Wave energy and flow reduce the abundance and size of benthic species on oyster reefs

Jessica Lunt[1,2,*], Joseph Reustle[1], Delbert L. Smee[1]

[1]Texas A&M University-Corpus Christi, Department of Life Sciences, Corpus Christi, TX 78412, USA

[2]*Present address:* Smithsonian Marine Station, Fort Pierce, FL 34949, USA

ABSTRACT: Hydrodynamic forces associated with waves influence the structure and function of rocky intertidal communities, but their effects on species composition and morphology within other marine communities have not been well studied. We measured wave characteristics and current speeds with acoustic Doppler velocimeters (ADVs) at oyster (*Crassostrea virginica*) reefs in St Charles and Aransas Bays, Texas. We investigated wave effects on communities at these reefs by comparing species composition, relative abundance, and species morphology on windward versus leeward sides. In addition, acorn barnacles *Amphibalanus eburneus* were used as biological indicators of flow because they develop larger basal diameters and shorter feeding appendages in faster flows. Waves were higher and current speed was faster on the windward sides of oyster reefs. Leeward sites had a greater abundance and diversity of species. Brachyuran crabs were significantly larger and more abundant when shielded from waves. Porcelain crabs *Petrolisthes armatus* were smaller and, in contrast to brachyuran crabs, more abundant at windward sites. Windward sites had fewer fish species though there was no difference in the size of fish found on either side of the reef. Barnacles settling in late spring had larger basal diameters but relatively shorter feeding appendages in windward areas, compared to leeward areas; these morphological differences mirrored ADV measurements, verified long-term differences in flow and were indicative of bigger waves and higher flow velocities in windward locations. Thus, oyster reefs can reduce wave height and slow current velocity and influence the diversity, abundance, and morphology of associated species. The decrease in wave height can provide shoreline protection, an ecosystem service of oyster reefs often mentioned but rarely measured.

KEY WORDS: Community structure · Flow · Turbulence · Barnacle · Crab

INTRODUCTION

Hydrodynamic forces are important community regulators in rocky intertidal communities (Sousa 1979, Denny et al. 1985), influencing species' composition (McQuaid & Branch 1984, Bloch & Klingbeil 2016), distributions (Leonard et al. 1998, García-March et al. 2007), morphologies (Denny & Gaylord 1996, Boulding et al. 1999, Denny 1999), and interactions (Powers & Kittinger 2002, Smee et al. 2010, Robinson et al. 2011). Species generally are more abundant and species diversity is higher in areas where stress is low (Ortega 1981, McQuaid & Branch 1984, Bloch & Klingbeil 2016), though some individual species presence or abundance may be positively affected by stress (e.g. wave exposure) (McQuaid & Branch 1984, Blanco et al. 2008, Bueno et al. 2015).

The effects of hydrodynamics on community composition vary among habitats and species assemblages (Ortega 1981, Bloch & Klingbeil 2016, Leps et al. 2016, Neumann et al. 2016). In rocky intertidal systems, diversity tends to be higher on protected shorelines (McQuaid & Branch 1984, Bloch & Klingbeil 2016), and biomass can be positively influenced because of

increased filter feeder abundance (McQuaid & Branch 1984, Guichard & Bourget 1998, Bueno et al. 2015). For example, mussel *Mytilus* spp. abundance increased with increased flow, which was attributed to food availability and filtering capacity (Guichard & Bourget 1998). On oyster reefs, diversity of sessile organisms decreased in exposed areas because scorched mussels *Brachiodontes exustus* are more tolerant of wave impacts and outcompete oyster spat and algae commonly found on protected reefs (Ortega 1981). However, the effects of wave exposure on mobile species or their size have not been assessed. Disturbance in oceanic soft sediment communities caused by tidal stress increased opportunistic species abundance, thereby altering community composition (Neumann et al. 2016). Hydrodynamics may benefit one species while impairing another. For example, Bueno et al. (2015) found that amphipod abundance increased on wave-exposed rocky shorelines while tanaidacean abundance decreased. These species-specific responses are not always directly related to exposure stress and may be an indirect effect of hydrodynamics. The decorator crab *Microphrys bicornutus*, for instance, is more prevalent on protected shorelines because the algae beds that it prefers are more abundant in these conditions (Blanco et al. 2011).

Species are often smaller and/or have different morphologies in areas subjected to waves than conspecifics in wave-protected areas (Denny et al. 1985, Denny 1999). For example, *Pinna nobilis*, a large bivalve mollusk, are smaller in areas of increased wave energy and further reduce drag associated with waves by altering their body orientation (García-March et al. 2007). Shingle urchins *Colobocentrotus atratus* live in the surf zone with intense wave action and have lost their identifying spines, thereby adapting their morphology to intense hydrodynamic forces (Denny & Gaylord 1996). Species' morphology may also be affected by interactions between hydrodynamic forces and predation. For example, periwinkle snails (Littorinidae) on wave-swept shores are smaller and have thinner shells and larger apertures than those in wave-protected areas, to better secure themselves to the substrate (Currey & Hughes 1982, Boulding et al. 1999). These morphological adaptations compensate for increased hydrodynamic stress associated with waves, but littorinids with smaller, thinner shells are more vulnerable to predation (Currey & Hughes 1982, Boulding et al. 1999). Similarly, dogwhelks *Nucella lapillus* have thinner, lighter shells with larger aperture openings on wave-swept shores where crushing predators are not typically found (Large & Smee 2013).

Wave forces and flow velocity can render predation effects unimportant and act as the primary agent of community regulation in rocky intertidal systems by limiting predator foraging ability and increasing competition (Menge 1976, Menge & Sutherland 1987, Leonard et al. 1998). However, even at levels that do not prevent predator movement, hydrodynamic forces influence predatory interactions by altering perceptive abilities in both soft sediment and rocky intertidal systems. The effects of flow on predation success are dependent on predator identity. For example, blue crabs are less effective predators in fast flows with high turbulence, but knobbed whelks are more efficient in these same conditions (Powers & Kittinger 2002). In the Damariscotta River estuary, Maine, USA, green crabs are more abundant in high flow sites than adjacent low flow sites, but green crab predation is reduced by hydrodynamic forces that compromise the ability of crabs to locate and handle prey (Leonard et al. 1998, Robinson et al. 2011).

The effects of hydrodynamics on oyster reef-associated species, especially on mobile fauna, are not well known, although the effects of flow and turbulence on spat settlement, growth, and survivorship have been examined (Turner et al. 1994, Lenihan 1999, Knights & Walters 2010). Here, we elected to study the relationship between waves and the size and distribution of organisms on oyster reefs. Oyster reefs are one of the most degraded marine habitats, but there is considerable interest and efforts in restoring them because they provide numerous ecosystems services (Coen & Luckenbach 2000, Coen et al. 2007, Beck et al. 2009). Besides being a commercially viable fishery, oyster reefs provide essential habitats for other recreational and commercially important organisms, protect shorelines, and remove harmful organisms and excess nutrients from the water through filtration (Grabowski et al. 2005, Grabowski & Peterson 2007). Despite interest in restoration, the success of oyster reef restoration efforts are variable (Coen & Luckenbach 2000, Coen et al. 2007, Plutchak et al. 2010). Understanding how environmental conditions shape oyster reef communities may improve restoration success. Abiotic variables such as salinity and dissolved oxygen are known to affect oyster recruitment, growth, and survival as well as the diversity and abundance of associated fauna on oyster reefs (Gunter 1955, Lenihan 1999, Kimbro & Grosholz 2006, Beseres Pollack et al. 2011). However, wave attenuation by oyster reefs and wave effects on oyster reef fauna require further investigation.

MATERIALS AND METHODS

Study site

Natural, intertidal oyster (*Crassostrea virginica*) reefs near Goose Island State Park in St. Charles and Aransas Bays, Texas, USA were selected for an empirical study on the effects of waves on community composition and organism size. To ensure selection of oyster reefs that differed in wave action but otherwise experienced similar abiotic variables and had similar habitat structure, we selected paired sampling locations on either side of a series of oyster reefs at the interface of St. Charles and Aransas Bays (Fig. 1). The thin white lines between the stars in the figure represent the reef crest which is generally exposed. These sampling locations were separated by approximately 100 m to ensure independence of samples, and reef sides were connected by small channels that provided a natural distinction between sampling locations. All study reefs were approximately 0.5 m below mean low water (MLW). However, this area is microtidal with very little water exchange or influence of tidal currents (Solis & Powell 1999), and waves and tides are strongly influenced by wind.

The oyster reefs within this area were low relief (very little vertical complexity created by the oys-

ters), being a mix of oyster clusters (live and boxes) and loose shell. The reefs slope gradually to deeper waters where the shell matrix is replaced by muddy sand sediments. Oyster population sampling on these reefs has been assessed, and the numbers of live oysters, oyster growth, and oyster size distribution are consistent throughout St. Charles Bay (Beseres Pollack et al. 2011, 2012, George 2013). Other structure-creating species were abundant in previous reef assessments but not found in our study (George 2013). Habitat structure in our study sites was qualitatively similar and was typical of other shallow reefs in the surrounding area but was not assessed directly as part of this study. Instead, we collected paired samples using similar artificial substrates because we were primarily interested in the associated fauna.

In this area, waves are created by prevailing southeastern winds (www.windfinder.com/windstatistics/ corpus_cristi_airport). The southern-facing side of oyster reefs in Aransas Bay are windward and frequently battered by waves, while those facing St. Charles Bay are leeward and receive little wave action (D. L. Smee pers. obs.). Additionally, the Aransas Bay system is microtidal (Solis & Powell 1999), and flow is primarily wind driven. Because of the proximity of the windward and leeward sites, water quality parameters such as salinity and temperature were similar, and species could move be-
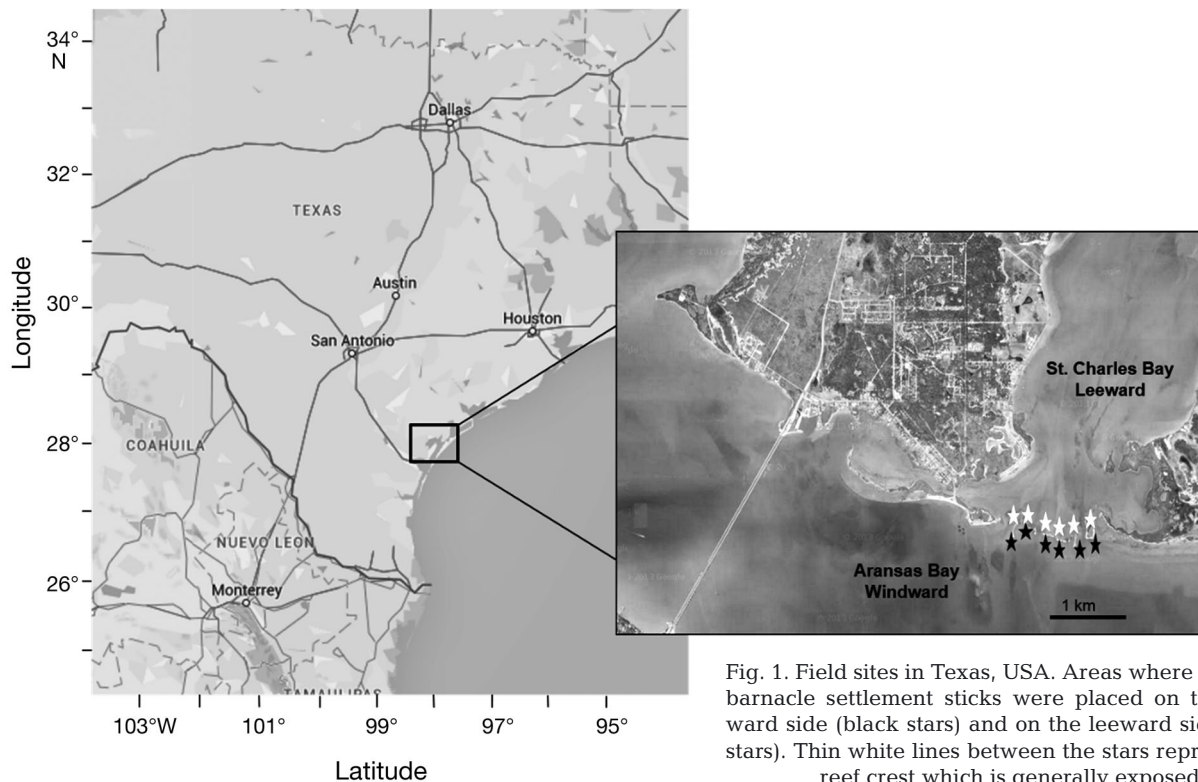

Fig. 1. Field sites in Texas, USA. Areas where trays and barnacle settlement sticks were placed on the windward side (black stars) and on the leeward side (white stars). Thin white lines between the stars represent the reef crest which is generally exposed

tween leeward and windward areas. Abiotic parameters were assessed using Hydrolab Data Sondes deployed in experimental sites intermittently for 5 d periods. Sonde deployment was limited by instrument capacity, logistical needs, and avoidance of peak usage of the state park waters for recreation. Sondes were deployed 8 times over the course of the experiment. Salinity ranged from 20 to 30 ppt and temperature ranged from 25 to 30°C on both sides of the reef over the course of the experiment, and no differences between leeward and windward sites were found. Thus, we could compare differences in the morphology of organisms as well as the abundance and diversity of associated reef fauna between areas in close proximity that differ primarily by wave regime.

Wave energy monitoring

Acoustic Doppler velocimeters (ADV, Nortek Vectrino Model) were deployed within windward and leeward sites to measure relative differences in waves. Four instruments measured waves simultaneously, with 2 pairs of ADVs deployed so that one was in St. Charles Bay on the leeward reef side and another was deployed on the windward reef side in Aransas Bay. A second pair was similarly deployed approximately 100 m away. Instruments were deployed approximately 50 m from the reef crest to ensure they were constantly submerged. ADVs were deployed for 1 wk in May 2013 and were programmed to record for 20 s every 15 min at 8 Hz. Wave data were processed with the QuickWave 2.10 and Explore V Pro © software packages (Nortek™). These software packages summarized wave height, wave period (i.e. frequency), unidirectivity index (scale 0 to 1, with 1 meaning waves move in the same direction and 0 in many directions) as well as speed and turbulence (see Table 1). These hydrodynamic parameters are known to affect species' assemblages, interactions, and morphologies on rocky shores.

Biological hydrodynamics monitoring

Barnacles *Amphibalanus eburneus* are phenotypically plastic, and react to faster flows by growing broader basal diameters and relatively shorter feeding appendages (Leonard et al. 1998, Marchinko 2003, Marchinko & Palmer 2003). We therefore used barnacles as biological flow meters by comparing

long-term effects of flow on their morphology. ADVs were constrained to a 1 wk deployment because of logistical issues. So, barnacles were used in addition to the ADVs to provide a continuous picture of hydrodynamic conditions on each side of the reef. We placed clean, 2.0 m PVC poles pressed 0.5 m into the sediment on both the windward and leeward sides of oyster reefs to allow natural barnacle recruitment onto the poles to occur. After 5 mo, poles were retrieved and returned to Texas A&M University-Corpus Christi (TAMU-CC). Barnacles settled approximately 5 to 20 cm above the sediments, which roughly corresponded to the height of community sampling trays described in the section below. Barnacles analyzed were taken from an area approximately 5 to 10 cm above the sediment (or the bottom half of the settlement area) to ensure they were at a similar height as oyster reef-associated species. All barnacles settled on the PVC poles that were at least 2.0 cm from any other barnacles were removed and measured. Barnacle body sizes were measured using 2 parameters: basal diameters (BD) and prosomal wet mass (PWM). Basal diameters were measured across the aperture or operculum, from rostrum to carina, using digital calipers. PWM was measured by removing the prosoma from the surrounding opercular plates (excluding egg masses), blot dried for 15 s using a dry Kimwipe®, and then weighed to the nearest 0.1 mg (Marchinko 2003, Marchinko & Palmer 2003). The sixth pair of cirri from each barnacle were removed and mounted in water on a slide. Cirri are often damaged in this process, and mounting 2 ensures 1 intact cirrus is available for measurement. Barnacles without intact cirri were not measured. Dissected sixth cirri were photographed using a Nikkon SMZ1000. Ramus and setae lengths were all measured using ImageJ (Marchinko & Palmer 2003).

Community sampling

Within each study site, a 0.25 m^2 area was cleared of large oyster clumps and a 0.25 m^2 (0.5 m × 0.5 m × 5 cm) lumber and Vexar mesh (1 × 1 cm) tray containing 25 l of sun-bleached oyster shells was anchored flush to the natural reef. A total of 24 trays were placed in the following arrangement: 6 pairs on the windward side and 6 pairs on the leeward side. Trays within pairs were approximately 3 m apart, and distances between pairs were approximately 100 m. We were concerned that oyster shells might be jostled easily or even knocked off trays by waves. To mini-
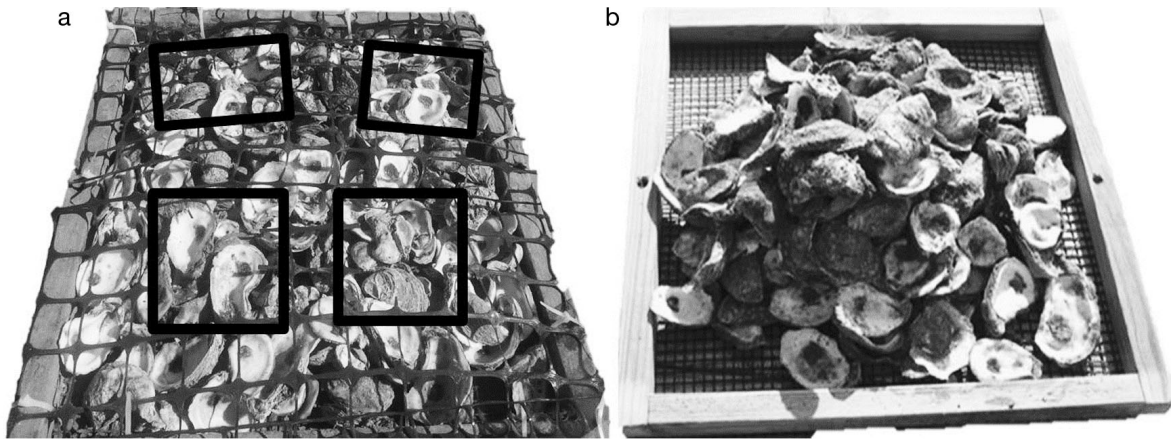
Fig. 2. Trays used for oyster reef community sampling. (a) Tray covered in Vexar mesh to retain shells. Black boxes highlight areas where mesh is not present, allowing predator access. (b) Tray with no Vexar mesh covering

mize shell movement, shells on 1 tray per pair were secured with Vexar mesh (5 × 5 cm openings; cut to have 15 × 15 cm openings at each corner) that would secure shells but not exclude predators (Fig. 2). This treatment allowed us to determine if stabilizing the substrate would change wave effects on reef fauna. The trays were deployed in the field in March and natural recruitment occurred until tray retrieval in August.

Collection and analysis

In August, all mobile organisms were collected from the trays using a modified, 1 m³ throw trap (sensu Rozas & Minello 1997), placed in ethanol, and transported to the laboratory for sorting, identification, measurement, and enumeration. This method of sampling is an effective way to collect oyster reef-resident fauna (Johnson et al. 2014, Lunt & Smee 2014). The throw trap was placed over the tray before the tray was removed from the substrate. After placement of the trap, the tray was removed, and a sweep net was used to collect any mobile organisms within the throw trap while animals in the tray were collected by hand. The number of oyster spat on 10 haphazardly selected oyster shells were counted on each tray to estimate oyster recruitment. Spat recruitment in windward and leeward sites were compared with a 2-way ANOVA, with tray cover (Vexar mesh, open) and location (leeward, windward) as factors. A 2-way ANOVA, with tray cover and location as factors, was used to determine differences in diversity, species richness, and overall abundance. Community differ-

ences were compared using multivariate analyses in PRIMER 6™. Species abundances were square root-transformed because porcelain crabs were an order of magnitude more abundant than other species. A 2-factor permutational multivariate analysis of variance (PERMANOVA) was used to compare community differences using location (windward vs. leeward) and tray cover (Vexar mesh present or not) as factors. No significant differences caused by Vexar mesh were found. An analysis of similarity (ANOSIM) was then performed using location (windward vs. leeward) as the sole factor followed by SIMPER analysis to determine which species contributed to community differences.

Using digital calipers, we measured the total lengths of all fish and shrimp collected and the carapace width of all collected crabs. The following species were found on both the leeward and windward sides of each reef in enough abundance for comparison: snapping shrimp *Alpheus* sp., pinfish *Lagodon rhomboides*, skillet fish *Gobiesox strumosus*, gulf toadfish *Opsanus beta*, porcelain crabs (Porcellanidae), mud crabs (Panopeidae), Xanthid crabs (Xanthidae, crabs too small to determine species), and gulf stone crabs *Menippe adina*. For size analysis, all brachyuran crabs (*Panopeus herbstii*, *P. turgidus*, *Eurypanopeus depressus*, and *M. adina*) were combined into a single category because of low abundance of several species and their similar morphologies. The sizes of these organisms were compared between windward and leeward areas using a 2-way ANOVA with location and Vexar mesh presence as fixed factors using JMP Pro version 12. All data tested using ANOVA met statistical assumptions.

Table 1. Mean and range of values for wave characteristics in windward (WW) and leeward (LW) areas of oyster reefs. Significant height is the mean height of the highest third of all waves recorded, zero crossing period is the average period for all the waves in a burst, unidirectivity index is how much of the wave energy is going in 1 direction on a 0 to 1 scale, with 1 meaning the energy is coming from a single direction

	Significant height (m)		Zero crossing period (s)		Unidirectivity index	
	Avg.	Range	Avg.	Range	Avg.	Range
LW	0.03	0.01–0.13	1.31	1.22–1.39	0.95	0.24–1
LW	0.07	0.01–0.15	1.29	1.24–1.37	0.96	0.4–1
WW	0.18	0.01–0.35	1.31	1.23–1.35	0.98	0.24–1
WW	0.26	0.02–0.59	1.38	1.24–1.43	0.99	0.27–1

Table 2. Flow and turbulence values for the windward (WW) and leeward (LW) areas of oyster reefs. Current speed (Speed; cm s^{-1}) and turbulence (Turb; cm s^{-1}) measurements are also reported from simultaneous measurements made at 2 leeward and 2 windward areas with an acoustic Doppler velocimeter. Turbulence was calculated as the root mean square (standard deviation) of the reported speed. X, Y, and Z represent directional velocity components

	Combined		X		Y		Z	
	Flow	Turb.	Speed	Turb.	Speed	Turb.	Speed	Turb.
LW	2.44	4.88	1.31	1.79	0.55	2.89	1.75	3.53
LW	5.06	1.83	1.82	0.99	2.61	1.19	3.78	0.92
WW	5.17	18.53	4.86	8.18	1.37	11.19	0.49	7.36
WW	8.19	18.76	6.53	10.34	4.71	13.47	0.74	7.49

RESULTS

Wave energy monitoring

Wave height (average: leeward 0.05 m, windward 0.22 m) and current speed (average: leeward 3.75 cm s^{-1}, windward 6.68 cm s^{-1}) were highest on the windward side of oyster reefs (Tables 1 & 2), but wave period (average: leeward 1.3 s, windward 1.35 s) and direction (average unidirectivity index: leeward 0.96, windward 0.99) was not different between windward and leeward areas. The unidirectivity index was >0.95, indicating that most waves were coming from the same direction. Thus, oyster reefs attenuated wave height and slowed fluid speed.

Biological hydrodynamics monitoring

Barnacles had significantly larger basal diameters on the windward side of reefs ($F_{1,50} = 50.5$, p < 0.001

Fig. 3a), and barnacle basal diameter was significantly correlated with prosomal wet mass ($t = 9.18$, p < 0.001, $r^2 = 0.80$). Barnacle ramus and setae lengths were significantly shorter in windward sites when standardized by basal diameter (ramus $F_{1,50} = 25.1$, p < 0.001; setae $F_{1,50} = 34.6$, p < 0.001, Fig. 3b,c).

Community sampling

Oyster spat numbers were not different between windward and leeward sites or treatments (average 3 spat per tray; $F_{1,19} = 0.014$, p = 0.90; $F_{19} = 0.347$, p = 0.56). Leeward sites were more diverse and had higher species richness than windward sites ($F_{1,19} = 43.08$, p < 0.0001; $F_{1,19} = 8.36$, p = 0.001; Fig. 4a,b). However, windward sites had higher abundances of organisms than did leeward sites ($F_{1,19} = 20.64$, p = 0.0002; Fig. 4c). There was no effect of the Vexar mesh cover or an interaction between the Vexar
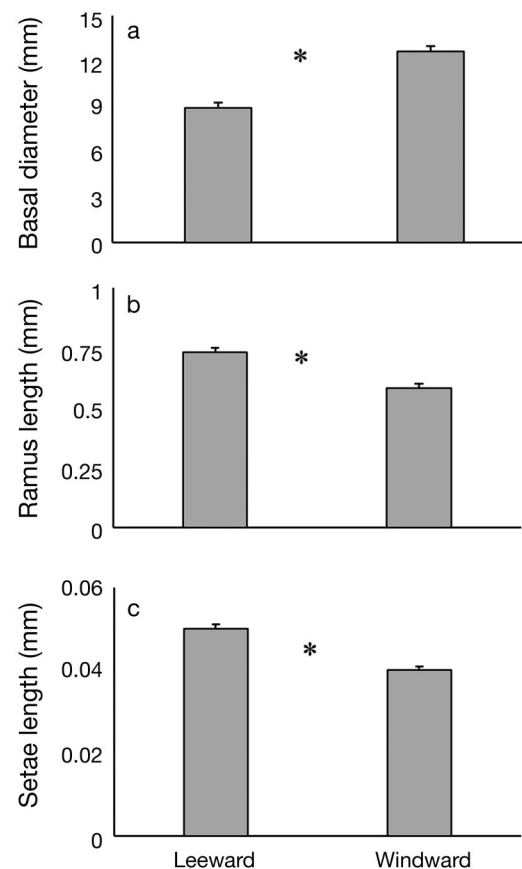

Fig. 3. Mean + SE sizes of barnacle (a) basal diameters, and (b) ramus and (c) setae lengths standardized by basal diameter. Barnacles had significantly larger diameters and relatively shorter ramus and setae lengths in windward areas. *p < 0.05, ANOVA
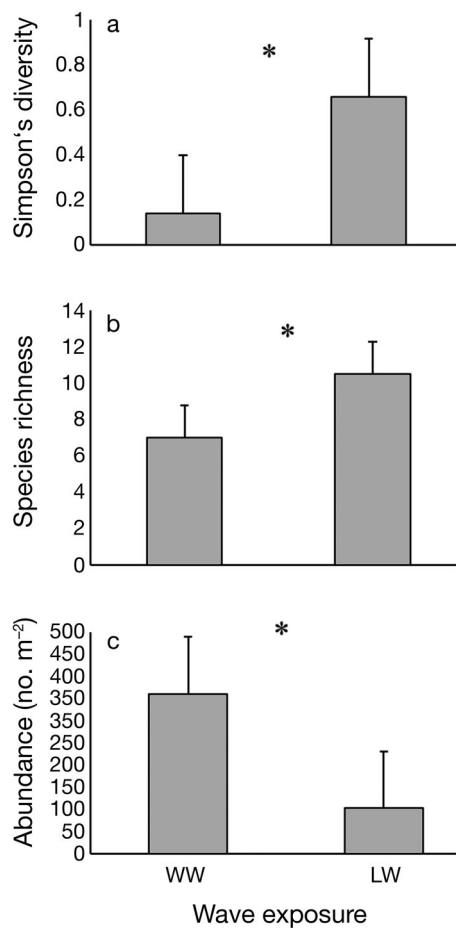
Fig. 4. Community measurements + SE. Comparisons of (a) Simpson's species diversity, (b) species richness, and (c) species abundance for windward (WW) and leeward (LW) sites. *p < 0.05, ANOVA

Table 4. Species collected on oyster reefs within St. Charles Bay during the study. Xanthid crabs refers to mud crabs found under 10 mm in carapace width because at this size, mud crab species are difficult to distinguish. WW: capture in windward sites; LW: capture in leeward sites

Common name	Scientific name	Site
Bigclaw snapping shrimp	*Alpheus heterochaelis*	WW, LW
Arrow shrimp	*Tozeuma carolinense*	LW
Crested blenny	*Hypleurochilus geminatus*	LW
Flatback mud crab	*Eurypanopeus depressus*	WW
Gastropod	Gastropoda	WW, LW
Goby unidentified	Gobiidae	WW
Inland silverside	*Menidia beryllina*	LW
Pinfish	*Lagodon rhomboides*	WW, LW
Gulf stone crab	*Mennipe adina*	WW, LW
Hooked mussel	*Ischadium recurvum*	WW, LW
Naked goby	*Gobiosoma bosc*	LW
Atlantic mud crab	*Panopeus herbstii*	WW, LW
Ridgeback mud crab	*Eurypanopeus turgidus*	WW, LW
Grass shrimp	*Palaemonetes* spp.	LW
Penaeid shrimp	Penaeidae	LW
Chain pipefish	*Syngnathus louisianae*	WW, LW
Green porcelain crab	*Petrolisthes armatus*	WW, LW
Shrimp eel	*Ophichthus gomesii*	LW
Skilletfish	*Gobiesox strumosus*	WW, LW
Eastern oyster	*Crassostrea virginica*	WW, LW
Longnose spider crab	*Libinia dubia*	WW
Gulf toadfish	*Opsanus beta*	WW, LW
Xanthid crabs	Xanthidae	WW, LW

Table 3. ANOVA table for community assemblage metrics. Simpson's diversity, species richness, and total abundance for each sample collected on St. Charles Bay oyster reefs were compared between wave exposure (windward and leeward sites) and presence of Vexar mesh

Factor	df	*F*-statistic	p-value
Simpson's diversity			
Wave exposure	1,19	43.0800	0.0001
Vexar	1,19	0.0232	0.8805
Interaction	1,19	0.0001	0.9939
Species richness			
Wave exposure	1,19	13.65	0.0014
Vexar	1,19	0.12	0.7286
Interaction	1,19	1.98	0.1746
Total abundance			
Wave exposure	1,19	20.64	0.0002
Vexar	1,19	0.8385	0.3707
Interaction	1,19	0.5779	0.4560

mesh and location with p > 0.2 for all ANOVA; (Table 3). Communities were significantly different between windward and leeward sites (Pseudo-F = $7.0_{1,19}$, p = 0.001) but not between treatments with and without Vexar mesh (Pseudo-F = $0.55_{1,19}$, p = 0.77). The interaction between location and Vexar mesh presence was not significant (Pseudo-F = $0.95_{1,19}$, p = 0.44), suggesting that hydrodynamic differences between sites accounted for community differences and that securing shells did not change these effects. ANOSIM also revealed significant differences between communities on windward versus leeward areas (R = 0.44, p = 0.001). An R-value of 0.44 suggests hydrodynamic differences account for much of the variation between community samples. Porcelain crabs *Petrolisthes armatus* and gastropods were more abundant in windward areas, but grass shrimp *Palaemonetes* sp., penaeid shrimp, crabs (Brachyura), and snapping shrimp *Alpheus heterochaelis* were more abundant in leeward areas. Grass and penaeid shrimp were not found in windward areas (Table 4). SIMPER analysis revealed leeward and windward sites to be 65% dissimilar (Table 5).

Table 5. SIMPER analysis of community composition on windward (WW) and leeward (LW) areas. Abundances are per 0.25 m^2 and were square root transformed for analysis. diss.: dissimilarity; contr.: contributed

| Species | Mean abund. | | WW vs. LW[a] | |
	WW	LW	Mean diss.	Contr. (%)
Porcellanidae	12.53	6.18	22.4	34.5
Palaemonetes sp.	0	3.12	7.3	11.3
Gastropoda	2.54	0.83	4.6	7.1
Penaeidae	0	2.0	4.5	7.0
Alpheus heterochaelis	0.24	1.92	4.2	6.5
Brachyura	1.56	2.18	3.2	4.9
[a]Average dissimilarity = 65.1				

Brachyuran crabs were larger in leeward sites than in windward sites ($F_{1,24}$= 3.86, p = 0.03; Fig. 5a), but snapping shrimp were larger in the windward sites ($F_{2,11}$= 10.48, p = 0.01; Fig. 5b). Porcelain crabs were smaller in the windward sites ($F_{2,22}$= 24.07, p < 0.0001; Fig. 5c), despite being more abundant in these areas. Pinfish *Lagodon rhomboides*, skilletfish *Gobiesox strumosus* and toadfish *Opsanus beta* lengths were not different between leeward and windward areas ($F_{2,7}$ = 0.53, p = 0.50; $F_{2,7}$ = 0.01, p =

Table 6. ANOVA results for analyses of organism size (mm) reported as carapace width for crabs and total length for all other species from windward and leeward sides of St. Charles Bay oyster reefs. Sizes were compared by wave exposure (windward and leeward) and presence of Vexar mesh. Too few pinfish and snapping shrimp were collected to compare between Vexar mesh treatments

| Factor	df	*F*-statistic	p-value
Brachyuran crabs			
Wave exposure	1, 24	3.86	0.03
Vexar	1, 24	0.74	0.40
Interaction	1, 24	0.56	0.58
Porcelain crabs			
Wave exposure	1, 22	24.07	0.0001
Vexar	1, 22	1.24	0.28
Interaction	1, 22	0.05	0.83
Skilletfish			
Wave exposure	1, 7	0.01	0.9428
Vexar	1, 7	0.02	0.9014
Interaction	1, 7	0.02	0.9014
Toadfish			
Wave exposure	1, 16	1.05	0.33
Vexar	1, 16	0.001	0.98
Interaction	1, 16	1.1494	0.30
Snapping shrimp			
Wave exposure	1, 11	10.48	0.01
Pinfish			
Wave exposure	2, 7	0.53	0.50
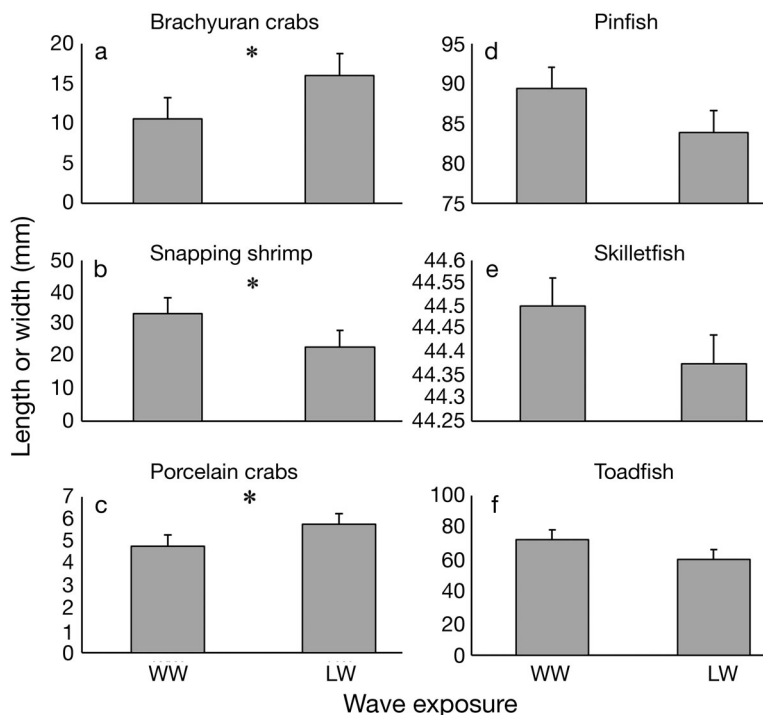
Fig. 5. Mean + SE size of organisms collected (carapace width for crabs, body length for other species) in windward (WW) and leeward (LW) sites. *p < 0.05, ANOVA

0.94; $F_{2,16}$ = 1.05, p = 0.33; respectively; Fig. 5d,e,f). Too few pinfish and snapping shrimp were collected to test for an effect of the Vexar mesh treatment. There was no significant effect of Vexar mesh and no interaction between the Vexar mesh treatment and location for any of the other species (p > 0.2 for all ANOVAS; Table 6).

DISCUSSION

Wave forces are well-known community regulators within rocky intertidal communities, influencing the morphology, diversity, forging strategy, and composition of communities (Sousa 1979, Denny et al. 1985, Denny & Gaylord 1996, García-March et al. 2007). Our data indicate that waves can also affect the size and distribution of species inhabiting oyster reefs. Like rocky intertidal habitats, we found species composition and size to differ significantly between windward and leeward sites. The waves in our study area are wind driven within a large

bay and do not reach the sizes or speeds of waves breaking on open coastlines. Yet in both habitat types, mobile species tended to be larger and more abundant, and species size patterns and growth rates were consistent with observations in rocky intertidal areas (Menge 1976, Leonard et al. 1998). Within oyster reef communities, species richness and crab sizes decreased in areas with higher wave height and current speed. Communities on windward and leeward sites were significantly different, though they did not differ in oyster recruitment. Flow velocity can affect recruitment only in the short term (Knights & Walters 2010), since we sampled in August (peak spawn in April to May), it is likely any initial differences in oyster recruitment were missed by our study (Beseres Pollack et al. 2011). Communities were 65% dissimilar between windward and leeward areas with windward areas dominated by porcelain crabs and gastropods while shrimp were the most abundant species in leeward areas.

Windward sites had higher waves and faster current speeds than leeward sites, which is consistent with 10 yr of personal observations in this area (D. L. Smee pers. obs.). The study area is microtidal, with currents primarily wind-driven, and current speed differences are the result of wave attenuation by the oyster reefs. Barnacles were used as biological flow meters because they are phenotypically plastic, and they grow larger basal diameters with relatively shorter, thinner feeding appendages in faster flows (Leonard et al. 1998, Marchinko 2003, Marchinko & Palmer 2003). Consistent with personal observations and measured hydrodynamic parameters, barnacles had larger basal diameters and shorter feeding appendages in windward areas that received direct wave energy and faster flows created through prevailing southeasterly winds.

Windward sites did not contain grass or penaeid shrimp and had fewer fish species. Porcelain crabs were more abundant than all other species combined. In windward sites, we collected approximately 340 porcelain crabs per tray, while leeward sites had a much lower abundance, averaging approximately 50 crabs per tray. Leeward sites had higher species richness and diversity, but an overall lower abundance of organisms than windward sites, due to the high number of porcelain crabs in windward areas. Brachyuran crabs (mostly mud crabs, Panopeidae) were much more abundant and larger in leeward than windward sites. Porcelain crabs are readily consumed by mud crabs (Hollebone & Hay 2008), and we found an inverse relationship between porcelain crab and mud crab abundance. Our work-

ing hypothesis is that waves restrict mud crab movement and release porcelain crabs from predation. Faster flows decrease porcelain crab foraging efficiency (Achituv & Pedrotti 1999), perhaps contributing to their smaller sizes in the faster flow sites. Given the negative effects of flow on porcelain crab feeding, it does not seem likely that porcelain crabs would elect to live in faster flow sites, but rather, may move to them or survive better in them where their brachyuran crab predators are less abundant.

Faster flows can provide more access to food for suspension feeding organisms by increasing food delivery to the substrate and resuspending benthic particles (Jorgensen 1966, Sebens 1984, Lesser et al. 1994), potentially leading to higher abundances and growth rates of suspension feeders (Leonard et al. 1998). However, the effects of flow differ between active and passive suspension feeders. For passive feeders like barnacles, the higher particle flux increases feeding efficiency and growth until feeding appendage deformation occurs (Sebens 1984). For active feeders, flow can impede particle capture, causing slower growth (Eckman et al. 1989, Leonard et al. 1998). Porcelain crabs are active suspension feeders and their feeding efficiency is inhibited by faster flows (Achituv & Pedrotti 1999).

A total of 12 taxa were found in both windward and leeward sites, but only 6 were abundant enough to allow statistical comparison of body size: brachyuran crabs, snapping shrimp, porcelain crabs, pinfish, skilletfish, and toadfish. For the purpose of size comparisons, all mud crab species, xanthid crabs, and stone crabs were grouped as Brachyura. This was necessary to ensure enough crabs were collected in windward sites for statistical comparison and because these crabs have similar morphologies and likely experience similar hydrodynamic forces. Crabs were significantly smaller and snapping shrimp significantly larger in windward than in leeward areas, while fish sizes did not differ. Porcelain crabs were smaller but more abundant in windward sites than in leeward sites, perhaps due to lower feeding ability in faster flows (Achituv & Pedrotti 1999). Smaller sizes might be an effect of intraspecific competition, although food is readily abundant and this explanation does not seem likely. Brachyuran crabs (mud and stone crabs) were both smaller and less abundant in windward sites. The crabs found in windward sites had a carapace width of approximately 10 mm, a size that still allows them to utilize interstitial spaces within oyster reefs as a potential refuge from waves and predators (McDonald 1982). The larger crabs found in leeward sites were perhaps less able to find

sufficient interstitial spaces on windward reef areas and were resultantly removed from windward reefs by hydrodynamic forces.

Intense intraspecific competition generally prevents organisms from being both larger and more abundant (Alunno-Bruscia et al. 2000). Brachyuran crabs being both larger and more abundant in leeward sites suggests that flow is an important factor in determining distribution. Intraspecific competition in leeward areas is likely elevated over windward areas due to higher mud crab densities, but increased prey abundance coupled with less hydrodynamic interference in leeward areas may allow crabs to reach higher densities and larger sizes (Robinson et al. 2011). Snapping shrimp were larger and less abundant in windward sites. Unlike crabs, snapping shrimp project a smaller frontal area than crabs and experience less effects of hydrodynamic forces such as lift and drag (Denny 1999), and their higher density but decreased size in leeward areas is consistent with elevated competition (Alunno-Bruscia et al. 2000). Fewer fish in windward sites may also decrease predation risk for snapping shrimp, allowing them to achieve larger sizes.

A number of factors play a role in how hydrodynamics shape communities including lift, drag, and wave acceleration (Denny 1999). These forces often act in concert and it is rarely a single force that alters a species habitat use or morphology (Denny et al. 1985, Denny 1999). For example, shingle urchins *Colobocentrotus atratus* lack spines, which reduces drag but increases lift. Still, the loss of spines and subsequent drag reduction make this organism more resistant to the forces of water acceleration, allowing it to exist in the surf zone (Denny & Gaylord 1996). These same forces may influence the sizes of organisms inhabiting oyster reefs and account for the observed patterns. Larger mud crabs, not present in higher wave sites, may be washed off reefs with faster flows and larger waves through a combination of lift and drag forces that change with body size. This effect of hydrodynamics on organisms may influence habitat selection within oyster reefs by individual species and contribute to the overall community structure within an oyster reef.

Increased hydrodynamic stress can shape communities by alleviating predation pressure through actively interfering with predator movement and making finding prey more challenging (Menge 1976, Menge & Sutherland 1987, Leonard et al. 1998, Smee et al. 2008). In this study, fewer nektonic fish, such as inland silversides *Menidia beryllina* and pinfish *Lagodon rhomboides*, were found in the sites with higher flow and wave heights. The reduction in fish species richness and abundance among sites may be a result of fish being more limited by increased hydrodynamic stress than benthic species, which can utilize the reef as a refuge. This may also be the case for larger fish predators. However, the sampling method used in this study does not effectively sample large, mobile organisms (i.e. blue crabs *Callinectes sapidus* and red drum *Sciaenops ocellatus*) which are abundant, transient predators on oyster reefs. It is possible that hydrodynamic stress interacts with predation to shape the communities on the windward and leeward sides of the oyster reefs, but more research is needed to test this hypothesis.

Oyster reefs are a critically endangered habitat of both ecological and economic importance (Grabowski & Peterson 2007, Beck et al. 2009) and are currently the subject of widespread restoration efforts (Coen & Luckenbach 2000, Coen et al. 2007, Plutchak et al. 2010). In order to successfully restore the ecosystem services offered by oyster reefs, the effects of abiotic variables on their ecosystem functioning must be well understood. Lower abundance of prey species (mud crabs, silversides, penaeid shrimp) in areas of high wave energy may reduce prey availability for larger commercial and recreational species. However, oyster reefs also attenuate wave energy as an ecosystem service (Grabowski & Peterson 2007), and the interaction between wave attenuation and commercial and recreational benefits should be considered carefully. Oyster reef management plans should take wave energy into account when determining sampling locations for monitoring efforts. Areas along the reef subject to high waves and faster flows are not likely to be representative of all the species present on the reef. Finally, our findings indicate that oyster reefs can decrease wave height and can provide shoreline protection, an ecosystem service often mentioned but rarely measured.

LITERATURE CITED

Achituv Y, Pedrotti ML (1999) Costs and gains of porcelain crab suspension feeding in different flow conditions. Mar Ecol Prog Ser 184:161–169

Alunno-Bruscia M, Petraitis PS, Bourget E, Frechette M (2000) Body size-density relationship for *Mytilus edulis* in an experimental food-regulated situation. Oikos 90: 28–42

Beck MW, Brumbaugh RD, Airoldi L, Carranza A and others (2009) Shellfish reefs at risk: a global analysis of problems and solutions. The Nature Conservancy, Arlington, VA

Beseres Pollack JB, Kim HC, Morgan EK, Montagna PA (2011) Role of flood disturbance in natural oyster (*Crassostrea virginica*) population maintenance in an estuary in south Texas, USA. Estuaries Coasts 34:187–197

Beseres Pollack J, Cleveland A, Palmer TA, Reisinger AS, Montagna PA (2012) A restoration suitability index model for the eastern oyster (*Crassostrea virginica*) in the Mission-Aransas Estuary, TX, USA. PLOS ONE 7:e40839

Blanco S, Fernández-Aláez M, Bécares E (2008) Efficiency of top-down control depends on nutrient concentration in a Mediterranean shallow lake: a mesocosm study. Mar Freshw Res 59:922–930

Blanco CG, Gusmão-Junior JBL, Christofoletti RA, Costa TM (2011) Hydrodynamism and its influence on the density of the decorator crab *Microphrys bicornutus* (Mithracidae) on intertidal rocky shores from a subtropical region. Mar Biol Res 7:727–731

Bloch CP, Klingbeil BT (2016) Anthropogenic factors and habitat complexity influence biodiversity but wave exposure drives species turnover of a subtropical rocky intertidal metacommunity. PSZNI: Mar Ecol 37:64–76

Boulding EG, Holst M, Pilon V (1999) Changes in selection on gastropod shell size and thickness with wave-exposure on northeastern pacific shores. J Exp Mar Biol Ecol 232:217–239

Bueno M, Dena-Silva SA, Flores AAV, Leite FPP (2015) Effects of wave exposure on the abundance and composition of amphipod and tanaidacean assemblages inhabiting intertidal coralline algae. J Mar Biol Assoc UK 96: 1–7

Coen LD, Luckenbach MW (2000) Developing success criteria and goals for evaluating oyster reef restoration: ecological function or resource exploitation? Ecol Eng 15: 323–343

Coen LD, Brumbaugh RD, Bushek D, Grizzle R and others (2007) Ecosystem services related to oyster restoration. Mar Ecol Prog Ser 341:303–307

Currey JD, Hughes RN (1982) Strength of the dogwhelk *Nucella lapillus* and the winkle *Littorina littorea* from different habitats. J Anim Ecol 51:47–56

Denny M (1999) Are there mechanical limits to size in wave-swept organisms? J Exp Biol 202:3463–3467

Denny M, Gaylord B (1996) Why the urchin lost its spines: Hydrodynamic forces and survivorship in three echinoids. J Exp Biol 199:717–729

Denny MW, Daniel TL, Koehl MAR (1985) Mechanical limits to size in wave-swept organisms. Ecol Monogr 55:69–102

Eckman JE, Peterson CH, Cahalan JA (1989) Effects of flow speed, turbulence, and orientation on growth of juvenile bay scallops *Argopecten irradiansconcentricus* (Say). J Exp Mar Biol Ecol 132:123–140

García-March JR, Pérez-Rojas L, García-Carrascosa AM (2007) Influence of hydrodynamic forces on population structure of *Pinna nobilis* L., 1758 (Mollusca: Bivalvia): the critical combination of drag force, water depth, shell size and orientation. J Exp Mar Biol Ecol 342:202–212

George LM (2013) Relative habitat value of alternative substrates used in oyster reef restoration. MSc thesis, Texas A&M University, College Station, TX

Grabowski JH, Peterson CH (2007) Restoring oyster reefs to recover ecosystem services. In: Cuddington K, Byers JE, Wilson WG, Hastings A (eds) Ecosystem engineers: plants to protists. Academic Press, Burlington, MA, p 281–298

Grabowski JH, Hughes AR, Kimbro DL, Dolan MA (2005) How habitat setting influences restored oyster reef communities. Ecology 86:1926–1935

Guichard F, Bourget E (1998) Topographic heterogeneity, hydrodynamics, and benthic community structure: a scale-dependent cascade. Mar Ecol Prog Ser 171:59–70

Gunter G (1955) Mortality of oysters and abundance of certain associates as related to salinity. Ecology 36:601–605

Hollebone AL, Hay ME (2008) An invasive crab alters interaction webs in a marine community. Biol Invasions 10: 347–358

Johnson KD, Grabowski JH, Smee DL (2014) Omnivory dampens trophic cascades in estuarine communities. Mar Ecol Prog Ser 507:197–206

Jorgensen CB (1966) Biology of suspension feeding. Pergamon Press, Oxford

Kimbro DL, Grosholz ED (2006) Disturbance influences oyster community richness and evenness, but not diversity. Ecology 87:2378–2388

Knights AM, Walters K (2010) Recruit–recruit interactions, density-dependent processes and population persistence in the eastern oyster *Crassostrea virginica.* Mar Ecol Prog Ser 404:79–90

Large SI, Smee DL (2013) Biogeographic variation in behavioral and morphological responses to predation risk. Oecologia 171:961–969

Lenihan HS (1999) Physical–biological coupling on oyster reefs: how habitat structure influences individual performance. Ecol Monogr 69:251–275

Leonard GH, Levine JM, Schmidt PR, Bertness MD (1998) Flow-driven variation in intertidal community structure in a Maine estuary. Ecology 79:1395–1411

Leps M, Sundermann A, Tonkin JD, Lorenz AW, Haase P (2016) Time is no healer: Increasing restoration age does not lead to improved benthic invertebrate communities in restored river reaches. Sci Total Environ 557–558: 722–732

Lesser MP, Witman JD, Sebens KP (1994) Effects of flow and seston availability on scope for growth of benthic suspension-feeding invertebrates from the Gulf of Maine. Biol Bull 187:319–335

Lunt J, Smee DL (2014) Turbidity influences trophic interactions in estuaries. Limnol Oceanogr 59:2002–2012

Marchinko KB (2003) Dramatic phenotypic plasticity in barnacle legs (*Balanus glandula* Darwin): magnitude, age dependence, and speed of response. Evolution 57: 1281–1290

Marchinko KB, Palmer AR (2003) Feeding in flow extremes: dependence of cirrus form on wave-exposure in four barnacle species. Zoology 106:127–141

McDonald J (1982) Divergent life history patterns in the co-occurring intertidal crabs *Panopeus herbstii* and *Eurypanopeus depressus* (Crustacea: Brachyura: Xanthidae). Mar Ecol Prog Ser 8:173–180

McQuaid CD, Branch GM (1984) Influence of sea temperature, substratum and wave exposure on rocky intertidal communities: an analysis of faunal and floral biomass. Mar Ecol Prog Ser 19:145–151

Menge BA (1976) Organization of the New England rocky intertidal community: role of predation, competition, and environmental heterogeneity. Ecol Monogr 46:355−393

Menge BA, Sutherland JP (1987) Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. Am Nat 130:730−757

Neumann H, Diekmann R, Kröncke I (2016) Functional composition of epifauna in the south-eastern North Sea in relation to habitat characteristics and fishing effort. Estuar Coast Shelf Sci 169:182−194

Ortega S (1981) Environmental stress, competition and dominance of *Crassostrea virginica* near Beaufort, North Carolina, USA. Mar Biol 62:47−56

Plutchak R, Major K, Cebrian J, Foster CD and others (2010) Impacts of oyster reef restoration on primary productivity and nutrient dynamics in tidal creeks of the North Central Gulf of Mexico. Estuaries Coasts 33:1355−1364

Powers SP, Kittinger JN (2002) Hydrodynamic mediation of predator−prey interactions: differential patterns of prey susceptibility and predator success explained by variation in water flow. J Exp Mar Biol Ecol 273:171−187

Robinson EM, Smee DL, Trussell GC (2011) Green crab (*Carcinus maenas*) foraging efficiency reduced by fast flows. PLOS ONE 6:e21025

Rozas LP, Minello TJ (1997) Estimating densities of small fishes and decapod crustaceans in shallow estuarine habitats: a review of sampling design with focus on gear selection. Estuaries 20:199−213

Sebens KP (1984) Water flow and coral colony size: Inter-habitat comparisons of the octocoral *Alcyonium siderium.* Proc Natl Acad Sci USA 81:5473−5477

Smee DL, Ferner MC, Weissburg MJ (2008) Alteration of sensory abilities regulates the spatial scale of nonlethal predator effects. Oecologia 156:399−409

Smee DL, Ferner MC, Weissburg MJ (2010) Hydrodynamic sensory stressors produce nonlinear predation patterns. Ecology 91:1391−1400

Solis RS, Powell GL (1999) Hydrography, mixing characteristics, and residence times of Gulf of Mexico estuaries. In: Bianchi TS, Pennock JR, Twilley RR (eds) Biogeochemistry of Gulf of Mexico estuaries. John Wiley & Sons, New York, NY, p 55

Sousa WP (1979) Disturbance in marine intertidal boulder fields: the nonequilibrium maintenance of species diversity. Ecol Lett 60:1225−1239

Turner EJ, Zimmer-Faust RK, Palmer MA, Luckenbach M, Pentcheff ND (1994) Settlement of oyster (*Crassostrea virginica*) larvae: effects of water flow and a water-soluble chemical cue. Limnol Oceanogr 39:1579−1593