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Habitat-modifying invasive species can influence rates of predation on native prey either directly by providing protective structure or indirectly by modifying traits of prey species responding to the habitat. The alga Caulerpa taxifolia is one of the most successful invasive species of shallow-water marine systems globally, often provisioning habitat in areas previously lacking in vegetated structure. We experimentally evaluated the direct effect of Caulerpa to provide refuge for the native clam Anadara trapezia and how this balances with its influence on two trait-mediated indirect interactions that may increase Anadara's susceptibility to predators. Specifically, Caulerpa's alteration of physical and chemical properties of the surrounding water and sediment deteriorate Anadara's condition and predator resistance properties and also cause Anadara, though normally buried, to project from beneath the sediment, exposing it to predators. Our results show that Anadara are somewhat (but not consistently) protected from predators by living among Caulerpa. Shallow burial depth did not counteract this protective effect. However at times of year when predator activity diminishes and conducive environmental conditions develop, negative effects of Caulerpa habitat such as hypoxia and lowered flow may dominate. Under such situations, poor clam condition accentuates Anadara's susceptibility to mortality. Ultimately, a slight and inconsistent positive effect of Caulerpa to protect Anadara from predators is exceeded by the strong negative effect of Caulerpa on clam mortality, which is heightened by clams' weakened condition produced by chronic exposure to Caulerpa. Our results show that invasive habitat-modifying species can affect mortality of native species not simply through obvious positive direct effects of their protective structure, but indirectly through contrasting negative modification of the traits of prey species responding to the habitat.

Keywords

indirect, fauna, direct, native, variable, mortality, species, invasive, modifying, habitat, effects

Disciplines

Life Sciences | Physical Sciences and Mathematics | Social and Behavioral Sciences

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Variable direct and indirect effects of a habitat-modifying invasive species on mortality of native fauna

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Abstract. Habitat-modifying invasive species can influence rates of predation on native prey either directly by providing protective structure or indirectly by modifying traits of prey species responding to the habitat. The alga *Caulerpa taxifolia* is one of the most successful invasive species of shallow-water marine systems globally, often provisioning habitat in areas previously lacking in vegetated structure. We experimentally evaluated the direct effect of *Caulerpa* to provide refuge for the native clam *Anadara trapezia* and how this balances with its influence on two trait-mediated indirect interactions that may increase *Anadara*'s susceptibility to predators. Specifically, *Caulerpa*'s alteration of physical and chemical properties of the surrounding water and sediment deteriorate *Anadara*'s condition and predator resistance properties and also cause *Anadara*, though normally buried, to project from beneath the sediment, exposing it to predators. Our results show that *Anadara* are somewhat (but not consistently) protected from predators by living among *Caulerpa*. Shallow burial depth did not counteract this protective effect. However at times of year when predator activity diminishes and conducive environmental conditions develop, negative effects of *Caulerpa* habitat such as hypoxia and lowered flow may dominate. Under such situations, poor clam condition accentuates *Anadara*'s susceptibility to mortality. Ultimately, a slight and inconsistent positive effect of *Caulerpa* to protect *Anadara* from predators is exceeded by the strong negative effect of *Caulerpa* on clam mortality, which is heightened by clams' weakened condition produced by chronic exposure to *Caulerpa*. Our results show that invasive habitat-modifying species can affect mortality of native species not simply through obvious positive direct effects of their protective structure, but indirectly through contrasting negative modification of the traits of prey species responding to the habitat.

Key words: Anadara trapezia; *behavioral modification; benthic infauna;* Caulerpa taxifolia; *ecosystem engineering; foundation species; New South Wales, Australia; nonnative species; prey refuges; soft sediment communities; sublethal effects; trait-mediated indirect interactions.*

Introduction

Invasive species that create or modify structure and habitat often have profound community effects (Jones et al. 1994, Hastings et al. 2007). These so-called habitat-modifying ecosystem engineers can affect not only habitat complexity, but also related properties such as environmental chemistry and physical variables (Vitousek 1990, Crooks 1998, 2002, Chisholm and Moulin 2003, Gribben et al. 2009*b*). Such alterations of habitat and environmental properties may in turn alter the abundance and diversity of native species, as well as their many context-dependent interactions such as competition and predation (e.g., Bertness 1984, D'Antonio and Mahall 1991, Equihua and Usher 1993, Crooks 1998, Grabowski et al. 2005).

The large effects of habitat-modifying invasive species on populations of resident species stem from two routes. First, habitat structure is an important mediator of biotic interactions, especially predation (e.g., Crowder and Cooper 1982, Fraser and Cerri 1982, Irlandi 1994, Byers 2002, Ryer et al. 2004, Johnson 2007, Shima et al. 2008). In particular, habitat may directly mediate predation by providing prey or predators a refuge and influencing predator–prey encounter rates. Neira et al. (2006) showed crab densities were five times higher in invasive *Spartina* marsh grass habitat compared to adjacent mudflats. Within the *Spartina* refuge, heightened crab abundance subsequently led to a twofold higher reduction in benthic microfaunal prey.

Second, habitat itself, especially biogenic habitat, may also indirectly mediate biotic interactions, especially predation, by altering morphological and behavioral traits of prey that in turn influence predation rates

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(Grabowski 2004, Griffen and Byers 2006). Although invasive habitat-modifying species have been studied little in regard to eliciting trait changes in resident species, invasive species in general are known to alter behavioral and morphological traits of prey that in turn influence their predation rates (Freeman and Byers 2006, Trussell et al. 2006, Langkilde 2009). For example, Kiesecker and Blaustein (1998) showed that tadpoles of a native frog species altered their microhabitat use in the presence of an introduced bullfrog and, by reducing overlap with the bullfrog, maintained high survival.

The possibility that such trait alterations might also stem from an invasive biogenic habitat itself raises the interesting possibility that the habitat-modifying invader may simultaneously both directly (through habitat provisioning) and indirectly (through trait modification) influence subsequent biotic interactions such as predation. The likelihood of pervasive effects may be particularly heightened if the invasive species provisions habitat de novo, since native species would share little to no evolutionary history with the provisioned structure. In this study we quantify predation rates on a common native species via the direct influences of habitat supplied by an invasive ecosystem engineer, as well as via indirect influences stemming from trait modifications of the prey elicited by the novel habitat.

Study system

The semi-tropical green alga *Caulerpa taxifolia* ((Vahl) C. Agardh; hereafter *Caulerpa*) is one of the world's most invasive species (Lowe et al. 2000, Meinesz et al. 2001). *Caulerpa* can establish from a single fragment and typically spreads rapidly in invaded regions, forming dense monospecific beds that often negatively affect many native taxa including algae and seagrasses (Devillele and Verlaque 1995, Ceccherelli and Cinelli 1997, Ferrer et al. 1997), fish (York et al. 2006), and invertebrates (Gribben and Wright 2006*a*, Wright and Gribben 2008). The habitat conversion that *Caulerpa* creates is stark. Throughout invaded estuaries, *Caulerpa* has converted large areas of the unvegetated, soft-sediment substratum that previously existed into vast algal beds (State of New South Wales, Department of Primary Industries 2005, Wright 2005). Organisms in these estuaries accustomed to soft-sediment environments now find themselves dealing with novel structure. In addition to simply changing the habitat structure, *Caulerpa* is known to alter physical properties such as slowing water flow and increasing sediment and boundary layer hypoxia (Gribben et al. 2009*b*, McKinnon et al. 2009).

In estuaries of southeastern Australia where *Caulerpa* is invading, one of the abundant native species is the long-lived (7–10 years), infaunal bivalve *Anadara trapezia* (Arcidae, Deshayes 1840; hereafter *Anadara*), the Sydney cockle. Recruitment of *Anadara* is significantly greater to *Caulerpa* habitat (Gribben and Wright 2006*b*), perhaps due to enhanced capture and retention of particles resulting from its reduction of water velocities (Gribben et al. 2009*b*). However, ultimately *Anadara* populations are very negatively affected by *Caulerpa*, with the higher recruit densities inside *Caulerpa* driven to equally low levels within a year (Gribben et al. 2009*b*) and adult densities in *Caulerpa* as low as one-fifth of those in unvegetated areas (Wright et al. 2007). However, the manner in which *Anadara* populations are reduced is unclear. We hypothesized that in addition to direct negative effects, *Caulerpa* might exert indirect effects on *Anadara* via its influences on the rates of predation on juvenile and adult clams.

The influence of *Caulerpa* on *Anadara* appears different in magnitude and kind from effects of native vegetated structure. In several bays *Anadara* co-occurs in patches with the native seagrasses *Zostera capricorni* and *Halophila ovalis*. *Anadara* densities within native seagrasses are roughly intermediate between unvegetated and *Caulerpa* habitats (Wright et al. 2007). Physical variables within native seagrasses, especially redox potential, are much more similar to unvegetated habitat than to *Caulerpa* habitat (McKinnon et al. 2009).

Anadara are susceptible to a suite of benthic predators whose traditional foraging methods may be influenced by *Caulerpa*. Dominant predators of *Anadara* include blue swimmer crabs (*Portunus pelagicus*), yellowfin bream (*Acanthopagrus australis*), rays and stingarees (*Urolophus* spp.), and octopods (*Octopus tetricus*), all of which, especially crabs and rays, are adapted and accustomed to foraging in unvegetated sediments and thus likely influenced by the novel vegetative structure of *Caulerpa*. The predators also may be deterred by the altered abiotic environment (e.g., low dissolved oxygen, high sulfide) (Altieri 2008) created by *Caulerpa*. In addition to these protective direct means by which habitat could affect rates of predation on *Anadara*, *Caulerpa* produces pronounced differences in the traits of clams living among it that may in turn influence predation rates. Specifically, in response to habitat conversion by *Caulerpa*, *Anadara* alters its burial depth and condition (including shell thickness, shell strength, and resistance to opening) (Wright and Gribben 2008; J. T. Wright et al., *unpublished manuscript*), both of which are important antipredator traits in bivalves (Seitz et al. 2001). *Anadara* normally lives buried beneath the sediment with only 5–10 mm of its body protruding above the surface. Once an area has been invaded, *Anadara* "pop up" from the sediment, sticking 50% or more of their bodies above the sediment surface (Gribben et al. 2009*a*). The mechanism for this pop-up effect has been documented as a response to hypoxic conditions at the sediment–water interface (Wright et al., *in press*), possibly created by associated reducing bacteria in *Caulerpa* sediments (Chisholm and Moulin 2003). Although pop-up does appear to be a useful strategy in mitigating mortality from anoxia (Wright et al., *in press*), the strategy, along with direct effects of the

reducing environment inside *Caulerpa* beds, decreases the clams' adductor muscle strength and overall condition (as indexed with measures of shell and tissue health; Wright and Gribben 2008).

We designed several experiments to examine the influence of *Caulerpa* on rates of predation on *Anadara*. We first quantified rates of predation in *Caulerpa*-invaded substratum and in unvegetated substratum, which is characteristic of a pre-invaded state. We then experimentally isolated the roles of one direct and two indirect mechanisms of the invader's influence on predator–prey interactions. We hypothesized that a positive effect on *Anadara* may stem from the direct influence of *Caulerpa* provisioning novel habitat that may serve as a prey refuge, hiding and protecting the prey and decreasing the foraging efficiency of the predators. Conversely, we hypothesized that two modifications of *Anadara*'s traits due to *Caulerpa* exposure, reduced burial depth and poor condition, may subsequently increase the clams' vulnerability to predators in the presence of *Caulerpa*. Thus, in invaded *Caulerpa* areas, clams may be negatively affected by increased exposure to predators due to protruding above ground and by weakened defenses against predators due to weaker shell and poor condition. Our experiments address the manner in which these positive and negative factors interact and how these predation mediation mechanisms balance with direct effects of *Caulerpa* on *Anadara* survival.

Methods

Species and study location

In southeastern New South Wales (NSW), Australia, since its initial discovery in 2000, *Caulerpa* has spread rapidly to 14 different estuaries (State of New South Wales, Department of Primary Industries 2005). All of our work was conducted subtidally (2-m depth) in Sponge Bay, Lake Conjola, NSW (35°15′44.3″ S, 150°26′47.8″ E), a temporary barrier estuary ~210 km south of Sydney. *Caulerpa* was first discovered in Lake Conjola in 2000 (Creese et al. 2004) and within eight years spread to cover >25% of the benthos, including nearly all of the benthos in shallow water (0.25–3 m; State of New South Wales, Department of Primary Industries 2005). At our study site, *Anadara* occurs in increasingly rare patches of unvegetated sediments and in *Caulerpa*-invaded sediments, although at lower densities (Wright et al. 2007). Native seagrasses are present in Lake Conjola but they are sparse and restricted to shallow areas fringing the bay.

Experiment I: effects of habitat, burial depth, and predator exposure

We conducted a three-month (11 October 2007 to 5 January 2008) experiment (1) to quantify the baseline mortality rates of *Anadara* in *Caulerpa*-invaded substratum and unvegetated substratum and (2) to determine how predator exposure, habitat, burial depth, and their interactions influence the mortality rate of *Anadara* (see Plate 1). To ensure adequate numbers of healthy *Anadara* for the experiment, adult clams (40–60 mm shell length) were collected from an adjacent estuary, St George's Basin. At the time of the study, *Caulerpa* invasion was minimal in this estuary and clams could be collected from large areas of unvegetated sediments, ensuring all clams were of equally good condition. These clams were allowed to acclimate in Lake Conjola for one month while buried in an unvegetated area that we hand-picked clear of *Caulerpa*.

We used a split-plot design with pairs of habitat plots in four blocks. Specifically, each block consisted of one 1.5 × 1.5 m plot of *Caulerpa* and one similar-sized adjacent plot of unvegetated sediment (separated by 2 m) where *Caulerpa* was removed by hand three weeks prior to the start of the experiment. Throughout the course of the experiment unvegetated plots were maintained to ensure no encroachment of *Caulerpa* occurred. Blocks were separated by 10–20 m. We replicated each predator exposure × burial depth treatment twice in each of the four paired habitat blocks (for a total of eight replicates per treatment per habitat).

Each replicate consisted of 10 *Anadara* placed into plastic tubs (25 × 15 cm that were either 2 or 10 cm deep) that were filled with sediment from an unvegetated area. Sediment from an unvegetated area was used to eliminate any effects of *Caulerpa*-associated substances or conditions (e.g., phytotoxins, associated bacteria, anoxia) that might be present in the sediment and affect infauna, such as *Anadara*. The density of *Anadara* used (10 clams/0.0375 m^2) is high, but realistic (Wright, *in press*), and allowed us to have sufficient clams per tub to reliably resolve mortality estimates. To manipulate burial depth, both shallow (2-cm depth) and deep (10-cm depth) tubs were used. In the shallow tubs, clams were inserted to the full depth of the tub and thus remained with approximately half to two-thirds of their shell exposed aboveground, mimicking their exposure in *Caulerpa*-invaded areas (Gribben et al. 2009*a*; J. T. Wright et al., *unpublished manuscript*). In deep tubs, clams were pushed to their full burial depth (90% submerged). Because the surrounding sediment in the tub was of good quality, i.e., from an unvegetated habitat, it helped ensure that the clams in the deep treatment would remain buried throughout the experiment. Predator exposure was manipulated by completely covering half of the tubs with wire mesh (19 mm) that extended 5 cm in height over the tubs. We installed a 5 cm high wire mesh rim around all the open-topped tubs to prohibit emigration of clams. These rims also functioned as a cage control since these tubs only differed from the fully caged treatment in not having a mesh top. By surrounding each tub, the mesh rim was perpendicular to the primary direction (horizontal) of water flow and thus should capture any potential artifacts of caging. However, water flow is generally low in Lake Conjola anyway, especially within Sponge

Bay, as flows are tidally driven and tidal range is low (20% of adjacent ocean range; MHL 2003).

Full replicates (representing one of each treatment) were systematically grouped within each habitat plot to ensure adequate interspersion of treatments. To reduce potential biases from predators foraging in open-topped tubs spilling over onto adjacent open-topped tubs, we systematically interspersed topped and open-topped treatments. Assignment of burial depth treatments was randomized within each predator exposure treatment within each replicate set.

The burial depth and predation exposure treatments were further crossed with habitat by burying tubs of all treatments inside the unvegetated and *Caulerpa* plots. Tubs were buried flush with the surrounding sediment and care was taken not to damage the canopy of *Caulerpa* when adding the tubs to this habitat. Because we suspected that the shallow-burial, uncaged treatment might exhibit the greatest and most variable loss rate of *Anadara*, we added a third replicate of it to each habitat plot, for a total of 12 replicates of this treatment per habitat type.

Approximately every 10 days we scoured the experimental plots for evidence of predation (e.g., cracked shells) and missing clams. At the end of the three-month experiment, tubs were removed, the contents sieved, and the clams enumerated. In some cases (especially under cage tops), dead shells remained and could be used to ascertain the cause of death. A split-plot ANOVA was used to test the effects of habitat, burial depth, predation, and their interactions (all fixed factors) and block and block × habitat (random factors) on the proportion of *Anadara* mortality in each experimental tub (Anscombe arcsine square-root transformed; Zar 1996) (proc mixed, SAS 9.1; SAS Institute, Cary, North Carolina, USA). To handle the unbalanced, larger sample size for the shallow uncaged treatment, we used type III sums of squares to analyze significance (Quinn and Keough 2002), though there are no changes in significance if these extra replicates are excluded altogether. Because caged clams had low mortality rate among plots and treatments and predator exposure did not interact significantly with other variables (see *Results*), in a second more-focused, higher power analysis we examined the effects of block, habitat, and burial depth on survival of *Anadara* only in the predator exposed, open-topped tubs.

Concomitantly in the same habitat blocks in which we conducted the larger orthogonal experiment, we quantified mortality rates under unmanipulated conditions. Into a 25 × 15 cm area of ambient sediment we inserted 10 *Anadara* from our collection to 80% of their body length (which clams could then subsequently adjust). We established two replicates within each habitat plot, i.e., one within each grouped full replicate set, for a total of eight replicates overall per habitat type. The two replicates within a single plot were separated by at least 0.6 m.

Predator surveys

To complement our habitat × burial depth × predation experiment, we indexed the abundance of predators within *Caulerpa* and unvegetated habitats in each of our experimental plots. These measurements not only determine predator use of the two habitat types, but also whether such habitat associations might help explain *Anadara* losses we observed in the experiment. We visually surveyed the number of clam predators (crabs, octopus, rays) in each plot approximately every 10 days. Immediately upon arrival at the site we visited each plot using scuba equipment. The substrate was typically prodded with a stick to ensure buried predators were uncovered.

Also, throughout the duration of experiment I, we conducted a number of baited video trials in nearby areas of Sponge Bay to assess the willingness and ability of predators to forage in *Caulerpa* vs. unvegetated habitat. Both this assessment and the predator surveys help to illustrate to what degree any predation alleviation *Anadara* experiences in *Caulerpa* is due to predators avoiding *Caulerpa* as opposed to *Anadara* simply being better hidden. Video cameras were encased in underwater housing and submerged typically to 2 m depth in *Caulerpa* beds and in unvegetated areas of at least 1 × 1 m that were either created by us or that occurred naturally in patches. Three *Anadara* were crushed and placed under protective mesh in the center of the field of view. Cameras were deployed in pairs with one in each habitat ~15 m apart. Two pairs (i.e., four cameras) were deployed at once and recordings lasted 90 min. Cameras were deployed on nine occasions for a total of 27 h in each habitat type spread over various times of daytime and dusk hours over three months.

We analyzed the videotapes noting predatory species that visited the bait (principally blue swimmer crabs and octopus), when they arrived, and how long they stayed (which was computed only for the videos in which a predator left before the end of the 90-min recording). Although healthy *Anadara* unlikely emit such strong olfactory cues as the cracked individuals we used, this experiment was designed to gauge how readily each habitat type is entered by predators. For example, if cracked bait clams in *Caulerpa* were relatively disfavored or avoided by predators even with this strongest of attractants, that would suggest that under normal circumstances when more subtle cues are present, the clams may benefit from even greater protection.

Experiment II: effects of predator exposure on juvenile clams

To examine the influence of habitat and predator exposure on the rates of predation on small (20–25 mm shell length) infaunal *Anadara*, we conducted a split-plot designed experiment. We created three experimental blocks consisting of a pair of unvegetated and *Caulerpa* plots (1 × 1 m each). Each block contained

one replicate of each habitat × predator exposure treatment. Specifically, into each of these six plots we inserted two mesh cages (16 × 24 × 9 cm high; 6 mm mesh size) to a depth of 4 cm into the sediment. Each cage received 11 juvenile *Anadara* (except one plot of *Caulerpa* in which both cages received 10). Clams were two years old and had been raised to this age and size in protective mesh bags in unvegetated sediments in Sponge Bay. A mesh top was added to one of the two cages in each habitat plot. Given the height of the cage walls and the depth of insertion, clams that were missing at the end of the experiment could not have emigrated and were assumed to have been taken by predators. Because of rapid predation rates in open-topped cages, this experiment was run over a two-week period (18 October to 1 November 2007). The proportion of clams surviving per cage were Anscombe transformed and analyzed using a split-plot ANOVA structure with habitat, predator exposure, and their interaction as fixed factors and block and block × habitat as random factors.

Experiment III: effects of habitat and clam condition

To determine the role of habitat and clam condition on clam mortality, we undertook another split-plot experiment. We collected 300 clams from Sponge Bay from both unvegetated habitat and within *Caulerpa* to get clams of both good and poor condition, respectively. Although it is well established that *Anadara* residing in *Caulerpa* have many aspects of inferior condition (Wright et al. 2007, Wright and Gribben 2008, Gribben et al. 2009*b*), we measured length and dry tissue masses of 10–15 clams from each habitat to verify that initial conditions were different. Both clam length and habitat of collection significantly affected *Anadara*'s initial condition; the interaction was not significant and was removed. Adjusted least squares means of ANCOVA between sites showed ~10% lower tissue mass standardized by size for *Anadara* from *Caulerpa* compared to those from unvegetated substratum (condition effect: $n = 23$, $t = -2.90$, $P = 0.0096$), a difference consistent in magnitude with detailed data collected on habitat effects on many *Anadara* metrics (Wright et al. 2007, Wright and Gribben 2008). Furthermore, J. T. Wright et al. (*unpublished manuscript*) demonstrated that *Anadara* collected from *Caulerpa* habitat also have significantly thinner shells and lower shell strength and resistance to opening compared to *Anadara* from unvegetated habitat.

Experimental clams collected from each of the two habitats were blotted dry and coded with black paint to denote their condition (good or poor) in accordance with the habitat from which they originated. Clams were held overnight in seawater and the following day (1 March 2008) were placed back into the field into 12 0.72-m^2 circular pens that were 10 cm high and extended 5 cm deep into the sediment (mesh size = 19 mm). Pens were deployed in groups using three of the same habitat blocks (numbers 1, 2, and 4) that had been used in experiment I. In each of the three blocks we inserted two pens in *Caulerpa* and two in unvegetated plots that had now been free of *Caulerpa* for approximately six months. Fifteen marked clams originating from each of the two habitat types were placed in each pen and inserted into the sediment. This density (30 *Anadara*/0.72 m^2) is a typical density for these clams in the study area in unvegetated areas (Wright et al. 2007). For comparative purposes, to gauge clam mortality rates in the absence of predation, in the third block we covered one of the pens in each habitat with mesh netting (mesh size = 10 cm) to prevent predator access. Because clam condition is altered by habitat and because we did not want the condition of clams to change appreciably from their assigned treatment over the course of the experiment (Wright and Gribben 2008), we terminated the experiment after two months and collected and enumerated the clams.

Pens were monitored approximately every 10 days to search for dead clams. At the end of the experiment (30 April), we retrieved the clams from each pen. Two divers separately excavated the bottom of every pen to ensure all clams had been recovered. In addition to tabulating total clam losses from each pen, we could also roughly attribute mortality sources to two broad categories based on forensic evidence on recovered shells, the position from which a clam was recovered, or whether a clam was recovered at all. (In the previous habitat × burial depth × predator exposure experiment [experiment I], of the predator-exposed clams only 12% of dead clams were recovered, essentially rendering shell forensics moot for that experiment). Dead clams found outside pens, cracked clams, and missing clams were treated as predator losses. Dead clams found inside a pen with both valves intact (and often stained black) were most likely attributable to non-predatory mortality sources such as hypoxia, starvation, or senescence. The proportion of mortality we attributed to predation may be slightly conservative since octopus can occasionally eat a clam in place and leave no marks on the shell (J. T. Wright and P. E. Gribben, *personal observation*).

The larger pen size and lower clam density in this experiment allowed us to treat each clam as a pseudo-independent replicate, which permitted more powerful analysis and also could easily handle the mixture of good- and poor-condition clams in each pen. Specifically, the mortality of *Anadara* in the open-topped pens was analyzed with logistic regression with individual clam responses clustered by pen to determine the effect of condition, habitat, condition × habitat, block, and block × habitat on mortality (proc surveylogistic, SAS 9.1). For each habitat we also parsed the overall mortality rate into suspected predator-caused and non-predatory deaths and compared loss rates to the clams in the predator-protected pens.

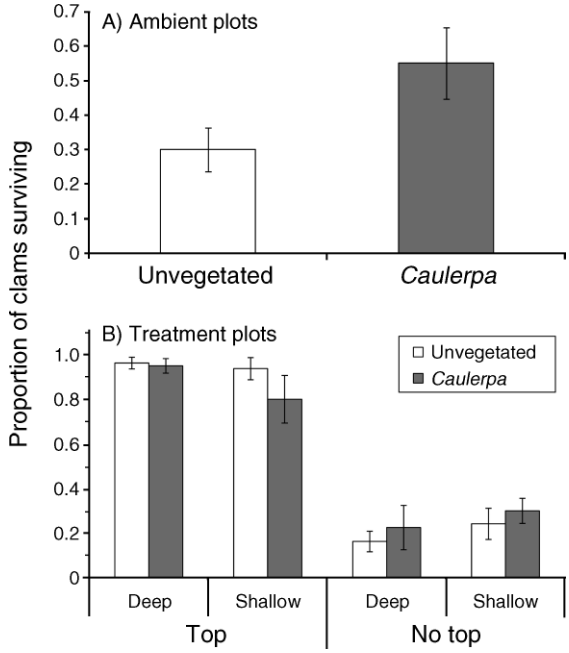

FIG. 1. Survivorship of the native clam *Anadara trapezia* (mean ± SE) over 12 weeks in the habitat × burial depth × predator exposure experiment (experiment I) for (A) clams placed into the sediment in 0.0375-m^2 ambient plots and (B) clams in each of the eight treatment combinations. The treatments reflected in the figure are predator exposure (top, protected; no top, exposed), burial depth (deep or shallow), and habitat (unvegetated substratum or with the habitat-modifying invasive algal species *Caulerpa taxifolia*). The work was conducted subtidally (2-m depth) in Sponge Bay, Lake Conjola, New South Wales, Australia, a temporary barrier estuary ~210 km south of Sydney.

RESULTS

Experiment I: effects of habitat, burial depth, and predator exposure

Over the 12-week experimental period under unmanipulated conditions, *Anadara* in our ambient *Caulerpa* plots survived better than *Anadara* in ambient unvegetated plots (55% surviving vs. 30%; one-tailed t test on Anscombe-transformed data, $t = 1.82$, df = 10.4, $P = 0.049$, assuming unequal variances; Fig. 1).

In the main factorial experiment, deaths within predator exclusion cages averaged only 9% per tub and were slightly higher in *Caulerpa* (12.5%) as opposed to unvegetated treatments (5%; Fig. 1). Losses were consistently large (an average of 76%) across all open-topped treatments. Comparatively low losses of the caged clams underscore that the majority of losses of exposed clams were due to predation. The mortality rate of exposed clams due to predation was at least 67% (loss and mortality of predator-exposed clams minus clam mortality in cages). In formal analyses only predator exclusion was a significant factor on clam mortality ($P < 0.0001$) and block was marginally nonsignificant ($P = 0.059$; Table 1A).

TABLE 1. Summary of split-plot analyses of the mortality of *Anadara trapezia* in the habitat × burial depth × predator exposure experiment (experiment I) examining treatment effects for (A) the full experiment and (B) predator-exposed, open-topped tubs only.

Factor	df	F	P
A) Full experiment			
Habitat	1, 58	0.15	0.723
Predation exposure	1, 58	205.95	<0.001
Burial depth	1, 58	0.02	0.897
Habitat × predator exposure	1, 58	1.90	0.174
Habitat × burial	1, 58	0.39	0.534
Predator exposure × burial	1, 58	3.35	0.072
Habitat × burial × predator exposure	1, 58	0.74	0.392
Block	3, 58	2.62	0.059
Block × habitat	3, 58	1.06	0.372
B) Predator-exposed, open-topped tubs			
Habitat	1, 30	0.29	0.625
Burial depth	1, 30	1.64	0.210
Habitat × burial depth	1, 30	0.03	0.860
Block	3, 30	3.12	0.040
Block × habitat	3, 30	1.89	0.152

Note: The work was conducted subtidally (2-m depth) in Sponge Bay, Lake Conjola, New South Wales, Australia, a temporary barrier estuary ~210 km south of Sydney.

When focusing exclusively on the uncaged, predator-exposed clams, only block was significant (Table 1B). Block 2 exhibited the most extreme mortality, with <10% survivorship. Habitat × block was not significant ($P = 0.15$) but showed a trend toward *Caulerpa* being safer for *Anadara* in blocks 1 and 4, whereas this trend was reversed for block 3 (Fig. 2). Neither burial depth nor any of its interactions were significant in either the full analysis or in the analysis of the predator-exposed clams exclusively (Table 1).

Predator surveys

In our 10 predator surveys of experimental plots over the three-month duration of the experiment, we never found a crab or stingaree in the four *Caulerpa* plots. In contrast, we found 20 crabs (*Portunus pelagicus*) and

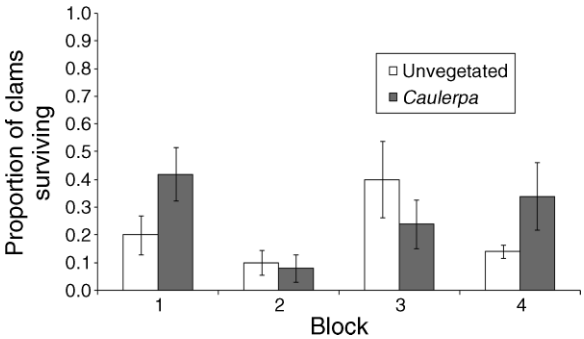

FIG. 2. The effect of habitat (unvegetated substratum or with the habitat-modifying invasive algal species *Caulerpa taxifolia*) on the proportion of *Anadara trapezia* clams surviving (mean ± SE) in the open-topped, predator-exposed tubs, by block, in experiment I.

TABLE 2. Summary of paired baited video deployments in each of the two habitat types (unvegetated substratum or with the habitat-modifying invasive algal species *Caulerpa taxifolia*).

Habitat type	No. video deployments	Videos with crabs	Time until crab arrival (min)		Duration of crab visit (min)
			Mean	SD	
Unvegetated	18	5	49.1	31.5	17.2
Caulerpa	18	4	45.7	21.9	16.1

Notes: Each video deployment recorded for 90 min. The table reports the number of deployments in which predatory crabs (*Portunus pelagicus*) were observed, the mean and standard deviation of the length of time after initial deployment that a crab appeared (for all nonzero values), and the duration of time the crab stayed on the bait. This latter category was only calculated for crabs that had left the field of vision before the end of the 90-min recording.

four stingarees (*Urolophus* spp.) in the unvegetated plots. Among the unvegetated plots, collectively we saw at least one predator on eight of the 10 survey days. Of the unvegetated plots, block 3 had the fewest observed predators (three crabs, no rays); block 1 had seven crabs; blocks 2 and 4 each had five crabs and two rays.

In baited video surveys, crushed *Anadara* clams attracted predatory crabs nearly identically into *Caulerpa* and unvegetated habitats (Table 2). Of 18 camera deployments in each habitat type, crabs appeared in five videos in unvegetated areas and in four videos in *Caulerpa*. The average time until the crab arrived was 49 min in unvegetated and 46 min in *Caulerpa*. The average duration of a crab's visit was 17 min in unvegetated and 16 min in *Caulerpa*. An octopus was observed on three occasions, all in unvegetated habitat. However, in two of these the octopus passed right over or by the bait cage; the one legitimate exploratory bout by an octopus lasted 6 min.

Experiment II: effects of predator exposure on juvenile clams

Predator exposure (i.e., cage tops) had a significant effect on the survival of juvenile clams ($F_{1,4} = 34.05$, $P = 0.004$). Also, fewer clams survived in unvegetated sediments than *Caulerpa* ($F_{1,4} = 23.58$, $P = 0.04$). Mortality also varied significantly by block ($F_{2,4} = 17.92$, $P = 0.05$). The interaction of habitat with predator exposure was not significant ($F_{1,4} = 0.33$, $P = 0.60$), nor was the interaction of block × habitat ($F_{2,4} = 0.13$, $P = 0.89$; Fig. 3). Based on our observations of the experiment, large yellowfin bream (*Acanthopagrus australis*) were likely the dominant predator of this size class of clam given their interest in the cages and their documented predation on recruits and small clams (4–10 mm shell length; Gribben and Wright 2006*b*).

Experiment III: effects of habitat and clam condition

In this experiment, block ($\chi^2 = 24.77$, $P < 0.0001$), habitat ($\chi^2 = 40.63$, $P < 0.0001$), condition ($\chi^2 = 9.97$, $P = 0.0016$), and block × habitat ($\chi^2 = 35.90$, $P < 0.0001$) were all significant factors on the loss rate of *Anadara*. Habitat × condition was not significant ($\chi^2 = 0.13$, $P = 0.72$). Block × habitat was significant because although loss was greater in *Caulerpa* in all blocks, it was extreme in *Caulerpa* in block 4 (Fig. 4). Compared to the habitat × burial depth × predation experiment (experiment I), overall loss rate of predator-exposed clams was low (21%). Of 64 clam deaths, 52 were in *Caulerpa* (81%) and 41 were poor-condition clams (64%; Table 3). If all clams had died at the rate of the good-condition clams, the expected total mortality would have been 46 clams, meaning the poor condition of clams resulting from prior living in *Caulerpa* increased the death rate by 18 (39%).

The majority of loss in this experiment was not attributable to predators, which were infrequently observed during this experiment. Predators accounted for 28 out of 64 clam losses, an overall mortality rate from predation of 9% (28 clams out of 300). *Anadara* in unvegetated habitat had 8% mortality overall (12 clams out of 150), with eight of these deaths suspected due to predators. In *Caulerpa* the overall loss rate was considerably higher at 34.7% (52 clams out of 150), with only 20 losses suspected due to predators. Overall loss rates due to non-predatory sources, most likely effects of poor environmental quality (e.g., hypoxia, low flow, high sulfides), was 12% overall, but very different between habitats: 21.3% in *Caulerpa* and 2.7% in unvegetated habitat. These values compare similarly to the *Anadara* loss rates in the topped, predator-exclusion pens, where there was a 23% loss in *Caulerpa* and 0% in

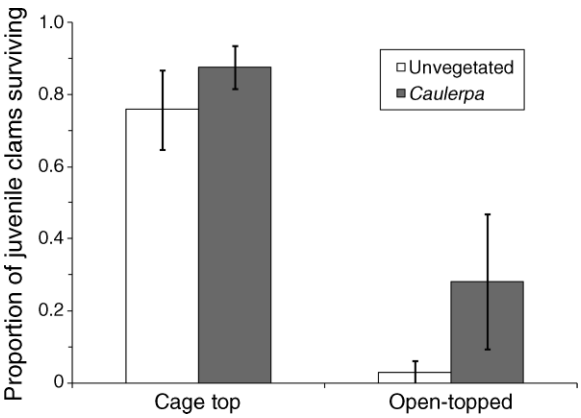

FIG. 3. Proportion of juvenile *Anadara trapezia* clams surviving (mean ± SE) over a two-week experiment as a function of habitat (unvegetated substratum or with the habitat-modifying invasive algal species *Caulerpa taxifolia*) and predator exposure (experiment II).

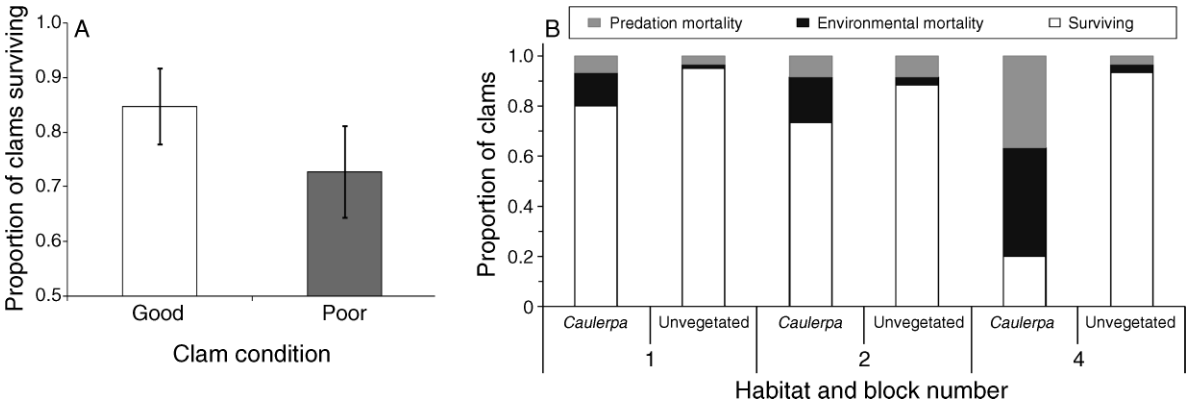

FIG. 4. Results for all predator-exposed *Anadara trapezia* clams in the habitat × clam condition experiment (experiment III). (A) Effect of condition on survival after two months (clams for the good-condition treatment were initially collected from unvegetated habitat; clams for the poor-condition treatment were initially collected from *Caulerpa taxifolia* habitat). Data shown are survival proportions averaged among pens (mean ± SE). (B) The effect of habitat on total clam survival within each block. Blocks 1 and 2 had two predator-exposed pens in each habitat; block 4 had one pen in each habitat. Each pen contained 30 clams (15 of each condition, good and poor).

the unvegetated habitat. The correspondence in values of these non-predator deaths in topped cages and those calculated for exposed clams via shell forensics not only indicates that we accurately attributed non-predator deaths, but also that mortality from multiple sources was largely additive.

DISCUSSION

The relative importance of biotic influences governing post-invasion interactions between native and exotic species can vary in time and space (Bruno et al. 2005). Our initial experiment (experiment I) found high levels of predation on *Anadara*, considerably higher than predation rates estimated in Sponge Bay three years earlier (Wright and Gribben 2008). During experiments I and II conducted during late spring and summer, low losses of cage-protected clams underscored that predation was responsible for the losses of most exposed clams. However the influence of *Caulerpa* in these experiments, which always trended toward mitigating *Anadara* losses to predation, varied considerably in strength. For example, in the habitat × burial depth × predator exposure experiment (experiment I), clams (all initially in good condition) survived 6% better overall in *Caulerpa* compared to unvegetated sediment. In our least manipulated clams in that experiment, i.e., the *Anadara* that were inserted into predator-exposed, ambient sediment plots, the net effect of *Caulerpa* was to nearly double *Anadara*'s survival rate, increasing its overall survival by 25 percentage points (Fig. 1A). Likewise in the juvenile clam experiment (II) predator-exposed *Anadara* inside *Caulerpa* survived better (28%) compared to unvegetated habitat (3%). However by autumn in the condition experiment (III), predators were seldom observed, and *Caulerpa*, now with little predator protection role to serve, became relatively more dangerous for clams compared to unvegetated habitat, with 81% of *Anadara* deaths occurring in *Caulerpa*.

Our predator surveys demonstrated that predators were abundant and active in the area during our spring and summer experiments (I and II). Although our video trials demonstrate that the predators do not avoid *Caulerpa* and will willingly forage within *Caulerpa*, from the clam survival data it seems predators forage more (or more effectively) in the unvegetated areas where we also observed them most often in our visual predator surveys. Any differential predation protection afforded *Anadara* by *Caulerpa* however was gone in the condition experiment (III). Not only were few predators observed, but clam losses to predation dropped almost an order of magnitude compared to experiment I, such that losses from non-predatory sources predominated. *Anadara* in unvegetated plots benefited greatly from predation decreasing, exemplified by the fact that mortality of predator-exposed *Anadara* in experiment III was essentially equal to mortality of cage-protected clams in

TABLE 3. Number of native clams (*Anadara trapezia*) lost as a function of habitat (unvegetated substratum or with the habitat-modifying invasive algal species *Caulerpa taxifolia*) and clam condition (good or poor) over two months in experiment III.

	Caulerpa		Unvegetated	
Source of mortality	Good	Poor	Good	Poor
Predation	9	11	2	6
Environmental influences	11	21	1	3

Notes: Starting number of clams for each condition type in each habitat was 75, for a total of 300 clams overall. The condition of experimental clams was determined by the habitat from which they were initially collected. It is well documented that clams that have lived in *Caulerpa* have poor condition; those in unvegetated areas have good condition. To verify we also quantified condition on a subset of our collected clams. *Anadara* from *Caulerpa* had ~10% lower tissue mass standardized by size compared to clams from unvegetated substratum.

experiment I (8% vs. 5%, respectively). *Anadara* in *Caulerpa* experienced decreased predation mortality as well, but the benefit of this alleviation was offset by an increase in non-predation mortality. Specifically, in experiment III the time-standardized non-predatory loss rate in *Caulerpa* was 32%, a nearly threefold increase over the 12.5% mortality in predator exclusion cages in experiment I. Thus, the change in the net effect of *Caulerpa* on *Anadara* we observed between experiments I and III is partly due to predation decreasing and unmasking a persistent negative influence of *Caulerpa* on *Anadara* and partly due to negative environmental influences of *Caulerpa* increasing.

Thus, even though *Caulerpa* appears to protect *Anadara* somewhat from predation at certain times of year when predators are active, this influence must eventually be outweighed by the negative non-predatory influences of *Caulerpa* because ultimately adult *Anadara* in *Caulerpa*-invaded areas are at one-fifth the density compared to adjacent unvegetated areas (Wright et al. 2007). Furthermore, because *Anadara* recruitment is significantly higher in *Caulerpa* (Gribben and Wright 2006*b*) and because mortality on small *Anadara* life stages (4–10 mm) is high and results in equally low *Anadara* abundances in both *Caulerpa* and unvegetated habitats (Wright and Gribben 2008, Gribben et al. 2009*b*), the differentially lower adult *Anadara* density in *Caulerpa* must result during the subsequent juvenile and adult life stages. In other words, the intermittent predation benefit to juvenile and adult *Anadara* from living in *Caulerpa* is ultimately overwhelmed by longer-term negative environmental effects of the alga.

Caulerpa likely affected *Anadara* mortality through several different environmental stresses known to be produced by the seaweed immediately below its canopy and in the sediment. These stresses include low levels of dissolved oxygen (DO) and flow (Gribben et al. 2009*b*) and high concentrations of sulfides, bacteria (Chisholm and Moulin 2003, Gribben et al. 2009*b*, McKinnon et al. 2009), and phytotoxins (Pedrotti et al. 1996). Recovered dead *Anadara* often exhibited the telltale signs of death consistent with these factors (intact shells, gaping and blackened). The localized nature of *Caulerpa*'s negative environmental effects in the sediment and in the benthic boundary layer beneath its canopy suggests why predation can still be high in *Caulerpa* (experiment I). Specifically, because the negative environmental effects are not large-scale, system-wide effects, large roving predators, i.e., those that eat adult *Anadara*, can move through and within degraded areas and strata and do not have to avoid invaded bays or *Caulerpa* patches.

Negative effects of *Caulerpa* are seemingly exacerbated by environmental stresses that vary temporally or stochastically. Wright and Gribben (2008), in a year-long study of *Anadara* survivorship in *Caulerpa*, identified a relatively long period of low mortality punctuated by a strong episodic die-off, suggesting that stochastic events (in their case a large freshwater input event) could drive mass mortalities that are accentuated in *Caulerpa*. In our study, low DO in the benthic boundary layer under *Caulerpa* may be more pronounced in autumn, the season immediately following luxuriant *Caulerpa* growth and metabolism, especially since such localized hypoxia is also associated with detrimental by-products (e.g., sulfides, bacteria, phytotoxins; Chisholm and Moulin 2003, Gribben et al. 2009*b*, McKinnon et al. 2009). Whatever the specific cause, non-predatory deaths were clearly accentuated in experiment III in *Caulerpa*, where they were an order of magnitude higher than in unvegetated habitat (21% vs. 2.7%, respectively; Table 3).

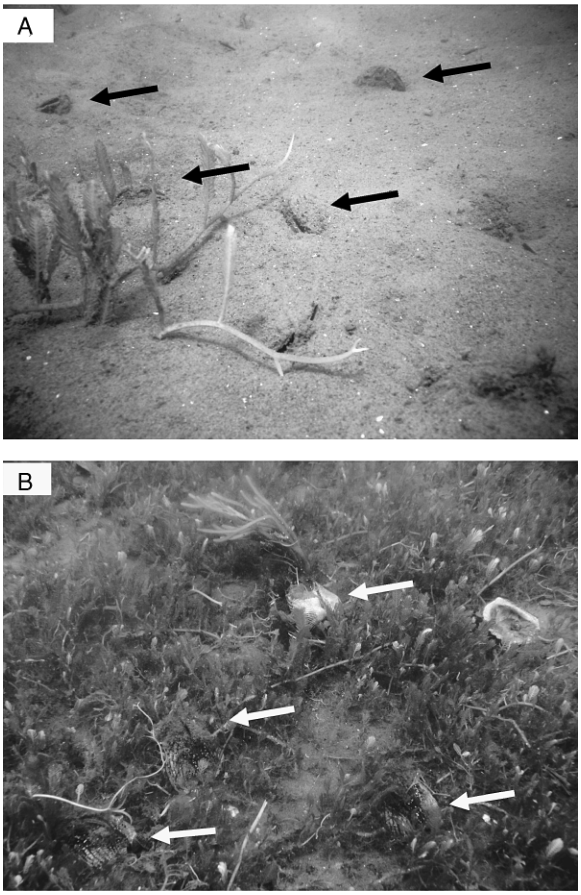

PLATE 1. (A) *Anadara trapezia* in natural, unvegetated habitat (though *Caulerpa taxifolia* is just beginning to invade from left). Several *Anadara* individuals, marked by arrows, are slightly visible with only a few mm of shell lip protruding above the surface. (B) Inside *Caulerpa* habitat, *Anadara* "pop-up" to expose often >50% of their bodies above the sediment. Photo credits: (A) J. T. Wright, (B) P. E. Gribben.

In addition to this negative effect via environmental conditions, *Caulerpa* also increased non-predatory mortality of *Anadara* through chronic effects on clam condition, a trait-mediated response of clams to living in *Caulerpa*. Specifically, clams in poor condition, i.e., those that had lived in *Caulerpa* longer, had lower

survival. Compared to good-condition clams, poor-condition clams were 55% more susceptible to predators and twice as susceptible to death by non-predatory/environmental causes (Table 3). So although environmental conditions may have degraded in *Caulerpa* during our final experiment, long-term exposure to *Caulerpa* and the resulting deterioration of clam condition is what appears to have set the stage for *Anadara*'s enhanced mortality quantified in this experiment. Ultimately, *Caulerpa*'s effect on *Anadara* via poor condition and environmental stress are the only negative ones we identified and thus the likely mechanisms responsible for drastically lower adult *Anadara* densities in *Caulerpa*.

Burial depth, a second trait-mediated response of clams to living in *Caulerpa*, does not help to account for *Anadara*'s density differential between habitats, as burial depth did not significantly affect *Anadara* mortality. (Although in the long term, shallow burial depth should indirectly increase mortality because it weakens *Anadara*'s adductor muscles and thus contributes to the clam's poor condition.) The lack of effect of burial depth was especially surprising considering that our predator surveys enumerated many predators in our experimental unvegetated patches and none in *Caulerpa* patches. Accordingly, the experimental shallow clams in unvegetated habitat should have been remarkably vulnerable. However, the shallow clams experienced loss rates nearly identical to all other predator-exposed clams. The lack of effect of burial depth suggests that visual cues may be of lesser importance for prey detection for *Anadara*'s predators or that visual cues even from mostly buried clams are sufficient.

Although it did not play a role in mediating predation, *Anadara*'s strategy to rise up to a shallower burial depth in *Caulerpa* habitat has been shown to mitigate negative effects of *Caulerpa* such as death by hypoxia, at least over the short term (Wright et al., *in press*). However, we did not observe negative direct effects of deep burial depth on mortality in *Caulerpa* clams in experiment I. This is perhaps not surprising because *Anadara* were placed in (initially) good sediment inside their experimental tubs and therefore had less immediate contact with any potential sediment anoxia, sulfides, and phytotoxins. Furthermore, with the exception of block 4, reasonably high survival of clams in ambient sediment within *Caulerpa* indicates no severe adverse environmental conditions during the time course of that experiment.

The temporal variation in predator influence led to a big difference between our two main experiments (I and III) that were run in different seasons. However, even within experiment I we observed much variability in *Anadara* survivorship, which was likely driven by two primary factors. First, predators themselves are spatially variable. Block 3 had the fewest observed predators by more than half in our surveys. This block also was the only block in which survival was appreciably better in unvegetated habitat than in *Caulerpa* (Fig. 2). Second, the variability in the net influence of predator protection by *Caulerpa* between experimental groups of clams in experiment I (i.e., neutral on *Anadara* in tubs; positive on clams in ambient plots) is likely driven by differences in experimental approaches used on these two groups. Importantly, the difference may point to the specific mechanism of *Caulerpa*'s protective effect. The stronger protective influence of *Caulerpa* on *Anadara* in ambient plots seems to stem not simply from the *Caulerpa* canopy covering the clams, which was a factor similar for both sets of clams. Rather, the major difference was that the main experimental clams in *Caulerpa* were placed into tubs containing sediment from unvegetated areas, while ambient clams were placed directly into the ambient sediment. Therefore, in the ambient treatments, roots and stolons of *Caulerpa* that enmeshed the clams could have served as a physical barrier to foraging crabs. Also, the silt and organic matter characteristic of ambient *Caulerpa* sediments (McKinnon et al. 2009) may mask the smell of clams, obscure predator visibility, or make it harder for predators to get leverage necessary to excavate *Anadara*. Interestingly, the positive effect of *Caulerpa* on *Anadara* in ambient plots seemingly outweighed the negative effects of the clams being in direct contact with *Caulerpa* sediment and its associated environmental alterations, at least during this short-term experimental time period.

Spatial variability in *Caulerpa*'s influence was apparent even when predator activity was minimal, as it was in our condition experiment (III). In that case the spatially variable effect of *Caulerpa* habitat is likely due at least in part to differences in *Caulerpa* biomass that influence consequent abiotic environmental changes. For example, block 4 had the thickest, densest *Caulerpa* and showed the highest non-predation mortality in the condition experiment. Losses of predator-protected, caged clams in *Caulerpa* in experiment I was also greatest in block 4.

If *Caulerpa* biomass is in fact an important factor governing its ultimate effects on *Anadara,* the temporal scale of invasion could also be important to consider in weighing *Caulerpa*'s effects. Our findings suggest a likely switch in *Caulerpa*'s average net effect as its invasion progresses, with initially positive effects outweighed by negative ones. Especially when *Caulerpa*'s coverage and biomass is moderate in early invasion stages, predation protection for juvenile and adult *Anadara* may at first produce a net positive effect for *Anadara*. But as *Caulerpa* gets denser and *Anadara* exposure to *Caulerpa* increases, clam condition declines in concert with degrading environmental conditions generated by *Caulerpa*, and *Caulerpa*'s negative effects dominate.

In summary, despite changes to antipredatory behavior and morphological traits of *Anadara*, *Caulerpa* exerted no measurable trait-mediated indirect influences that affected predation rates on the clam. Rather, *Caulerpa* exerted a slight, variable, positive effect via

its habitat provisioning. However, the slight mitigation of predation by *Caulerpa* is counterbalanced by a large negative direct effect of environment-associated mortality (especially when *Caulerpa* is thickest). Such negative effects of *Caulerpa* were abetted by *Caulerpa*'s influence to chronically weaken *Anadara* living within it, enhancing the clams' susceptibility to reduced environmental quality. Negative effects of degraded environmental conditions induced by *Caulerpa* must be strong (Gribben et al. 2009*b*) because ultimately they reverse the trend of a positive or benign effect of *Caulerpa* to decrease predation on juveniles and adults and to attract and (initially) protect recruits from predation (Gribben and Wright 2006*b*), resulting in adult *Anadara* densities in *Caulerpa* that are one-fifth of those in uninvaded, unvegetated habitat (Wright et al. 2007). Thus, our results emphasize that invasive habitat-modifying species can affect mortality of native species not only through obvious direct effects of their protective structure, but also indirectly through modifying environmental properties and traits of prey species responding to the habitat.

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