

Differences in anti-predator traits of a native bivalve following invasion by a habitat-forming seaweed

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Abstract. Invasive habitat-forming species cause large changes to the abiotic environment, which may lead to lethal and sublethal effects on native fauna. In this study, we tested whether morphological anti-predator traits of an infaunal bivalve, *Anadara trapezia*, differed between areas invaded by the habitat-forming seaweed *Caulerpa taxifolia* and uninvaded habitats in estuaries in New South Wales, Australia. *Caulerpa* changes the abiotic environment in ways that may affect traits of native species. In particular, there is lower water flow, lower dissolved oxygen in the water and sediments are more silty and anoxic than in unvegetated habitat. To test our hypotheses, we collected *Anadara* from *Caulerpa* and uninvaded habitats and measured shell thickness, shell strength and resistance to opening of valves. We found that all three traits were reduced in *Anadara* from *Caulerpa* habitat compared with *Anadara* from uninvaded habitats. These findings are consistent with the idea that trait modifications in native fauna in response to invasive habitat-forming species can potentially increase susceptibility to predation.

Additional keywords: *Anadara trapezia*, bivalve, *Caulerpa taxifolia*, invasive seaweed, predation, shell strength, traits.

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Introduction

Habitat-forming invasive species are a major perturbation to many natural ecosystems where they change a range of environmental variables (Crooks 2002). In marine soft-sediment systems, the establishment of invasive habitat-forming macrophytes changes key variables, including water flow, dissolved oxygen, concentrations of Chlorophyll *a*, the deposition of organic matter and sediment chemistry (Neira *et al.* 2006; Gribben *et al.* 2009; McKinnon *et al.* 2009). Such environmental changes have major effects on native fauna. For example, sediment anoxia, high concentrations of sulfides and hypoxic water can all be lethal to infauna (Shumway *et al.* 1983; Diaz and Rosenberg 1995; King *et al.* 2004). These environmental changes may also result in sublethal effects on the body and shell condition and reproductive traits of infauna (Gribben and Wright 2006; Wright and Gribben 2008). Traits of particular interest are those that deter predation because a reduction in the effectiveness of anti-predator strategies may leave prey more vulnerable to predation.

Infaunal bivalves have the following three main strategies to minimise the effects of predators: escape via burial in the sediment to avoid surface-feeding or digging predators (Seitz *et al.* 2001; Meyer and Byers 2005); morphological defence via strong shells to deter shell crushing, cracking or drilling predators (e.g. crabs, rays; Juanes and Hartwick 1990; Seitz *et al.* 2001; Bishop and Peterson 2006); and defence via strong adductor muscles to deter predators that pull or pry shells apart (e.g. sea stars, octopus; Ross *et al.* 2002; Steer and Semmens 2003). Although genetic factors will partly determine these traits, environmental factors including temperature, food availability (Schöne *et al.* 2003) and anoxic or anaerobic conditions (Crenshaw and Neff 1969; Gordon and Carriker 1978) all influence the expression and, subsequently, the effectiveness of these traits. Invasive predators can induce anti-predator traits of native prey, potentially decreasing their susceptibility to predation (Trussell 2000; Freeman and Byers 2006; Pangle *et al.* 2007). To our knowledge, there are no examples of whether habitat-forming invasive species can also affect

anti-predator traits of native fauna and, thus, whether they are likely to decrease or increase susceptibility to predation.

In the present study, we determined differences in three morphological anti-predator traits of the native infaunal bivalve *A. trapezia* (Arcidae, hereafter *Anadara*), following invasion by the habitat-forming seaweed *C. taxifolia* (hereafter *Caulerpa*). Previously, we have shown differences in behaviour (a decrease in burrowing depth) in *Anadara* in *Caulerpa* habitat (Wright *et al.* 2010). *Caulerpa* has invaded several temperate regions worldwide (Jousson *et al.* 2000; Meinesz *et al.* 2001; Creese *et al.* 2004) where it forms high-biomass (>500 g m⁻² dry weight) stands in previously unvegetated sediment (Wright 2005). These dense stands have anoxic sediments, low water flow and low dissolved oxygen (Gribben *et al.* 2009; McKinnon *et al.* 2009), all of which potentially affect the anti-predator traits of bivalves. Given these changes to the abiotic environment in *Caulerpa* habitat, we tested the following hypotheses: (1) shell thickness of *Anadara* will differ between *Caulerpa* and uninvaded habitats (seagrass and unvegetated sediment), (2) shell strength of *Anadara* will differ between *Caulerpa* habitat and unvegetated sediment and, (3) the ability of *Anadara* shells to resist opening when force is applied to pull valves apart will differ between *Caulerpa* habitat and unvegetated sediment.

Materials and methods

Study system and sites

Caulerpa occurs in 14 estuaries in New South Wales, Australia (Creese *et al.* 2004). Our study was conducted between April and October 2006 in two of the invaded estuaries, namely St Georges Basin (35°12'S, 150°35'E) and Lake Conjola (35°26'S, 150°50'E). *Caulerpa* was discovered in Lake Conjola in 2000 and in St Georges Basin in 2004 (Creese *et al.* 2004). See Creese *et al.* (2004) for a detailed description of these estuaries and their history of invasion by *Caulerpa*. At the time of the study, both estuaries had thick infestations of the alga where there would previously have been unvegetated sediment. Many areas of the benthos invaded by *Caulerpa* also contained *Anadara* (Wright *et al.* 2007).

Anadara is a large (up to 70-mm shell length), thick-shelled suspension-feeding infaunal bivalve that occurs fully or partially buried at the sediment surface in estuaries (Wright *et al.* 2010). Populations of *Anadara* are dominated by large individuals (Wright *et al.* 2007) and at least some adult *Anadara* present in the sediment before *Caulerpa* invasion have survived for at least 6 years after invasion (J. T. Wright, P. E. Gribben, pers. obs.), although at lower densities than in uninvaded habitat. We have observed several bivalve predators in these estuaries, including the blue swimmer crab, *Portunus pelagicus*, the octopus, *Octopus tetricus*, and stingarees, *Urolophus* spp.. These predators occur in *Caulerpa* and unvegetated habitats but are more frequently observed in unvegetated sediment (Byers *et al.* 2010).

Differences in *Anadara* shell thickness and strength among habitats

To determine whether the shell thickness differed among habitats, *Anadara* individuals ($n = 25$ per habitat) were collected from intermingling patches of unvegetated sediment, *Caulerpa* and the native seagrass *Halophila ovalis* at Smiths Bay

in St Georges Basin. We included *Halophila* in our initial assessment of shell thickness because it is an important habitat for *Anadara* in St Georges Basin, and as a habitat-forming macrophyte, it may have effects on shell thickness that are similar to those of *Caulerpa* (Wright *et al.* 2007). The right valve from each individual was sectioned along a standard axis perpendicular from the apex of the umbo to the ventral margin using a 250-mm diatremm saw blade (Model E2G34, Shelleys Lapidary Supplies, Adelaide, SA). Shell thickness was measured at three positions (the umbo, the shell centre (midway point of the section) and 10 mm inward from the ventral margin) on each shell cross-section using digital callipers.

Differences in the shell thickness of *Anadara* among habitats were examined with one-factor Analysis of Covariance (ANCOVA) for each shell position, with shell length (anterior–posterior axis) as the covariate. For this and subsequent analyses, assumptions of analysis of variance were checked by examining distributions of residuals and plots of residuals *v.* means and data were transformed where necessary. ANCOVA assumptions were tested by examining homogeneity of slopes between treatments and determining whether covariate values were similar across groups (Quinn and Keough 2002).

To determine differences in the shell strength (i.e. resistance to a standard force) of *Anadara* between *Caulerpa* habitat and unvegetated sediment, we used an Instron tensile testing machine (Model 4302, 10 kN load cell, Instron Corporation, Canton, MA, USA). The 10-kN load was lowered onto *Anadara* shells at a speed of 0.5 mm min⁻¹ and the peak and break force for shells were determined. Peak force (kN) is the maximum force sustained by the shell before breakage and break force (kN) is the force at which a major drop in force occurred (i.e., the force at which the shell broke). *Anadara* individuals ($n = 20$ per habitat, size range 55–75-mm shell length) were collected from unvegetated and *Caulerpa* habitats in both St Georges Basin and Lake Conjola. We focussed here on *Anadara* collected from unvegetated sediment *v.* *Caulerpa* because there was no difference in shell thickness between the unvegetated sediment and *Halophila* habitat at the crucial ventral margin of the shell (see Results).

The force required to crack shells was determined on live clams to ensure a realistic test of the strength required by predators to crack shells. Shells were positioned on their side so the valve opening was horizontal, held steady in a clamp and an 11-mm-diameter metallic rod was lowered to a point on the right valve of each shell, ~10 mm from the end of the ventral margin, until the shell cracked. This position on the shell was chosen as crabs often crack bivalve shells here (Smith and Jennings 2000) and we have observed this type of damage in the field (Byers *et al.* 2010). Differences in peak and break force in shells from different habitats were examined separately at each site using ANCOVA, with the factor habitat (*Caulerpa* and unvegetated) and shell length as a covariate (measured before the shells were cracked).

Differences in *Anadara* shell resistance to opening between habitats

To mimic the opening of bivalve shells by octopi, we determined how long *Anadara* individuals from *Caulerpa* habitat and unvegetated sediment could keep their valves closed when a

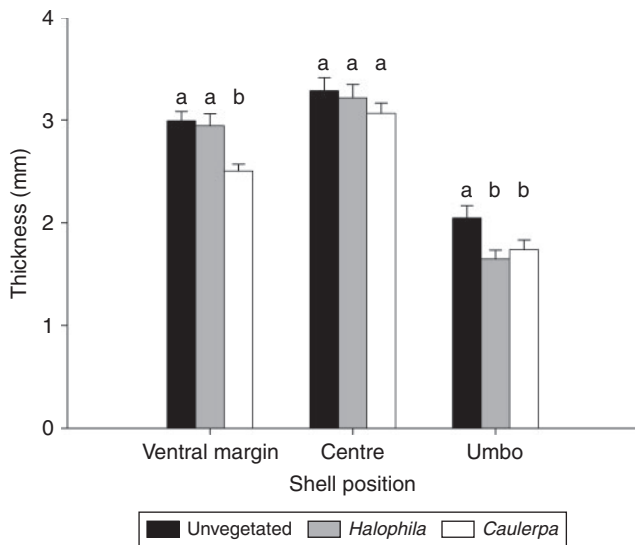


Fig. 1. Mean (\pm s.e.) shell thickness at three positions along sectioned *Anadara trapezia* shells ($n=25$) from unvegetated sediment, *Halophila ovalis* and *Caulerpa taxifolia* habitats. Habitats sharing a letter do not differ within position at $P=0.05$ (Tukey's analysis).

constant force was applied to pull the valves apart. *Anadara* individuals were collected from *Caulerpa* habitat ($n=11$) and unvegetated sediment ($n=10$, size range 53–75 mm shell length) in Lake Conjola, and transported back to the laboratory. Once there, a single 3-cm-long screw was glued at a standardised position, ~15 mm from the ventral margin to the outside of each valve so the screws sat perpendicular to the valve. Pieces of string (10 cm) were attached to each screw. A 0.45-kg weight was attached to one piece of string and each *Anadara* individual and associated weight were hung from a rod by the other piece of string. The time taken for the valves to be fully pulled apart (defined as a 5-mm gape) was recorded. The difference between habitats in the time to open shells was determined using ANCOVA, with the factor habitat (*Caulerpa* and unvegetated) and shell length as a covariate.

Results and discussion

Differences in anti-predator traits of *Anadara*

The main morphological traits of infaunal bivalves that often minimise predation were reduced in *Anadara* living in *Caulerpa*. First, at the ventral margin, *Anadara* had significantly thinner shells in *Caulerpa* habitat than in both unvegetated sediment and *H. ovalis* habitat (ANCOVA, Habitat: $F_{2,71}=6.989$, $P=0.002$; Shell length: $F_{1,71}=5.816$, $P=0.018$, Fig. 1). At the umbo, *Anadara* had significantly thinner shells in *Caulerpa* habitat than in unvegetated sediment (ANCOVA, Habitat: $F_{2,71}=4.171$, $P=0.019$; Shell length: $F_{1,71}=0.561$, $P=0.457$) but the shells had a thickness similar to those from *H. ovalis* (Tukey's $\alpha > 0.05$). In contrast, at the shell centre there was no significant difference in shell thickness among habitats (ANCOVA, Habitat: $F_{2,71}=0.914$, $P=0.406$; Shell length: $F_{1,71}=4.592$, $P=0.036$).

Second, in St Georges Basin, *Anadara* from *Caulerpa* habitat required approximately half the force to crack compared with *Anadara* from unvegetated sediment. There was a

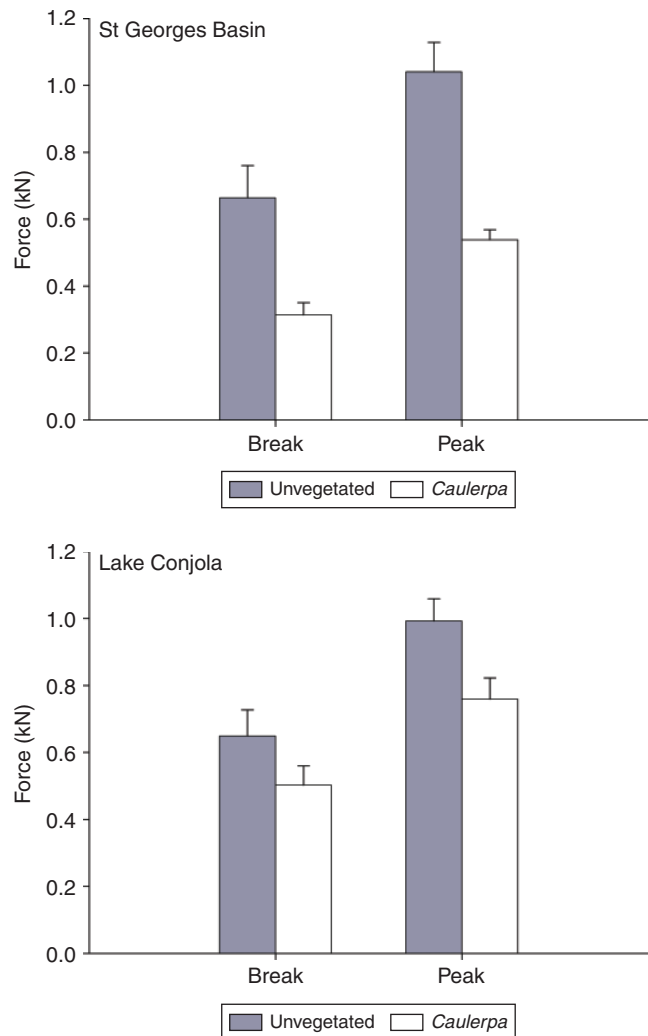


Fig. 2. Mean (\pm s.e.) break and peak force (kN) required to crack *Anadara trapezia* shells ($n=20$) in *Caulerpa taxifolia* habitat and unvegetated sediment from St Georges Basin and Lake Conjola.

significantly lower peak force (ANCOVA, Habitat: $F_{1,37}=31.842$, $P<0.001$) and break force (ANCOVA, Habitat: $F_{1,37}=10.355$, $P=0.003$) before cracking in *Anadara* from *Caulerpa* habitat than in *Anadara* from unvegetated sediment (Fig. 2). In Lake Conjola, *Anadara* from *Caulerpa* habitat required significantly lower peak force (ANCOVA, Habitat: $F_{1,37}=5.294$, $P=0.027$), but not break force (ANCOVA, Habitat: $F_{1,37}=1.175$, $P=0.285$) before cracking than did *Anadara* from unvegetated sediment. However, on average *Anadara* individuals from *Caulerpa* habitat had lower break forces than did those from unvegetated sediment. There was a significant covariate effect of size for break force in Lake Conjola only ($F_{1,37}=4.147$, $P=0.049$). The finding that shells of *Anadara* from *Caulerpa* habitat were both significantly thinner and required less force to crack at the ventral margin is important because this part of the shell is often targeted by predators such as crabs or rays that crack or crush bivalve shells (Smith and Jennings 2000). Importantly, shell thickness at the ventral margin was linked to shell strength in *Anadara* because

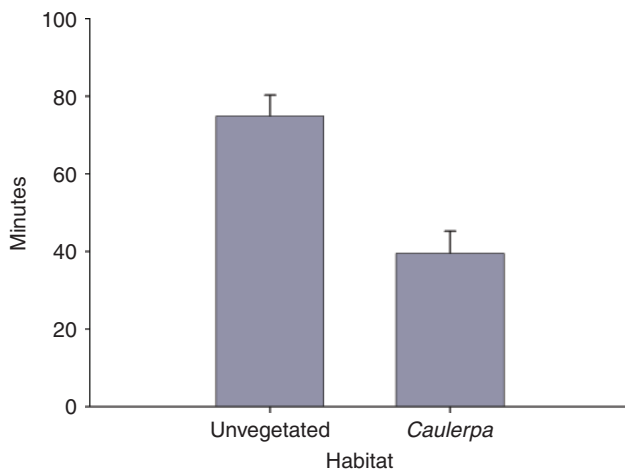


Fig. 3. Mean (\pm s.e.) time to open to a 5-mm gape for *Anadara trapezia* from unvegetated sediment and *Caulerpa taxifolia* habitat.

clams from *Caulerpa* habitat also required less force to crack in this region.

Third, *Anadara* individuals from *Caulerpa* habitat opened in approximately half the time of those from unvegetated sediment (ANCOVA: $F_{1,18} = 23.082$, $P < 0.001$, Shell length: $F_{1,18} = 8.483$, $P = 0.009$, Fig. 3). We observed many *Anadara* shells in the dens of *Octopus tetricus* at sites invaded by *Caulerpa*, suggesting they are a significant predation threat in these estuaries.

We have previously shown that *Anadara* individuals bury less deeply in *Caulerpa* habitat than in uninvaded habitats because of low dissolved oxygen (Wright *et al.* 2010). This behavioural change may have two important consequences for *Anadara*. First, it is likely to play a key role in *Anadara*'s morphological changes because the resulting decreased pressure on valves once unburied may lead to adductor-muscle atrophy. Second, shallow burrowing depth could also directly increase predation by increasing exposure to predators. However, experimental manipulations of burrowing depth and condition of *Anadara* in *Caulerpa* habitat and in unvegetated sediment demonstrated that the deteriorated condition of clams living in *Caulerpa* habitat had greater influence on clam mortality than the direct effects of shallow burial – although these effects are variable (Byers *et al.* 2010). Shallow burrowing depth did not increase predation mortality on *Anadara*.

Environmental changes following invasion

Environmental changes following *Caulerpa* invasion are likely to drive the reduced shell thickness, shell strength and resistance to opening in *Anadara* from *Caulerpa* habitat. There may be two main ways in which environmental changes caused by *Caulerpa* affect *Anadara*. First, there may be effects on clam physiology. The sediment anoxia and lower dissolved oxygen in the water column in *Caulerpa* habitat than in unvegetated sediment (Gribben *et al.* 2009) may reduce feeding and/or respiration and thus have an impact on shell growth, resulting in thinner, weaker shells. Alternatively, these environmental changes may affect body condition (Wright *et al.* 2007; Wright and Gribben 2008), resulting in weaker adductor muscles. Second, environmental

changes may cause direct effects on shell-dissolution rates (Crenshaw and Neff 1969; Gordon and Carriker 1978). Additionally, boring by spionid polychaetes results in weaker shells in molluscs (Dunphy and Wells 2001) and *Anadara* shells are more heavily infested by spionids in *Caulerpa* habitat than they are in unvegetated sediment (L. Collins, unpubl. data). Finally, although food limitation as a result of reduced water flow in seagrass results in lower shell growth and reproduction of an invasive mussel (Allen and Williams 2003) because phytoplankton abundance is higher in *Caulerpa* habitat than in unvegetated sediment (Gribben *et al.* 2009), food limitation is an unlikely explanation for the negative impacts on anti-predator traits of *Anadara*.

One constraint to any conclusions about *Caulerpa* (and its associated abiotic changes) causing differences in anti-predator traits is that we have not undertaken a *Caulerpa* transplant experiment here and, thus, we have not unambiguously isolated it as the agent causing the observed differences. However, *Anadara* experimentally transplanted to *Caulerpa* habitats have reduced shell and tissue weight compared with *Anadara* transplanted to unvegetated sediment (Wright and Gribben 2008), suggesting that *Caulerpa* is responsible for general differences in shell and tissue traits.

Conclusions

Our findings have highlighted the way in which changes to abiotic factors following the invasion of habitat-forming macrophytes may affect traits of native species, with potentially important ramifications for predator-prey interactions. Such changes in anti-predator traits of native species in response to invasive habitat-forming species are unlikely to be limited to marine algae. Invasive marine invertebrates (Castilla *et al.* 2004) and terrestrial and freshwater plants (Levine *et al.* 2003; Strayer 2010) modify a range of important abiotic factors, including soil and sediment physico-chemistry, water, light and oxygen availability and disturbance regimes. Given that many native species persist in these modified habitats (Crooks 2002), future work focussing on how traits of native species change following invasion by habitat-forming species and how these changes affect species interactions will enhance our understanding of the impacts of invasive species on native ecosystems.

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