Vol. 608: 61–72, 2019
https://doi.org/10.3354/meps12823

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published January 3

Co-occurring secondary foundation species have distinct effects on the recruitment and survival of associated organisms

Maria L. Vozzo[1,2,*], Melanie J. Bishop[1]

[1]Department of Biological Sciences, Macquarie University, North Ryde, NSW 2109, Australia

[2]*Present address:* Sydney Institute of Marine Science, Mosman, NSW 2088, Australia

ABSTRACT: There is growing realisation that foundation species often co-occur in nested or adjacent assemblages. Whether multiple co-occurring foundation species have additive or interactive effects on communities depends on the extent to which they are functionally redundant, and on the density-dependent functions within and across species. We compared how 2 secondary foundation species — the Sydney rock oyster *Saccostrea glomerata* and the free-floating fucalean algae *Hormosira banksii*, each facilitated by the grey mangrove *Avicennia marina* — influence the recruitment and survival of associated invertebrates. Field experiments revealed that effects of the 2 species on recruitment processes were generally distinct and additive. *S. glomerata* recruitment was enhanced in the presence of oysters but unaffected by algal biomass. Barnacle recruitment, however, decreased with oyster or algal habitat biomass. The efficacy of secondary foundation species in ameliorating predator–prey interactions was dependent on body size relative to the refuge space provided by the foundation species. The naticid gastropod *Conuber sordidum* was sufficiently small to penetrate habitats, such that neither foundation species influenced its predation on the gastropod *Batillaria australis*. By contrast, each foundation species reduced predation of the toadfish *Tetractenos hamiltoni* on small crabs, *Paragrapsus laevis*, which were able to seek refuge in the interstitial space provided by either habitat. Differential effects of co-occurring secondary foundation species on key ecological processes (recruitment and predation) will result in their facilitation of distinct ecological communities. Hence, models of community assembly should consider interactions among primary and secondary foundation species, and of co-occurring secondary foundation species, which may occur in complex networks.

KEY WORDS: Oysters · Recruitment · Foundation species · *Saccostrea glomerata* · Algae · *Hormosira banksii* · Mangroves · Predator–prey · Facilitation

1. INTRODUCTION

Foundation species (sensu Dayton 1972) are critical to the maintenance of biodiversity (Bertness & Callaway 1994, Stachowicz 2001, Bruno et al. 2003). They maintain complex habitat, and in doing so may ameliorate abiotic stressors such as temperature and desiccation, and biotic stressors such as competition and predation (e.g. Hay 1986, Jones et al. 1997, McAfee et al. 2016). Most studies have considered the effects of foundation species independently of one another, but many overlap in time and space (e.g. Altieri et al. 2007, Gribben et al. 2009, Dijkstra et al. 2012). In some instances, primary foundation species simultaneously facilitate multiple secondary foundation species that may form nested or adjacent configurations (Bishop et al. 2012, Hughes et al. 2014). There is growing evidence that habitat cascades — nested interactions whereby primary foundation species provide habitat for secondary foundation species that in

*Corresponding author: maria.vozzo@mq.edu.au

turn provide habitat for a focal community (Thomsen et al. 2010, Angelini et al. 2011) — are common in a wide range of terrestrial and aquatic ecosystems (e.g. Angelini et al. 2011, Thomsen et al. 2018, Gribben et al. in press).

The way in which spatially overlapping foundation species interact to facilitate biodiversity is determined by interspecific differences in their functional traits (Angelini et al. 2011) and by intraspecific variation in traits at the population- (e.g. density) and individual-level (e.g. morphology; Bishop et al. 2013). At a species level, foundation species that are functionally similar are more likely to compete (Krassoi et al. 2008, Angelini et al. 2011) and be functionally redundant in terms of the biodiversity that they support (e.g. Wilkie et al. 2012). By contrast, species that are functionally distinct and fill different niches can coexist (Angelini et al. 2011) and may have large additive or synergistic effects on biodiversity (e.g. Bishop et al. 2012, Dijkstra et al. 2012, Hughes et al. 2014). Within species, intraspecific variation in density, morphology and key functions can lead to variation in the biological communities they support (e.g. Bruno & Kennedy 2000, Bishop et al. 2009, Nicastro & Bishop 2013) and determine how foundation species interact (Bishop et al. 2012, 2013, Hughes et al. 2014). For example, in nested assemblages of foundation species, a critical density or particular morphology of the primary foundation species might be required to support the secondary foundation species, and particular densities or morphologies of the secondary foundation species might be required to facilitate a focal community (Bishop et al. 2013). How secondary foundation species interact to facilitate biodiversity has, however, received little attention (but see Hughes et al. 2014). Furthermore, the mechanisms by which secondary habitat formers enhance biodiversity remains poorly understood (Thomsen et al. 2018, Gribben et al. in press).

In estuarine and coastal environments of eastern Australia, the grey mangrove *Avicennia marina* is a primary foundation species that creates structure and shading in the otherwise sedimentary environment (Fig. 1A) (McAfee et al. 2016). Among the species facilitated by *A. marina* are the secondary foundation species the Sydney rock oyster *Saccostrea glomerata* (Fig. 1B) and the fucalean algae *Hormosira banksii* (Fig. 1C) (Bishop et al. 2012, 2013, Hughes et al. 2014). *S. glomerata* use the pneumatophores (peg-roots) and trunks of *A. marina* as a substrate for attachment, on which they build dense aggregations (Bishop et al. 2012, McAfee et al. 2016). Mangrove pneumatophores facilitate free-living *H. banksii* by providing a structure around which the alga's fronds — bead-like chains of spherical receptacles — become entangled and trapped (Bishop et al. 2012, 2013). The net effect is mosaics in which the 2 secondary foundation species *S. glomerata* and *A. marina* are found in overlapping (Fig. 1D) and adjacent configurations (Bishop et al. 2012). The indirect effect of mangroves on invertebrate biodiversity, arising from their facilitation of oysters and algae, overwhelms their direct effect (Bishop et al. 2012). In previous studies, the 2 secondary foundation species have been demonstrated to have additive effects on associated communities of invertebrates (Hughes et al. 2014). Nevertheless, the mechanisms by which their distinct effects arise have not been investigated.

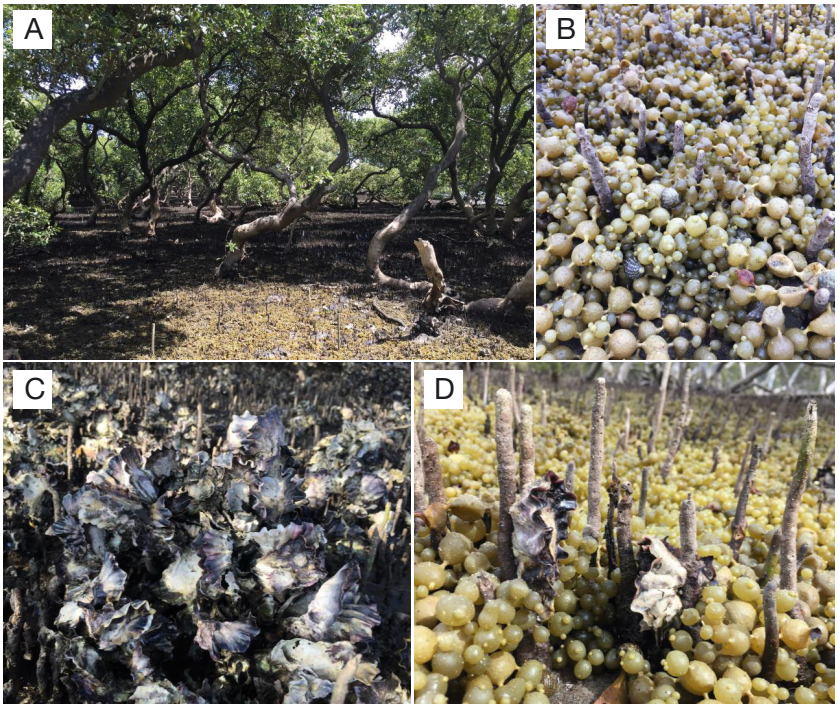

Fig. 1. In southeast Australia the (A) grey mangrove *Avicennia marina* is a primary foundation species. The peg-root pneumatophores of *A. marina* facilitate (B) the free-living *Hormosira banksii*, around which the alga becomes entangled and (C) the Sydney rock oyster *Saccostrea glomerata*, by providing hard structure for attachment. The 2 secondary foundation species, *S. glomerata* and *H. banksii*, are patchily distributed and may display adjacent or (D) overlapping distributions

The mechanisms by which *S. glomerata* and *H. banksii* facilitate invertebrates in temperate mangroves may include provision of substrate for attachment and grazing, modification of recruitment to co-occurring substrates, and provision of a microhabitat refuge from predation (Hughes et al. 2014, McAfee et al. 2016). In mangrove forests, hard substrate is generally limited to biogenic structures (e.g. mangrove trunks, pneumatophores and shell substrates), and competition for space and the food resources that grow on these surfaces is intense (Branch & Branch 1980, Minchinton & Ross 1999). Both *H. banksii* and *S. glomerata* offer a potential substrate for recruitment of organisms, but their functional roles may differ as a result of differences in the hardness and micro-complexity of their surfaces, as well as the biofilms they support (Anderson 1996, Minchinton & Ross 1999). Additionally, they may have differential effects on recruitment — not only to their own surfaces, but also to others — by influencing settlement cues, modifying small-scale currents and, in the case of filter-feeding oysters, larviphagy (Tamburri et al. 2008, Fulford et al. 2011).

Foundation species can provide critical protection for juvenile species which rely on complex habitat for protection from predators and from abiotic stressors such as desiccation (Altieri et al. 2007). Mangrove invertebrate communities can be subject to high rates of predation by marine fishes and invertebrates that feed in mangrove forests at high tide, shore and wading birds that forage at low tide, and invertebrate predators, such as crabs and muricid and naticid gastropods that are resident within the mangrove benthos (Warren 1990, Bishop et al. 2008, Nagelkerken et al. 2008). The match between invertebrate body size and habitat architecture can influence invertebrate habitat selection (Hacker & Steneck 1990). Additionally, at low saturation rates of habitats with prey (Toscano & Griffen 2013), habitat architecture may influence susceptibility of small prey to larger predators by determining whether there are suitable interstices between habitat units to provide protection (Pennings 1990, Eggleston & Lipcius 1992). Hence, *S. glomerata* and *H. banksii* may functionally differ in the protection they offer prey from predators.

Here, we utilised a combination of field and aquarium experiments to assess the independent and interactive effects of *H. banksii* and *S. glomerata* on invertebrate recruitment to a common substrate, survivorship and predator–prey interactions. We thereby add a mechanistic perspective to previous research that has focused on net effects on biodiversity of the 2 secondary foundation species (Hughes et al. 2014). We hypothesised that due to functional differences between the 2 foundation species, they will differ in their influence on 2 key ecological processes that shape community structure: recruitment and predation. We hypothesised that not only would there be interspecific differences in such functions of the 2 foundation species, but that these functions would also vary according to intraspecific variation in the density and habitat configuration of the foundation species. We expected that with increasing biomass and density of *H. banksii* and *S. glomerata*, invertebrate recruitment and survival would increase.

2. MATERIALS AND METHODS

2.1. Field experiments

2.1.1. Experimental design

Densities of the 2 secondary foundation species, *Saccostrea glomerata* and *Hormosira banksii*, were manipulated in the *Avicennia marina* mangrove forest of Quibray Bay (34.025° S, 151.180° E), within the Towra point Aquatic Reserve, Botany Bay, New South Wales (NSW), Australia. During March 2015, a total of 6 sites, each separated by at least 4 m, were established in the seaward pneumatophore fringe at a tidal elevation of mean low water springs +0.7 m and along a ~80 m length of shoreline. Sites had a similar pneumatophore density of 586 ± 26 m^{-2} (all measurements are presented as mean ± SE unless otherwise noted).

Within each site, 12 experimental plots (0.5 × 0.5 m^2), at least 1.5 m apart, were cleared of all oysters and algae. A 0.5 m area around each plot was also cleared to ensure that adjacent habitat structure did not dominate the effects of experimental interventions. Within each site, a single plot was randomly assigned to 1 of 12 habitat treatments arising from every possible combination from each of 4 oyster and 3 algal treatments. Oyster treatments contained naturally occurring clumps of oysters varying in number and size: no (0 clumps), low (2 small clumps), high (4 small clumps) or large (1 large clump). Oyster treatments were based on the range of naturally occurring densities within this system (Hughes et al. 2014). Small oyster clumps contained 9 ± 1 oysters, while large clumps contained 31 ± 2 oysters. The large oyster clumps contained a similar number of oysters to 4 small clumps, with the comparison between high and large oyster treatments

assessing whether the configuration rather than just density of oyster habitat influences community structure. The positioning of small clumps of oysters within low or high treatments was random whereas large clumps were placed in the center of their assigned experimental plots. Algal treatments were based on the range of naturally occurring densities within this system (Bishop et al. 2012, Hughes et al. 2014) and were no (0 kg), low (1.25 kg), or high (2.5 kg) biomass (wet weight), which were placed evenly throughout the 0.25 m^2 plot. All plots were checked every 2 wk to maintain habitat treatments and the cleared area around each plot.

2.1.2 Oyster and barnacle recruitment

To compare how the 2 secondary foundation species influence oyster and barnacle recruitment onto hard substrates, and to assess the extent to which their varying effects on predation drives differences between the two, caged and uncaged roughened pieces of polyvinyl chloride (PVC) were introduced into experimental plots as recruitment sticks. The PVC stakes were not intended to mimic pneumatophores, but rather introduced an identical recruitment substrate into habitats containing one or both secondary foundation species. Each plot received 6 randomly positioned 25 cm long and 1.9 cm diameter PVC posts that were pushed 15 cm into the sediment so that approximately 10 cm of PVC was exposed. Cylindrical cages that were 15 cm in length and 8 cm in diameter and constructed of 25 × 25 mm galvanised steel mesh enclosed the top section of 3 of the PVC posts per plot (caged treatment). The coarse mesh size of cages was designed to exclude predators such as fish and crabs that forage on oyster recruits at high tide, whilst minimising shading or sediment accretion artefacts of cages. Recruitment sticks were checked every 2 wk until recruitment of oysters and barnacles was observed. Once oyster recruitment was observed (September 2015), 1 randomly selected caged and 1 uncaged PVC stake was collected from each plot 2 wk later, and again after 4 and 6 wk, and the number of oyster spat and barnacles on each was quantified. Because sediment accretion in some plots affected the length of each stake that was exposed above the sediment, densities of barnacles and oysters were expressed as the number per unit area of surface exposed. Cages did not become fouled throughout the experiment and the change in sediment accretion did not significantly differ between caged and uncaged PVC stakes (ANOVA: $F_{1,360}$ = 3.16, p = 0.08; see Table S1 in the Supplement at www.int-res.com/articles/suppl/m608p061_supp.pdf for full ANOVA results), suggesting minimal cage artefacts (Peterson & Black 1994). Nevertheless, because our design did not include caging controls, the interpretation that differences in recruitment between caging treatments were due to predation must be made cautiously.

2.1.3. Juvenile invertebrate survival

The interacting effect of oysters and algae on the survival of juvenile *Bembicium auratum* and juvenile *S. glomerata* was monitored over 3 to 4 mo. The gastropod *B. auratum* is common within the mangrove forest and is found living on oysters, *H. banksii*, sediment and pneumatophores (Reid 1988, Bishop et al. 2009, Hughes et al. 2014). Juvenile *S. glomerata* recruit to pneumatophores, the shells of conspecifics and other molluscs, as well as any other hard substrates that may be present (Bishop et al. 2012, Hughes et al. 2014).

In May 2015, a total of 8 *B. auratum* snails (width: 7.12 ± 0.17 mm; height: 5.63 ± 0.19 mm) were tethered within each plot. Tethers consisted of a 25 cm piece of fishing line secured at one end to a single snail using SikaBond super glue gel, and at the other end to a galvanised steel mesh stake (approximately 2.5 cm in width and 6 cm in height) that was anchored beneath the sediment surface. The spire of each snail was marked with a small dot of red nail polish so that in the event that snails were missing from tethers, plots could be searched for marked individuals to determine if this was due to glue failure or predation. Pilot studies indicated that the nail polish did not influence snail survival.

In August 2015, a total of 9 juvenile *S. glomerata* oyster spat (shell height: 17.5 ± 0.24 mm) were marked with red nail polish and placed in each plot. In treatments with oysters, spat were attached using Sikaflex-291 marine sealant and evenly distributed among 3 clumps of dead oysters, comprising 4 ± 1 pieces of shell, that were in turn attached with marine sealant to the end of a wooden chopstick (23.0 cm length). In plots with no oysters, spat were evenly distributed among 3 bare chopsticks, with oysters attached to one end of each using the marine sealant. Chopsticks were used to mimic pneumatophores, onto which oysters recruit within this system (Bishop et al. 2012), and were secured in plots by depressing the end without oysters ~12 cm into the sediment.

Snails and spat were checked every month and classified as alive, dead or missing. Among dead molluscs it was noted whether they had drill-holes (indicative of predation by naticid or muricid gastropods), were cracked (likely from crab or finfish predators) or had entire shells intact (indicative of non-predatory mortality; Bishop et al. 2008). Where snails or spat were missing, the surrounding area was checked for painted individuals. On the rare occasion (6 occurrences) that a marked individual was found, it was recorded as alive and reattached. Monitoring of snail survival was terminated after 3 mo because simultaneous monitoring of tethered snails in bare 0.5 × 0.5 m plots (n = 3) caged with 25 × 25 mm galvanised steel mesh to exclude predators revealed that glue failure occurred over longer time intervals. Although oyster spat remained attached to wooden pegs over longer time intervals, their monitoring was terminated at 4 mo, because almost all spat had been consumed by this time.

2.2. Aquarium experiments

To assess the interactive and independent effect of algae and oysters on predator–prey interactions, we conducted 2 aquarium experiments. Each followed the same fully orthogonal design as the field experiments, with 4 oyster treatments (no clumps, low density of small clumps, high density of small clumps, single large clump) and 3 *H. banksii* treatments (no algae, low biomass, high biomass). The first experiment, conducted in October–December 2015 (Austral spring and summer), considered how the 2 foundation species influence predation by common toadfish *Tetractenos hamiltoni* on shore crabs *Paragrapsus laevis.* The second experiment, run in March–April 2016 (Austral fall), considered how the foundation species affect moon snail *Conuber sordidum* predation on the mud whelk *Batillaria australis.* Both toadfish and moon snails are generalist predators of invertebrates in temperate Australian mangrove forests, which in tethering and mesocosm experiments have been demonstrated to account for a significant proportion of predatory mortality (Warren 1990, Bishop et al. 2008). Toadfish forage in mangrove forests at high tide (Warren 1990), with decapods comprising a majority of their diet (Bell et al. 1984). Moon snails are resident on and in mangrove sediments (Bishop et al. 2008), sometimes living in association with *H. banksii* (Bishop et al. 2009). Shore crabs are ubiquitous across intertidal oyster habitat (Hughes et al. 2014) and are often found hiding in and beneath oyster shells (M. L. Vozzo pers. obs.). *B. australis* is an epibenthic species that displays enhanced abundances under *H. banksii* (Bishop et al. 2009, 2012, Hughes et al. 2014).

Experiments examining toadfish predation on shore crabs were conducted in the Macquarie University seawater facility, a recirculating system utilising seawater trucked from Sydney Harbour, while experiments examining moon snail predation on mud whelks were run in the Sydney Institute of Marine Science (SIMS) aquarium, a flow-through system which directly sources water from the harbour. *Paragrapsus laevis* (carapace width: 10.81 ± 0.35 mm), *B. australis* (shell height: 18.71 ± 0.30 mm) and *C. sordidum* (18.65 ± 0.24 mm) for use in experiments were collected by hand from the Quibray Bay mangrove forest at low tide, the day before commencement of each experiment. Toadfish (total length: 10.1 ± 0.2 cm) could not be collected from Quibray Bay due to the status of this site as an Aquatic Reserve, and were instead collected by seine net from Tambourine Bay, Lane Cove River, Sydney, 5–7 d prior to experiments. Until the start of experiments, toadfish were housed in 55 l tanks supplied with ~18°C recirculating seawater; the tanks were exposed to a natural lighting regime and cleaned daily. Toadfish were fed a varied diet of prawns, oysters and crabs daily, but were starved 36 h prior to use in the experiment. Predatory snails were kept in individual 0.5 l containers and prey snails were kept in two 10 l containers of aerated seawater (22–24°C) supplied by the SIMS flow-through water system.

Experiments at Macquarie University utilising toadfish and crabs were conducted in 27 l tanks (47 × 35 × 25 cm, length × height × width). The tanks were each closed systems, filled with seawater and individually aerated. The air temperature in the seawater facility was set to match water temperatures recorded in Sydney Harbour to mimic natural conditions (18.5–20.5°C) in the housing and trial tanks. A total of 72 tanks were established, and randomly assigned to each of 4 oyster treatments, to give 18 tanks of each oyster treatment. The percentage covers of oysters in treatments (0 [no], 8.5 ± 0.53 [low], 17.33 ± 1.05 [high], or 15.33 ± 0.56 [large]) and number of oyster clumps matched those of oyster clumps within plots of the field experiment, with small clumps positioned randomly and large clumps positioned in the center of the aquarium. Clumps were smaller due to the aquarium setup and contained 5 ± 1 oysters in small clumps and 22 ± 4 oysters in large clumps. For each oyster treatment, 6 tanks were randomly assigned to each of 3 algal treatments: no algae, 0.82 kg (towel-

dried wet weight) or 1.65 kg to match the densities (0, 0.5 or 1 kg per 0.25 m^2) utilised in field experiments. Once the habitats were constructed, an individual toadfish and 10 shore crabs were added to each tank. The number of shore crabs added to tanks was based on pilot studies that indicated that even in the absence of structured habitat, toadfish would consume no more than 9 crabs over the experimental duration of 9 h. Fish were added 30 min prior to crabs to give them time to acclimate, but were gently kept to the side of the tank when crabs were added, allowing the crabs time to hide within the habitat. Trials (n = 6 for each of the 12 habitat treatments) were run during daylight hours, as toadfish are omnivorous scavengers that are active during the day and night (Miller & Skilleter 2006). After 9 h, fish were removed from tanks, tanks were thoroughly searched for crabs and the number of crabs remaining was quantified. Fish were only used once in the experiment to eliminate any learned foraging behavior, and were returned to their collection site at the end of the experiment.

Experiments at SIMS utilising *C. sordidum* and *B. australis* were run in 4 l plastic ice cream tubs (19 × 19 × 12 cm, length × height × width) that were fully submerged in one of two 20 cm deep water tables. Seawater from Sydney Harbour, ranging from 22–24°C during February–April 2016, was supplied to the water tables via a flow-through system at a constant flow rate (1 l min^{-1}). As with the first predator–prey experiment, oyster treatments were established so that they had the same percent cover of oysters as the 4 treatments used in the field experiment (0% [no], 8.5 ± 0.53% [low], 17.33 ± 1.05% [high] or 15.33 ± 0.56% [large]) and the same number and positioning of oyster clumps. Small oyster clumps contained 3 ± 1 and large oyster clumps contained 12 ± 1 oysters. There were 18 tubs of each oyster treatment that were randomly assigned to each of 3 algal treatments (no, low or high biomass of *H. banksii*) to give n = 6 for each of the 12 treatments. The low biomass treatment received 0.06 kg of algae tub^{-1}, and the high biomass treatment, 0.11 kg tub^{-1}, to match the biomass per unit area of algae in the field experiment.

Once the habitats were constructed, an individual moon snail and 10 mud whelks were added to each tank. The number of mud whelks added to tanks was based on a pilot study that indicated that in unstructured habitat, moon snails consumed no more than 10 snails within the experimental period of 12 d. The mud whelks were added to the tanks first to allow them time to explore the habitat before adding the predatory snail, approximately 30 min later. Tubs were covered and sealed with wire screen mesh to prevent escape of snails, and were aerated via an individual airline fed through a small hole in the mesh for each tub. After 12 d, the moon snails were removed from tubs and the number of mud whelks with drill holes (indicative of moon snail predation) was quantified. Moon snails and mud whelks were only used once and released to Quibray Bay after use in the experiment.

2.3. Statistical analyses

Four-way ANOVAs, with the factors oyster habitat (4 levels: zero oyster clumps [no], low density of small clumps [low], high density of small clumps [high] and large [large] clump), algal habitat (3 levels: no, low and high biomass), caging (2 levels: caged, uncaged) and time (3 levels: 2, 4 and 6 wk) examined sources of variation in the recruitment of barnacles and oysters to PVC stakes and their subsequent survival. Time was considered an independent factor because different PVC stakes were sampled each time. Site was not considered as a factor because these were used solely for the purposes of ensuring interspersion of plots, with the distance between sites the same order of magnitude as the distance among plots. Separate 2-way fully orthogonal ANOVAs tested for effects of oyster and algal habitat on the survivorship of juvenile *B. auratum* snails after 1, 2 and 3 mo, and *S. glomerata* oysters after 1, 2, 3 and 4 mo in field plots, and on *P. laevis* and *B. australis* over the duration of the laboratory predator–prey experiments. For these, sampling times were analysed separately as the same invertebrates were sampled through time and times were, hence, non-independent. Prior to each analysis, Cochran's *C*-test was performed to confirm homogeneity of variance, and where necessary, data were square root (recruitment counts) or arcsine (surviving invertebrate percentages) transformed (Underwood 1997) to achieve homogeneity of variance. After transformation, the 3 and 4 mo *S. glomerata* survival data still did not meet homogeneity of variance requirements for ANOVAs; therefore, significant differences were determined at p = 0.01 (Underwood 1997). Where ANOVAs found significant treatment effects, Tukey's HSD tests were conducted *a posteriori* to determine significant differences among means ($\alpha = 0.05$). A Welch's *t*-test was done to test whether there was any difference in the mean percentage of damaged *B. auratum* snails that had been drilled and cracked across all treatments. Statistical tests were conducted in R version 3.0.2.

3. RESULTS

3.1. Field experiment

3.1.1. Oyster and barnacle recruitment

Neither the density of oysters nor barnacles on recruitment sticks displayed interacting effects of any combination of algal habitat, oyster habitat, time and caging (ANOVA, p > 0.05 for interaction terms; see Table S2 in the Supplement for full ANOVA results), allowing for the interpretation of main effects. No differences in the densities of either oysters (ANOVA: time, $F_{2,360}$ = 0.03, p = 0.97) or barnacles ($F_{2,360}$ = 2.16, p = 0.12) were detected through time (Fig. S1). Densities of oysters (ANOVA: cage, $F_{1,360}$ = 11.54, p = 0.001) and barnacles ($F_{1,360}$ = 15.47, p = 0.001) were greater on caged than uncaged recruitment sticks (62.8 cm^2 surface area; oysters: 3.29 ± 0.21 caged vs. 2.36 ± 0.18 uncaged; barnacles: 30.45 ± 3.32 caged vs. 15.78 ± 2.07 uncaged; Tukey tests: p ≤ 0.001). Oyster habitat had differing effects on each of oyster and barnacle recruitment to PVC stakes. Whereas greater oyster recruitment to stakes occurred in plots with oyster habitat of any type than in plots that received no oyster habitat (ANOVA: oysters, $F_{3,360}$ = 7.84, p < 0.001; Fig. 2A), less barnacle recruitment occurred to stakes in plots with than without oyster habitat, although this trend was not significant (Fig. 2C). Among treatments with oyster habitat, there was no significant difference in oyster recruitment to stakes between plots with a low or high density of small oyster clumps, or a single large oyster clump (Tukey: p > 0.05; Fig. 2A). While the algal habitat had no effect on the density of oyster recruits (ANOVA: algae, $F_{2,360}$ = 2.50, p = 0.084; Fig. 2B), barnacle density varied with algal biomass (ANOVA: algae, $F_{2,360}$ = 9.94, p < 0.001), with lower barnacle recruitment occurring in the high algal biomass treatment than the no or low algal biomass treatments which, in turn, did not significantly differ (Tukey: p ≤ 0.02; Fig. 2D).

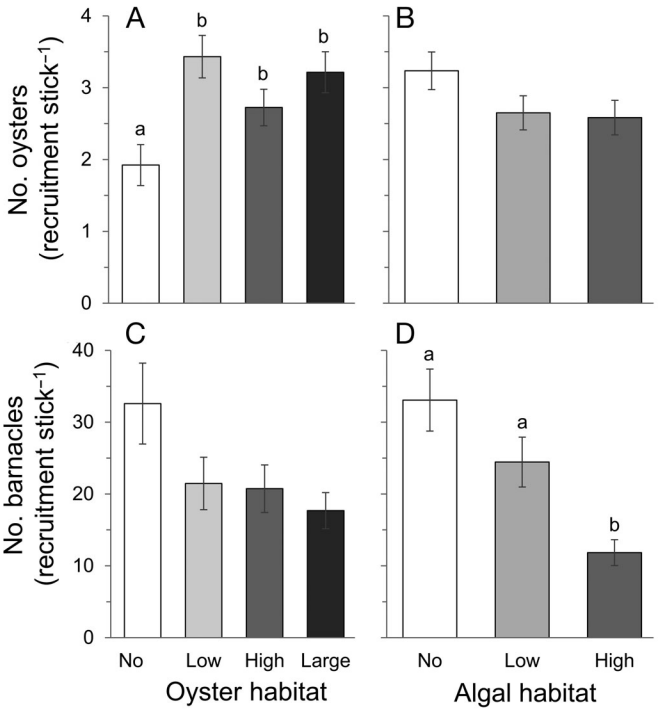

Fig. 2. Mean (±SE) density of (A) *Saccostrea glomerata* oysters and (B) barnacles (*Amphibalanus* spp. and *Hexaminius* spp.) recruiting to PVC stakes in plots with no, low, high or large oyster biomass and of (C) oysters and (D) barnacles recruiting to PVC stakes (62.8 cm^2) in plots with no, low or high algal biomass after 4 mo. Letters above bars: significant differences (ANOVA, Tukey: p < 0.05; see Table S2 in the Supplement for full ANOVA results)

3.1.2. Juvenile invertebrate survival

One and 3 mo after tethering, survival of the snail *B. auratum* was not significantly affected by oyster habitat, algal habitat or the interaction (ANOVA: p > 0.05, see Table S3 for full ANOVA results). By contrast, snail survival displayed an effect of algal (ANOVA: $F_{2,60}$ = 3.49, p = 0.037) but not oyster habitat (ANOVA: $F_{3,60}$ = 1.29, p = 0.29) or the interaction between oysters and algae (ANOVA: $F_{6,60}$ = 1.10, p = 0.37) after 2 mo of tethering. Snail survival was greater in plots with low than no algal biomass (Tukey test: p = 0.031), but there were no significant differences among other pairwise comparisons of no, low and high algal biomass treatments (Tukey tests: p > 0.05; Fig. 3A). Among damaged snails, a significantly greater (t_{87} = 3.30, p = 0.001) percentage were drilled (7.61 ± 1.6 %) than cracked (1.62 ± 0.55 %) but there were no effects of habitat (oysters, algae, or the interaction) on the percentages of drilled and cracked snails (p > 0.05, Table S3).

Oyster survival was not influenced by the interaction between oyster and algal habitat at any of the 4 sampling times (ANOVAs: p > 0.05; Table S3) allowing for the interpretation of main effects. At the 1 mo time interval, algae but not oysters had a significant effect on oyster survival (ANOVA: algae, $F_{2,60}$ = 5.46, p = 0.007; oysters, $F_{3,60}$ = 1.72, p = 0.17), with survival greater in low than no or high algal biomass treatments (Tukey tests: p ≤ 0.02; Fig. 3B). There were no differences in oyster survival due to main effects of

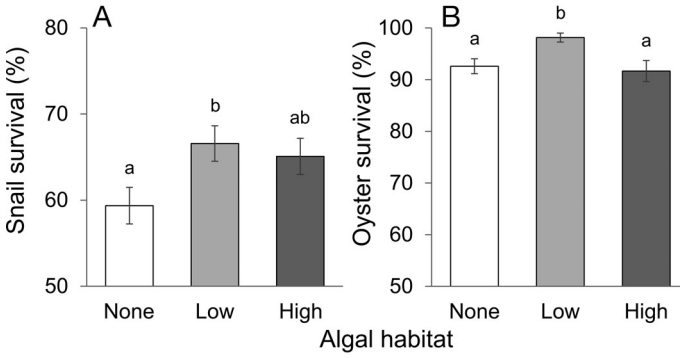

Fig. 3. Mean (±SE) percentage of (A) *Bembicium auratum* snails surviving after 2 mo and (B) oysters surviving after 1 mo in each algal habitat treatment (no, low or high algal biomass). Letters above bars: significant differences (ANOVA, Tukey: $p < 0.05$; see Table S3 in the Supplement for full ANOVA results)

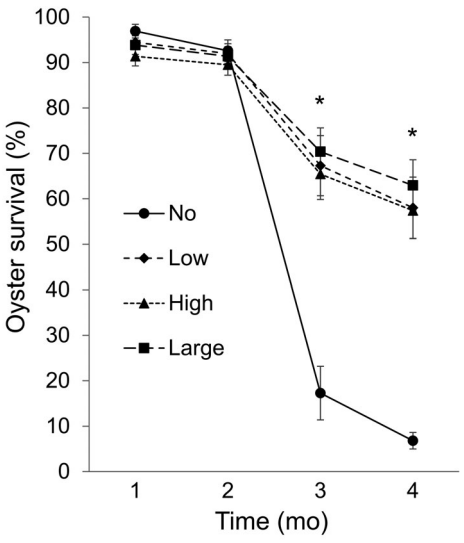

Fig. 4. Mean (±SE) percentage of oysters surviving in each oyster habitat treatment across the 4 mo of monitoring. Plots received no oyster habitat (No), 2 small clumps (Low), 4 small clumps (High) or a single large clump (Large). After 3 and 4 mo, survival was greater in plots that contained any oyster habitat than plots without oyster habitat. Asterisks indicate significant differences (ANOVA, Tukey: $p < 0.001$; see Table S3 in the Supplement for full ANOVA results)

oysters or algae after 2 mo (ANOVA: oysters, $F_{3,60}$ = 0.51, p = 0.68; algae, $F_{2,60}$ = 2.02, p = 0.14), but at each of the 3 and 4 mo time intervals, the main effect of oyster treatment but not algal biomass had a significant effect on oyster survival (ANOVA, 3 mo: oysters, $F_{3,60}$ = 16.34, $p < 0.001$; algae, $F_{2,60}$ = 0.1, p = 0.91; 4 mo: oysters, $F_{3,60}$ = 21.78, $p < 0.001$; algae, $F_{2,60}$ = 0.02, p = 0.98). During the third and fourth month, oyster survival was greater in plots with any density of oyster habitat than plots without oysters (Tukey test: $p < 0.001$; Fig. 4).

3.2. Aquarium experiments

Predation by toadfish on crabs was determined by the interacting effect of oyster and algal habitat (ANOVA: $F_{6,60}$ = 4.99, $p < 0.001$; see Table S4 for full ANOVA results). In the absence of oysters, survivorship was significantly greater at low or high biomasses of algae than in the absence of algae (Tukey test: $p \leq 0.004$), but in the presence of oysters, of any habitat configuration, there was no effect of algae on crab survivorship (Tukey test: $p > 0.05$; Fig. 5). Similarly, in the absence of algae, survivorship was greater in tanks with oysters than in those without oysters (Tukey test: $p < 0.001$), which in turn did not significantly differ, and at the low biomass of algae, there was lower survivorship in tanks without oysters than those with a large oyster clump (Tukey test: p = 0.05). At the high algal biomass, there was little effect of oysters on survivorship (Tukey test: $p > 0.05$; Fig. 5).

In trials examining *Conuber sordidum* predation on *Batillaria australis*, there was no significant effect of oysters, algae or the interaction on snail survivorship (ANOVA: main effect of oysters, $F_{3,60}$ = 1.34, p = 0.27; main effect of algae, $F_{2,60}$ = 0.46, p = 0.63; oyster by algae interaction, $F_{6,60}$ = 0.67, p = 0.67). Across all habitat treatments, the predatory snails consumed an average of 5 ± 1 snails per 12 d trial (Fig. S2).

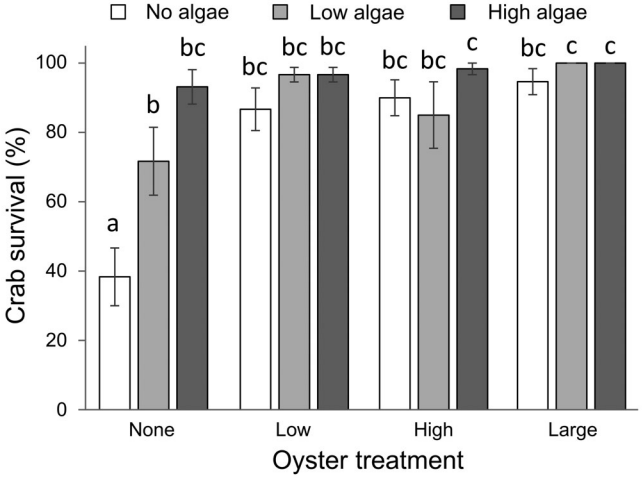

Fig. 5. Mean (±SE) percentage of shore crabs *Paragrapsus laevis* surviving in each of 12 habitats after the 9 h feeding trial with toadfish *Tetractenos hamiltoni*. Tanks received either no oyster habitat (None), 2 small clumps (Low), 4 small clumps (High) or a single large clump (Large), and either no, low or high algal biomass in a fully factorial design. Letters above bars: significant differences (ANOVA, Tukey: $p < 0.05$; see Table S4 in the Supplement for full ANOVA results)

4. DISCUSSION

Previous research in this system has demonstrated that co-occurring secondary habitat forming species can have distinct effects on the composition of associated communities (Hughes et al. 2014), but the mechanisms that give rise to such differences in community structure have not been explored. This study investigated how 2 secondary foundation species, the Sydney rock oyster *Saccostrea glomerata* and the free-floating fucalean algae *Hormosira banksii*, interact to influence 2 key biological processes critical to community assembly — recruitment and predator–prey interactions. Consistent with the hypothesis that the 2 foundation species would produce distinct, density-dependent effects on each of these processes, we found generally additive density-dependent effects of *S. glomerata* and *H. banksii* on the recruitment and survival of invertebrates. Nevertheless, some redundancy between the 2 secondary foundation species in their mediation of predator–prey interactions was apparent.

Barnacles and oysters displayed divergent patterns of recruitment to a common substrate embedded in experimental field plots, dependent on the identity of the 2 secondary foundation species present. Whereas *S. glomerata* recruitment to PVC stakes was positively influenced by the presence of oysters, it was unaffected by algal biomass. Barnacle (*Amphibalanus* spp. and *Hexaminius* spp.) recruitment to stakes, however, decreased with the biomass of surrounding oyster or algal habitat. Recruitment of sessile invertebrates is the net effect of larval supply, settlement and post-settlement mortality (Pawlik 1992). The divergent response of oyster recruitment to the 2 foundation species appeared to primarily be due to differences in settlement, with the absence of an interaction between the caging and habitat treatments suggestive of no differential effect of the 2 foundation species on post-settlement predation. Nevertheless, because caging can also influence settlement as well as predation (Schmidt & Warner 1984), it remains possible that any differential predation between treatments was swamped by a caging artefact.

Oysters are known to be gregarious settlers, responding positively to the chemical cues of conspecifics (Tamburri et al. 2007, 2008). The mechanism by which the algae and oysters diminished barnacle recruitment is unclear. Larviphagy of barnacles by adult oysters could contribute to lower barnacle recruitment in plots with oysters (Tamburri & Zimmer-Faust 1996, Fulford et al. 2011). It has been hypothesised that algal canopies may reduce barnacle recruitment by reducing larval supply to substrates below (Hatton 1938, Southward 1956, Connell 1961). The whip-lash effects of algae on barnacle recruits that have been observed on rocky shores (Leonard 1999, Beermann et al. 2013) are unlikely to have occurred here due to the sheltered environment of the mangrove forest. The smothering effect of algae on barnacle recruits observed on rocky shores (Denley & Underwood 1979), although plausible in sheltered environments, is also unlikely within this study system. At low tide the vertical distributions of *H. banksii* and barnacles did not overlap, because *H. banksii* rested on the muddy substrate, sitting below the band on recruitment sticks at which barnacles were found. The negative influence of oysters on barnacle settlement is to the benefit of oyster recruits, which can compete with barnacles for space and food resources (Luckens 1975, Anderson & Underwood 1997).

The survival of oysters in the field displayed similar responses to the 2 habitat forming species as recruitment, with greater survival of oysters in the presence than absence of conspecifics over periods of 3 mo or longer, irrespective of oyster habitat biomass or configuration (as determined by the number and size of oyster habitat clumps). By contrast, effects of algae on oyster recruitment were seen only after 1 mo, and were generally non-linear, with survivorship of oysters greater at the low biomass of algae than the high or no algae treatments. Whereas low densities of algae may protect oysters from finfish predators, high densities may disrupt feeding by inhibiting water flow, or facilitate predatory naticid gastropods which, unlike fish, are able to penetrate algal habitat and benefit from its structure (Bishop et al. 2009). Nevertheless, there was no difference across treatments in the percentage of oysters that were drilled. These results highlight the importance of examining effects of foundation species across a range of biomasses and patch configurations, as their interactions with associate species are not necessarily linear.

The effects of the secondary foundation species on survival of the 2 snail species were also generally independent. The 2 snail species used in this study, *Bembicium auratum* and *Batillaria australis*, were numerically dominant species in our mangrove study system, with *B. auratum* more common on oysters and *B. australis* often found under *H. banksii* (Reid 1988, Bishop et al. 2009, Hughes et al. 2014). Despite the stronger association of *B. auratum* with oysters than with algae in the field (Bishop et al. 2009, Hughes et al. 2014), in the tethering study, oysters had no influence on the snail's survivorship, as compared to weak positive effects of low densities of the

alga. This result suggests that small-scale variation in *B. auratum* abundance is not driven by predation, but by an alternative factor. For example, in mangrove forests where the availability of hard substrate is limited, *B. auratum* may use hard surface provided by oyster shell as a substrate for grazing (Reid 1988, Hughes et al. 2014). The weak positive effect of *H. banksii* but not oysters on *B. auratum* survival may reflect differences in the fit between the body size of the snail and the predator refuges provided by each of the habitats: whereas the body size of adult *B. auratum* is too large to fit in many of the interstices between oyster shells, the snail can move amongst the *H. banksii* habitat. Nevertheless, to confirm that differential effects of the 2 secondary foundation species arose from differences in habitat structure, structural mimics for each would need to be included in the experimental design.

In laboratory experiments, predation by *Conuber sordidum* on *B. australis* was influenced by neither the presence nor density of oysters or algae. This may be because *B. australis* was too large to shelter in the interstices provided by either habitat, and *C. sordidum* was sufficiently small to move freely into each habitat to forage. At low prey densities, large predator body size relative to interstitial protective spaces can reduce rates of predation on small prey (Toscano & Griffen 2013). However, at high prey densities at which the number of protective interstices is insufficient to shelter all prey, predation rate is instead determined by prey handling time (Toscano & Griffen 2013). In our study, prey handling, which can take anywhere from 36 to 60 h, rather than prey detection and capture limited the rate of prey consumption. Although the laboratory experiment only considered effects of secondary habitat forming species on predation by a single species on *B. australis*, this and a previous study (Bishop et al. 2008) indicate that this species, *C. sordidum*, is the dominant predator of shelled gastropods at our study site. Over 4 times more *B. auratum* were drilled than cracked in the field tethering study, indicating the greater significance of naticid gastropod than crab or fish predation on its survival. Hence, this study does not support the hypothesis that the aggregation of *B. australis* underneath *H. banksii* is a predator-avoidance strategy. Instead, this behavior may be driven by the enhancement of organic matter concentrations beneath the algal mats, upon which *B. australis* feeds (Bishop et al. 2009, 2012).

In contrast to the differential effects of the 2 habitats on snail predation, both algae and oysters reduced predation by toadfish on small crabs and appeared largely redundant in their effects. In the absence of the alga, the presence of the oyster enhanced crab survivorship. Conversely, in the absence of the oyster, increasing biomasses of *H. banksii* enhanced crab survivorship. However, if one foundation species was already present, adding a second had little or no effect. Although our experiments did not include the structural mimics necessary to disentangle structural from other effects, we hypothesise that in this case the 2 foundation species were functionally redundant in their effect on this predator–prey interaction, because the structure of each was largely impenetrable by toadfish, but each provided interstices in which crabs could seek refuge. Nevertheless, whereas crab survivorship responded only to the presence or absence of oysters, the alga had a density-dependent effect on the crabs. Theory (Bruno & Bertness 2001) and evidence (Bishop et al. 2012, 2013) suggest that above a certain threshold, the biomass of a foundation species can be less important in influencing associated communities than just its presence. Here, the threshold above which further increases in foundation species biomass produced no further enhancement of crab survivorship may have been lower for oysters than the alga. Previous studies suggest that in the intertidal zone, oysters, which provide a rigid 3-dimensional structure with persistent interstices between shells, are a higher value anti-predator refuge for small crabs than algae, which has a more malleable form that collapses at low tide when the alga is immersed (Bishop & Byers 2015).

Facilitative interactions can vary with foundation species abundance or biomass (Bracken et al. 2007, Irving & Bertness 2009, Dijkstra et al. 2012), with variation in these population-level traits in some instances influencing community assembly more than foundation species identity (Hughes et al. 2014). Effects of the biomass and configuration of individual secondary foundation species on recruitment and survivorship of colonists were apparent in this study. Overall, however, these effects were secondary to interspecific differences between the alga and oysters. The Foundation Species–Biodiversity model (Angelini & Silliman 2014) predicts that benefits to biodiversity will be greatest where the structure of secondary foundation species provides novel habitat compared to the primary foundation species. The present study extends this model by showing that multiple co-occurring secondary foundation species can have distinct effects on ecological processes such as recruitment and predation that are important in shaping biodiversity. This study did not attempt to disentangle

structural versus functional effects of the 2 foundation species through the inclusion of structural mimics in experimental designs. However, as with previous studies that have demonstrated a positive correlation between prey survival and habitat complexity, we suspect that effects of secondary foundation species on prey survival were predominantly due to the structural habitat they provide (see Heck & Thoman 1981, Crowder & Cooper 1982, Grabowski 2004). Irrespective, our study provides evidence that the pathways by which 2 secondary foundation species influence associate communities include the provision of refuge from predators and the modification of recruitment. Previous studies on habitat cascades have focused on the role of secondary foundation species in boosting the biodiversity facilitated by the primary foundation species (e.g. Altieri et al. 2007, Bishop et al. 2012, Angelini & Silliman 2014). Here, we have shown that where primary foundation species facilitate multiple secondary foundation species, these can each have distinct effects on processes that are important in shaping associated community structure. Hence, models of community assembly need to consider interactions among co-occurring foundation species, which may occur in complex networks.

Acknowledgements. This work would not have been possible without help of many field volunteers, especially V. Baca González, S. Bagala, J. Crosswell, B. Fernandes, F. Rose, R. Steel, N. Vitlin, and C. Yong. We thank Dr. Ken Cheng and 3 anonymous reviewers for helpful comments on earlier drafts of the manuscript. This research was supported by funding through the Department of Biological Sciences, Macquarie University. All applicable institutional and/or national guidelines for the care and use of animals were followed (MQ AEC ARA 2015/002).

LITERATURE CITED

Altieri AH, Silliman BR, Bertness MD (2007) Hierarchical organization via a facilitation cascade in intertidal cordgrass bed communities. Am Nat 169:195–206

Anderson MJ (1996) A chemical cue induces settlement of Sydney rock oysters, *Saccostrea commercialis*, in the laboratory and in the field. Biol Bull (Woods Hole) 190: 350–358

Anderson MJ, Underwood AJ (1997) Effects of gastropod grazers on recruitment and succession of an estuarine assemblage: a multivariate and univariate approach. Oecologia 109:442–453

Angelini C, Silliman BR (2014) Secondary foundation species as drivers of trophic and functional diversity: evidence from a tree–epiphyte system. Ecology 95:185–196

Angelini C, Altieri AH, Silliman BR, Bertness MD (2011) Interactions among foundation species and their consequences for community organization, biodiversity and conservation. Bioscience 61:782–789

Beermann AJ, Ellrich JA, Molis M, Scrosati RA (2013) Effects of seaweed canopies and adult barnacles on barnacle recruitment: the interplay of positive and negative influences. J Exp Mar Biol Ecol 448:162–170

Bell JD, Pollard DA, Burchmore JJ, Pease BC, Middleton MJ (1984) Structure of a fish community in a temperate tidal mangrove creek in Botany Bay, New South Wales. Aust J Mar Freshwater Res 35:33–46

Bertness MD, Callaway R (1994) Positive interactions in communities. Trends Ecol Evol 9:191–193

Bishop MJ, Byers JE (2015) Predation risk predicts use of a novel habitat. Oikos 124:1225–1231

Bishop MJ, Cole MR, Taylor SL, Wilkie EM, Kelaher BP (2008) Size-specific predation by dominant consumers maintains a 'trophic cul-de-sac'. Mar Ecol Prog Ser 354: 75–83

Bishop MJ, Morgan T, Coleman MA, Kelaher BP, Hardstaff LK, Evenden RW (2009) Facilitation of molluscan assemblages in mangroves by the fucalean alga *Hormosira banksii*. Mar Ecol Prog Ser 392:111–122

Bishop MJ, Byers JE, Marcek BJ, Gribben PE (2012) Density-dependent facilitation cascades determine epifaunal community structure in temperate Australian mangroves. Ecology 93:1388–1401

Bishop MJ, Fraser J, Gribben PE (2013) Morphological traits and density of foundation species modulate a facilitation cascade in Australian mangroves. Ecology 94:1927–1936

Bracken MES, Gonzalez-Dorantes CA, Stachowicz JJ (2007) Whole-community mutualism: associated invertebrates facilitate a dominant habitat-forming seaweed. Ecology 88:2211–2219

Branch GM, Branch ML (1980) Competition in *Bembicium auratum* (Gastropoda) and its effects on micro-algal standing stocks in mangrove muds. Oecologia 46:106–114

Bruno JF, Bertness MD (2001) Habitat modification and facilitation in benthic marine communities. In: Bertness MD, Gains SD, Hay ME (eds) Marine community ecology. Sinauer Associates, Sutherland, MA, p 201–218

Bruno JF, Kennedy CW (2000) Patch-size dependent habitat modification and facilitation on New England cobble beaches by *Spartina alterniflora.* Oecologia 122:98–108

Bruno JF, Stachowicz JJ, Bertness MD (2003) Inclusion of facilitation into ecological theory. Trends Ecol Evol 18: 119–125

Connell JH (1961) Effects of competition, predation by *Thais lapillus*, and other factors on natural populations of the barnacle *Balanus balanoides.* Ecol Monogr 31:61–104

Crowder LB, Cooper WE (1982) Habitat structural complexity and the interaction between bluegills and their prey. Ecology 63:1802–1813

Dayton PK (1972) Toward an understanding of community resilience and the potential effects of enrichments to the benthos at McMurdo Sound, Antarctica. In: Parker BC (ed) Proceedings of the colloquium on conservation problems in Antarctica. Allen Press, Lawrence, KS, p 81–95

Denley EJ, Underwood AJ (1979) Experiments on factors influencing settlement, survival, and growth of two species of barnacles in New South Wales. J Exp Mar Biol Ecol 36:269–293

Dijkstra JA, Boudreau J, Dionne M (2012) Species-specific mediation of temperature and community interactions by multiple foundation species. Oikos 121:646–654

Eggleston DB, Lipcius RN (1992) Shelter selection by spiny lobster under variable predation risk, social conditions, and shelter size. Ecology 73:992–1011

Fulford RS, Breitburg DL, Luckenbach M (2011) Differences in relative predation vulnerability between native and non-native oyster larvae and the influence on restoration planning in an estuarine ecosystem. Estuaries Coasts 34: 618–629

Grabowski JH (2004) Habitat complexity disrupts predator–prey interactions but not the trophic cascade on oyster reefs. Ecology 85:995–1004

Gribben PE, Byers JE, Clements M, McKenzie LA, Steinberg PD, Wright JT (2009) Behavioural interactions between ecosystem engineers control community species richness. Ecol Lett 12:1127–1136

Gribben PE, Angelini C, Altieri AH, Bishop M, Thomsen M (in press) Facilitation cascades in marine ecosystems: a synthesis and future directions. Oceanogr Mar Biol Annu Rev

Hacker SD, Steneck RS (1990) Habitat architecture and the abundance and body-size-dependent habitat selection of a phytal amphipod. Ecology 71:2269–2285

Hatton H (1938) Essais de bionomie explicative sur quelques espèces intercotidales d'algues et d'animaux. Ann Inst Oceanogr Monaco 17:241–348

Hay ME (1986) Associational plant defences and the maintenance of species diversity: turning competitors into accomplices. Am Nat 128:617–641

Heck KL Jr, Thoman TA (1981) Experiments on predator–prey interactions in vegetated aquatic habitats. J Exp Mar Biol Ecol 53:125–134

Hughes AR, Gribben PE, Kimbro DL, Bishop MJ (2014) Additive and site-specific effects of two foundation species on invertebrate community structure. Mar Ecol Prog Ser 508:129–138

Irving AD, Bertness MD (2009) Trait-dependent modification of facilitation on cobble beaches. Ecology 90: 3042–3050

Jones CG, Lawton JH, Shachak M (1997) Positive and negative effects of organisms as physical ecosystem engineers. Ecology 78:1946–1957

Krassoi FR, Brown KR, Bishop MJ, Kelaher BP, Summerhayes S (2008) Condition specific competition allows coexistence of competitively superior exotic oysters with native oysters. J Anim Ecol 77:5–15

Leonard GH (1999) Positive and negative effects of intertidal algal canopies on recruitment and survival of barnacles. Mar Ecol Prog Ser 178:241–249

Luckens PA (1975) Competition and intertidal zonation of barnacles at Leigh, New Zealand. N Z J Mar Freshw Res 9:379–394

McAfee D, Cole VJ, Bishop MJ (2016) Latitudinal gradients in ecosystem engineering by oysters vary across habitats. Ecology 97:929–939

Miller SJ, Skilleter GA (2006) Temporal variation in habitat use by nekton in a subtropical estuarine system. J Exp Mar Biol Ecol 337:82–95

Minchinton TE, Ross PM (1999) Oysters as habitat for limpets in a temperate mangrove forest. Aust J Ecol 24: 157–170

Nagelkerken I, Blaber SJM, Bouillon S, Green P and others (2008) The habitat function of mangroves for terrestrial and marine fauna: a review. Aquat Bot 89:155–185

Nicastro A, Bishop MJ (2013) Effects of tidal inundation on benthic macrofauna associated with the eelgrass *Zostera muelleri.* Estuar Coast Shelf Sci 117:238–247

Pawlik JR (1992) Chemical ecology of the settlement of benthic marine invertebrates. Oceanogr Mar Biol Annu Rev 30:273–335

Pennings SC (1990) Predator–prey interactions in opisthobranch gastropods: effects of prey body size and habitat complexity. Mar Ecol Prog Ser 62:95–101

Peterson CH, Black R (1994) An experimentalists challenge: when artifacts of intervention interact with treatments. Mar Ecol Prog Ser 111:289–297

Reid DG (1988) The genera *Bembicium* and *Risellopsis* (Gastropoda: Littorinidae) in Australia and New Zealand. Rec Aust Mus 40:91–150

Schmidt GH, Warner GF (1984) Effects of caging on the development of a sessile epifaunal community. Mar Ecol Prog Ser 15:251–263

Southward AJ (1956) The population balance between limpets and seaweeds on wave-beaten rocky shores. Rep Mar Biol Sta Pt Erin 68:20–29

Stachowicz JJ (2001) Mutualism, facilitation, and the structure of ecological communities: positive interactions play a critical, but underappreciated, role in ecological communities by reducing physical or biotic stresses in existing habitats and by creating new habitats on which many species depend. Bioscience 51:235–246

Tamburri MN, Zimmer-Faust RK (1996) Suspension feeding: basic mechanisms controlling recognition and ingestion of larvae. Limnol Oceanogr 41:1188–1197

Tamburri MN, Zimmer RK, Zimmer CA (2007) Mechanisms reconciling gregarious larval settlement with adult cannibalism. Ecol Monogr 77:255–268

Tamburri MN, Luckenbach MW, Breitburg DL, Bonniwell SM (2008) Settlement of *Crassostrea ariakensis* larvae: effects of substrate, biofilms, sediment and adult chemical cues. J Shellfish Res 27:601–608

Thomsen MS, Wernberg T, Altieri A, Tuya F and others (2010) Habitat cascades: the conceptual context and global relevance of facilitation cascades via habitat formation and modification. Integr Comp Biol 50:158–175

Thomsen MS, Altieri AH, Angelini C, Bishop MJ and others (2018) Secondary foundation species enhance biodiversity. Nat Ecol Evol 2:634–639

Toscano BJ, Griffen BD (2013) Predator size interacts with habitat structure to determine the allometric scaling of the functional response. Oikos 122:454–462

Underwood AJ (1997) Experiments in ecology: their logical design and interpretation using analysis of variance. Cambridge University Press, Cambridge

Warren JH (1990) Role of burrows as refuges from subtidal predators of temperate mangrove crabs. Mar Ecol Prog Ser 67:295–299

Wilkie EM, Bishop MJ, O'Connor WA (2012) Are native *Saccostrea glomerata* and invasive *Crassostrea gigas* oysters' habitat equivalents for epibenthic communities in south-eastern Australia? J Exp Mar Biol Ecol 420-421: 16–25

Editorial responsibility: Lisandro Benedetti-Cecchi, Pisa, Italy

Submitted: May 13, 2018; Accepted: November 12, 2018
Proofs received from author(s): December 8, 2018