0.0750)	NIM	NT	NT
ln[Total wet wt]	2.160	7	−0.037 (0.0068)	0.496 (0.1834)	−0.767 (0.2237)	NIM	NIM	−0.273 (0.2572)	NIM	NT	NT
ln[Tissue wet wt]	0.333	7	−0.024 (0.0035)	0.625 (0.1330)	−0.656 (0.1094)	NIM	NIM	−0.925 (0.1820)	NIM	NT	NT
ln[Tissue/Total wet wt]	−1.967	7	0.017 (0.0040)	NIM	−0.430 (0.0911)	NIM	NIM	NIM	NIM	0.077 (0.0911)	−0.003 (0.0007)

were not associated with any factors (Fig. 5, Table 2; Supplement 1). Heights decreased with distance from shore (slope = −0.001 mm d^{-1} km^{-1}; Fig. 5A, Table 2), but the depth-by-year interaction indicated that the effect of depth was larger in 2016 vs. 2015. The smallest estimated mean height growth rate was 0.02 mm d^{-1} (60 km to shore at 7 m in 2015), and the greatest was 0.13 mm d^{-1} (15 km to shore at 2 m in 2016). Tallness decreased with distance from shore (Fig. 5C, Table 2), but the depth-by-year interaction indicated that the effect of depth was larger in 2016 vs. 2015. The smallest estimated mean tallness was 0.36 (60 km to shore in 2016 & 7 m), and the greatest was 1.11 (15 km to shore, 2016 & 2 m).

The total and tissue wet weights (mg d^{-1}) of *A.* reticulatus decreased with increased distance from shore, were greater in 2016 vs. 2015 and were typically greater at 2 vs. 7 m (Fig. 6, Table 2; Supplement 1). Total weight gain decreased with increased distance from shore (Fig. 6A, Table 2). Total weight gain was generally higher at 2 vs. 7 m and in 2016 vs. 2015. But a depth-by-year interaction suggested differences between 2 and 7 m were more pronounced in 2016 than 2015 (Table 2). The smallest estimated mean total weight gain was 0.43 mg d^{-1} (60 km to shore at 7 m in 2015), and the greatest was 8.17 mg d^{-1} (15 km to shore, 2016 & 2 m). It is notable that the model for total weight gain described here had a similar AIC value as a model that replaced depth-by-year interaction with depth-by-distance (Supplement 1). The depth-by-distance model showed increased total weight gain with increased distance from shore at 2 m, which was apparently driven by the 2016 data. We chose the depth-by-year model as our final model because regression lines poorly fit the data for the depth-by-distance model. Nevertheless, the plot shows that the relationship with distance from shore at 2 m in 2016
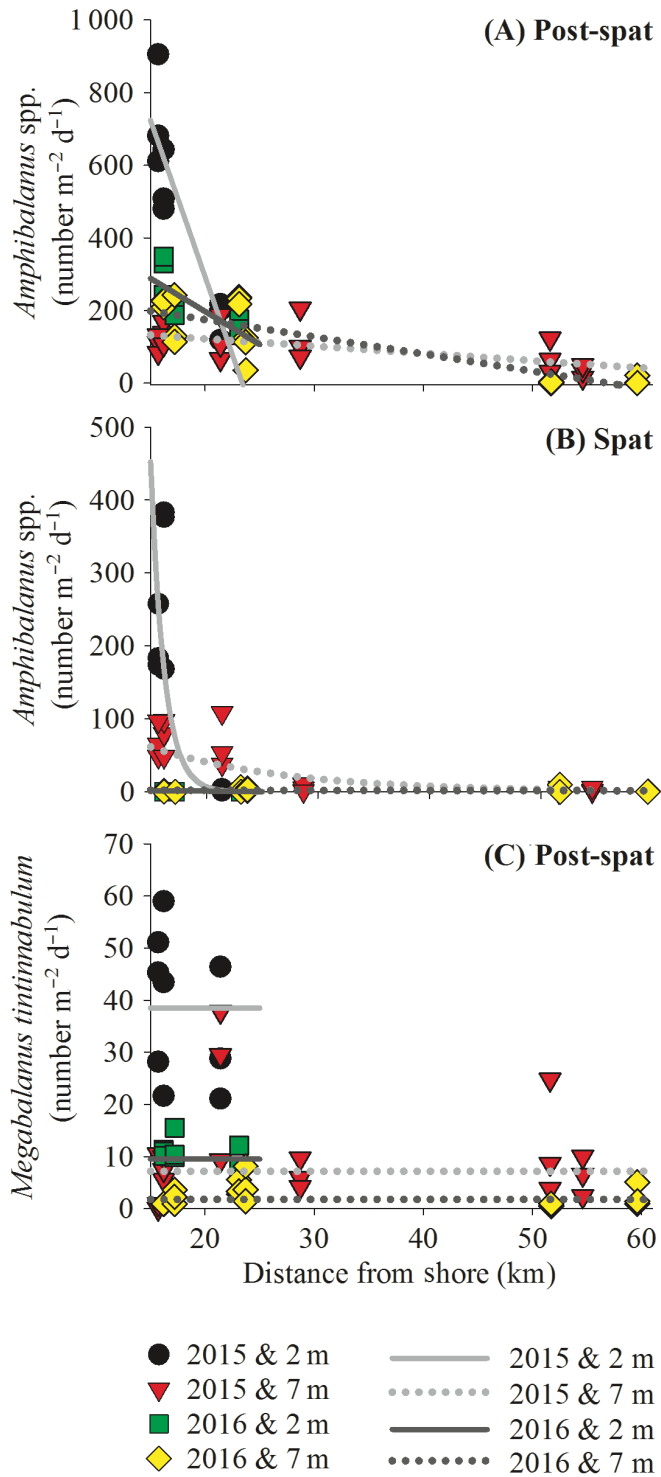
Fig. 4. (A) Post-spat and (B) spat *Amphibalanus* spp. abundances, and (C) post-spat *Megabalanus tintinnabulum* abundances for each year-by-depth combination of settlement plates (2015 & 2 m, 2015 & 7 m, 2016 & 2 m, 2016 & 7 m) with varying distance from shore. Regression lines were generated by the GLMM and were plotted for relationships identified as being important by AIC selection. Note the differences in scale for the 3 *y*-axes
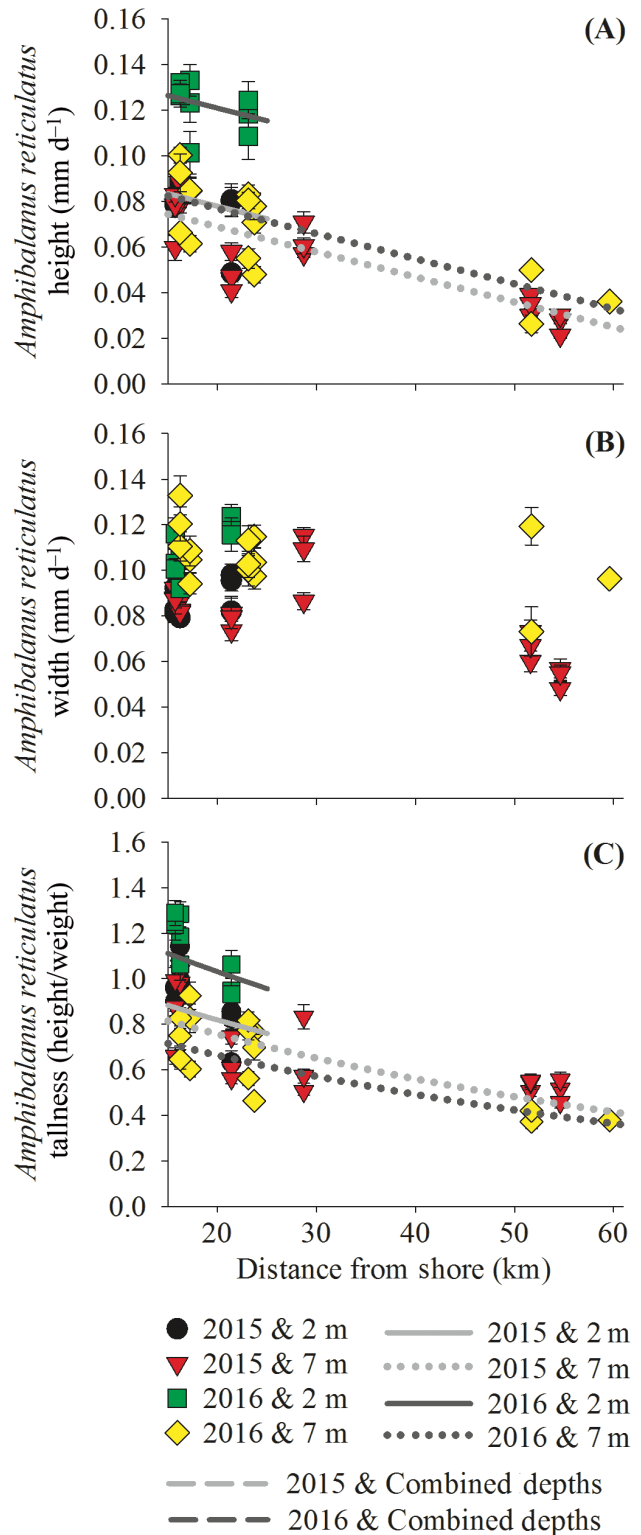
Fig. 5. *Amphibalanus reticulatus* (A) height (mm d⁻¹), (B) width (mm d⁻¹) and (C) tallness (height/width) for each year-by-depth combination of settlement plates (2015 & 2 m, 2015 & 7 m, 2016 & 2 m, 2016 & 7 m) with varying distance from shore. Regression lines were generated as described in Fig. 4
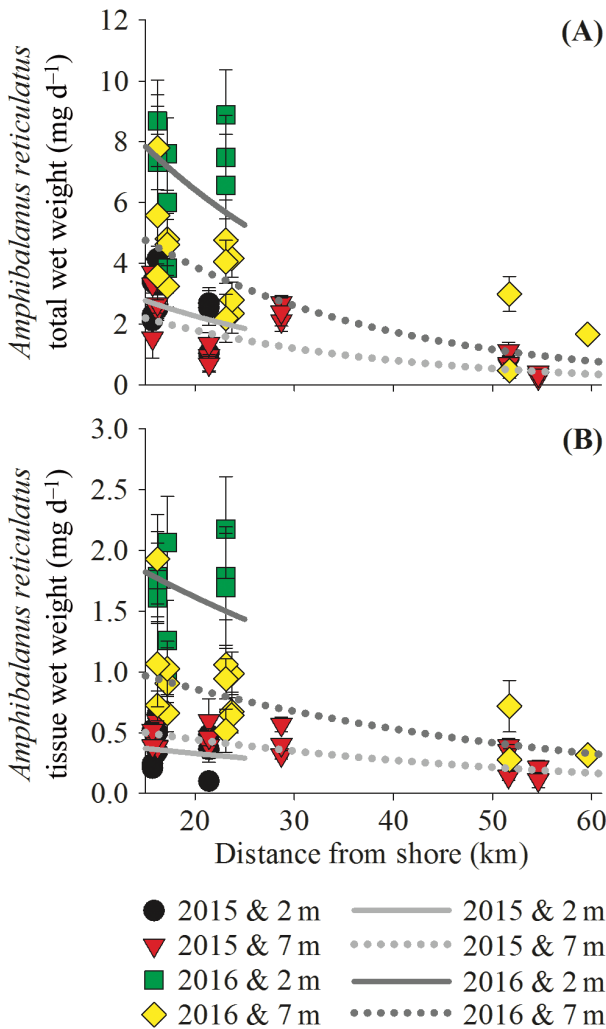
Fig. 6. *Amphibalanus reticulatus* (A) total wet weight (mg d^{-1}) and (B) tissue wet weight (mg d^{-1}) for each year-by-depth combination of settlement plates (2015 & 2 m, 2015 & 7 m, 2016 & 2 m, 2016 & 7 m) with varying distance from shore. Regression lines were generated as described in Fig. 4

was weak and possibly positive. Tissue weights decreased with increased distance from shore (Fig. 6B, Table 2), but the depth-by-year interaction indicated that the magnitude and direction of the depth effect changed across years. The effect of depth was more pronounced in 2016 vs. 2015, and weights were greater at 2 vs. 7 m in 2016 and 7 vs. 2 m in 2015. The smallest estimated mean tissue weight growth was 0.13 mg d^{-1} (60 km to shore at 2 m in 2015) and the greatest was 1.82 mg d^{-1} (15 km to shore at 2 m in 2016).

Percent wet tissue of *A. reticulatus* varied across distance from shore, height, and year (Fig. 7, Table 2; Supplement 2 at www.int-res.com/articles/suppl/
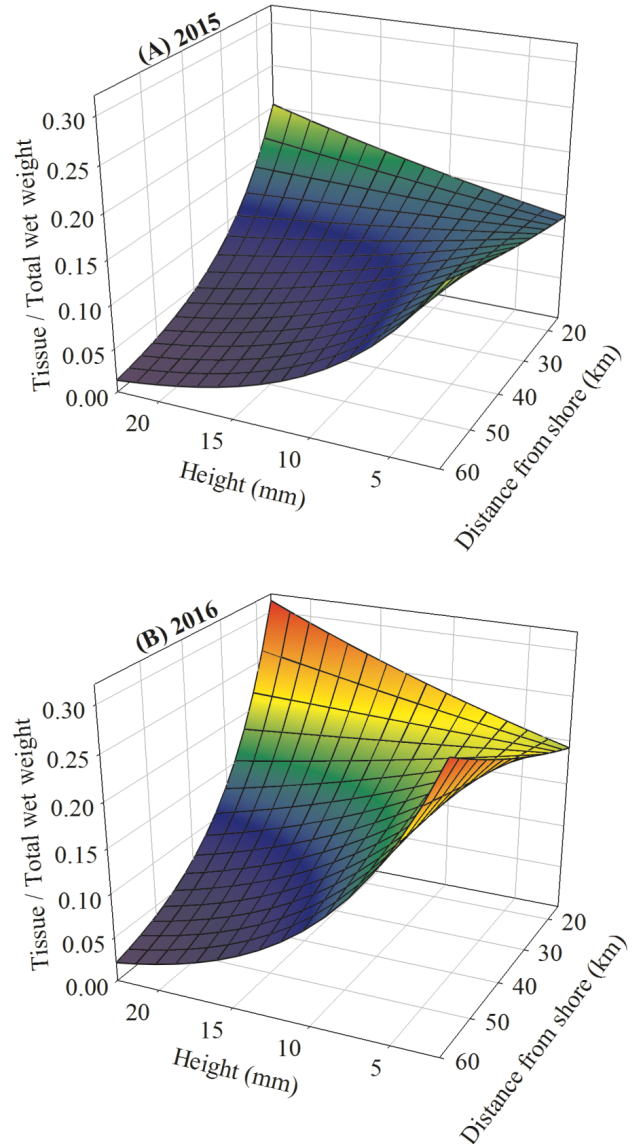

Fig. 7. Tissue/total wet weight (percent tissue) of *Amphibalanus reticulatus* across distance from shore and height in (A) 2015 and (B) 2016. Warmer colors correspond to greater percent tissue. The response surfaces were generated by the GLMM

m590p131_supp.pdf). Percent tissue was greater in 2016 vs. 2015 (Fig. 7, Table 2). A distance-by-height interaction suggested that percent tissue was similar at all distances from shore for smaller barnacles, but distance had a strong, negative effect for large barnacles and percent tissue peaked at ~25 to 30%.

DISCUSSION

Fouling accumulation, barnacle settlement, and barnacle growth were markedly higher in nearshore

waters where there was prolific primary and secondary production. It is well established that barnacle growth and settlement is greater in areas with higher phytoplankton (Bertness et al. 1991, Menge et al. 2003, Leslie et al. 2005) and zooplankton production (Sanford & Menge 2001). Thus, patterns of productivity probably drove the differences in barnacle settlement and growth described here. Primary and secondary production are generally greater closer to shore and near the surface off Louisiana's coast (Chen et al. 2000). These patterns are driven by discharge from the Mississippi and Atchafalaya rivers (Dortch & Whitledge 1992, Justic et al. 1993, Dagg & Breed 2003), which initially forms a low salinity layer in the surface water that gradually mixes with underlying sea water as distance from shore increases. Low salinity surface waters typically occur within the upper 4 m in Louisiana's nearshore waters (Munnelly 2016, Reeves et al. 2017a,b), where dense phytoplankton blooms are common (Grimes & Finucane 1991, Dortch & Whitledge 1992).

Greater percent tissue (tissue wet weight/total wet weight) of *Amphibalanus reticulatus* closer to shore and in 2016 vs. 2015 reflects a higher investment in tissue, but this relationship was only apparent for larger barnacles. Percent tissue is often positively related to tallness (height/width) and thus thinner and more brittle shells, but this relationship is species-specific (Wethey 1984) and was not observed here. This is an important consideration since brittle barnacles are more prone to crushing by conspecifics (Connell 1961). Tallness typically increases with barnacle density (Barnes & Powell 1950, Wethey 1984, Bertness 1989), and we found that plates with the highest barnacle settlement and tallness all occurred in the nearshore zone. Higher settlement and densities of barnacles may create a positive feedback by increasing ease of copulation (Crisp 1976).

Annual variability in the settlement and growth of barnacles may be related to later recruitment of *A. reticulatus* in 2016 than 2015. The highest *Amphibalanus* spp. settlement occurred for the plates at 2 m in 2015, but *A. reticulatus* growth rates were generally higher in 2016 than in 2015. This could reflect higher recruitment of *A. reticulatus* in 2015, but it more likely reflects a later recruitment. Barnacles tend to crush and displace their neighbors as they grow outwards in a crowded environment (Crisp 1960, Connell 1961), so settlement may have been similar in 2016 and 2015 but was masked by mortality of some 2016 recruits (see Bertness et al. 1992). Our strongest support for a later recruitment in 2015 was the substantially higher number of *Amphi-*

balanus spp. spat in 2015. For example, *Amphibalanus* spp. spat settlement at the 2 m plates closest to shore in 2015 exceeded 100 ind. m^{-2} d^{-1}, but spat were nearly absent in the same area during 2016. Later recruitment in 2015 may have also caused lower estimates of growth rates in 2015 vs. 2016.

Oceanographic features that may influence barnacle settlement and growth

Cross-shelf patterns of temperature and salinity may have influenced barnacle settlement and growth. Temperature is known to be positively related to barnacle growth (Phillips 2005, Inatsuchi et al. 2010), but interaction between temperature and productivity may dampen or intensify their individual effects (Sanford & Menge 2001). In this study, temperature was highest offshore where barnacle settlement and growth were lowest. Cross-shelf differences in plankton productivity may have overwhelmed the effects of temperature. Salinity also tended to increase with distance from shore. Salinity is one of the most important hydrographic features in determining species distributions (Gunter 1961), and it is possible that higher offshore salinity decreases suitability for *A. reticulatus*. However, we are unaware of research detailing *A. reticulatus* salinity suitability, and it is thus equally likely that higher salinities were more suitable for these barnacles. Barnacles are replaced by sponge and tunicate species as the dominant fouling organisms as distance from shore increases (Lewbel et al. 1987), but sponges and tunicates were not typically found on settlement plates. Barnacles were found on the settlement plates furthest offshore, but their settlement and growth were minimal.

Cross-shelf patterns of total depth and turbulence (wave height) may have also influenced barnacle settlement and growth. The 4 platforms 15 to 18 km from shore stood in waters with total depths of 7.6 to 8.2 m. Sand was often trapped between barnacles located on the 7 m plates at these platforms, and barnacles may have benefited from the resuspension of benthic microalgae and organic matter (Oviatt & Nixon 1975, Roman & Tenore 1978a,b). However, the 7 m plates at the other 8 platforms were >7 m from the bottom, and it was thus unlikely that there was notable influence from the benthos. Consistent declines in growth and settlement at 7 m plates across the entire transect and similar trends at 2 m plates (all >5 m from the bottom) suggest that the contribution of resuspended organic matter was not a

dominant factor. Turbulence also tended to increase with distance from shore and dislodged the 2 m settlement plates at the 6 platforms furthest offshore (18 plates total). There is often a positive relationship between turbulence and barnacle growth (Crisp 1960, Bertness et al. 1991, Sanford & Menge 2001) and settlement (Bushek 1988, Bertness et al. 1992), presumably because turbulence increases the encounter rate between barnacles and their food supply. However, high turbulence may decrease the ability of barnacles to capture prey by interfering with capture processes (Crisp 1955, Shimeta & Jumars 1991, Eckman & Duggins 1993), which may have contributed to lower barnacle growth offshore.

Currents and proximity to Terrebonne Bay may have influenced patterns of barnacle settlement. There is a strong current off Louisiana's coast that flows longshore (east to west) and dwarfs onshore/offshore transport (Shaw et al. 1985). Shaw et al. (1985) hypothesized that the transfer of fish and invertebrate larvae between bays and the coastal ocean likely occurs during and after the passage of cold fronts when water is advected offshore and then onshore, respectively. If concentrations of barnacle larvae are higher in the bays, proximity of nearshore platforms to Terrebonne Bay may help explain the trend of increased barnacle settlement with decreased distance from shore, given the long larval duration of barnacles (7 to 13 d for *A. eburneus*; Costlow & Bookhout 1957). However, this would not explain cross-shelf differences in growth.

Dominance of nonindigenous species on settlement plates

All barnacles collected during this study are nonindigenous species that are widely distributed. It is well established that shipping is a vector of nonindigenous species (Gollasch 2002, Davidson et al. 2009), but the transit of semisubmersible drilling platforms may pose a greater risk because they support more developed fouling communities than ship hulls (Ferreira et al. 2004). The transit of semisubmersible drilling platforms is known to move entire communities of fishes and invertebrates across biogeographic boundaries (Wanless et al. 2010, Yeo et al. 2010) and may contribute to the spread and maintenance of nonindigenous barnacles in the Gulf of Mexico. Platforms in the Gulf of Mexico host many nonindigenous species including orange cup coral *Tubastraea coccinia* (Sammarco et al. 2004) and lionfish *Pterois* spp. (Schofield et al. 2017). Given the proximity of platforms to Louisiana's coastal wetlands and the shelf-edge reefs off the Louisiana–Texas coast, it is important to evaluate their potential as vectors of nonindigenous species. In terms of policy, the spread of nonindigenous species could be a substantial counterweight to ecological services provided by platforms (Page et al. 2006).

CONCLUSIONS: IMPLICATIONS FOR ARTIFICIAL REEF MANAGEMENT

Higher barnacle settlement and growth in nearshore waters suggests that prolific nearshore primary and secondary production translated to increased production of barnacles at nearshore platforms. The difference between barnacle production at 2 and 7 m is striking and supports the argument that the vertical dimension of platforms is an important aspect of their ecological value (Stanley & Wilson 2004, Reeves et al. 2017a,b). Moreover, higher barnacle production at nearshore platforms suggests that nearshore platforms provide a different ecological function than those further offshore, and distance from shore should be considered as a part of artificial reef management plans. These are important considerations because only toppled platforms are considered for inclusion in Louisiana's Artificial Reef Program (Kaiser 2006), and the shallowest platforms currently included in the program are in depths of ~30 m. It should also be noted that barnacle production at platforms is sometimes considered to be less important than primary production (see Daigle et al. 2013). However, without platforms, barnacles would undoubtedly be less common in Louisiana's nearshore waters because there is little naturally occurring hard bottom substrate in this area (Parker et al. 1983). Thus, we consider the production of barnacles and other associated organisms (stone crabs, amphipods, etc.) as being a novel and an important characteristic of nearshore fouling communities.

Nearshore barnacle production appears to be an important aspect of the ecological function of platforms because barnacles are prey for commercially and recreationally important species, and they feed on phytoplankton in a region with excessive phytoplankton production. Gray triggerfish *Balistes capriscus* (Gallaway et al. 1981, Beaver et al. 2003, Daigle et al. 2013), sheepshead (Gallaway et al. 1981, Hoskin & Reed 1984, Sedberry 1987), and black drum *Pogonias cromis* (authors' pers. obs.) are known barnacle predators. Stone crabs *Menippe* spp. are also known to feed on barnacles (Powell &

Gunter 1968, Gallaway et al. 1981), and their abundances are positively associated with living barnacle densities on small platforms (Reeves et al. 2017a). Barnacles are generalist filter feeders that consume a variety of organisms, including phytoplankton and zooplankton (Barnes 1959), and may be an important trophic link between phytoplankton and tertiary consumers (Beaver 2002). Barnacle consumption of plankton and the subsequent energy transfer to fish and invertebrate biomass may be especially beneficial to the fishes that prey upon them in coastal Louisiana, where the decomposition of plankton leads to the annual formation of the world's second largest hypoxic zone (Turner & Rabalais 1991, 1994, Rabalais et al. 1996). Platform barnacles capture and enhance food web productivity.

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