

Native species behaviour mitigates the impact of habitat-forming invasive seaweed

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Abstract Habitat-forming invasive species cause large, novel changes to the abiotic environment. These changes may elicit important behavioural responses in native fauna, yet little is known about mechanisms driving this behaviour and how such trait-mediated responses influence the fitness of native species. Low dissolved oxygen is a key abiotic change created by the habitat-forming invasive seaweed, *Caulerpa taxifolia*, which influences an important behavioural response (burrowing depth) in the native infaunal bivalve *Anadara trapezia*. In *Caulerpa*-colonised areas, *Anadara* often emerged completely from the sediment, and we experimentally demonstrate that water column hypoxia

beneath the *Caulerpa* canopy is the mechanism instigating this “pop-up” behaviour. Importantly, pop-up in *Caulerpa* allowed similar survivorship to that in unvegetated sediment; however, when we prevented *Anadara* from popping-up, they suffered >50% mortality in just 1 month. Our findings not only highlight the substantial environmental alteration by *Caulerpa*, but also an important role for the behaviour of native species in mitigating the effects of habitat-forming invasive species.

Keywords Ecosystem engineers · Hypoxia · Infauna · Marine algae · Soft-sediment ecology

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Introduction

Understanding the response of native species to invasive species is important in determining the extent of invader impact. Native species can respond to invasive species via behavioural and morphological changes (Trussell et al. 2003; Freeman and Byers 2006; Strauss et al. 2006). Behavioural responses by native fauna to invasive predators, such as reduced activity and feeding rates and increased use of refuges, depend on the ability of native fauna to detect invasive predators. Indeed, several studies have identified specific predator cues as the mechanism determining those responses (Kiesecker and Blaustein 1997; Trussell et al. 2003; Pearl et al. 2003).

Invasive habitat-forming species also represent a major perturbation to many natural ecosystems. These species are often considered ecosystem engineers (Jones et al. 1994, 1997) or foundation species (Dayton 1972) because of the way they modify the abiotic environment and influence community organisation (Crooks 2002; Levine et al. 2003). Moreover, the large abiotic changes caused by

habitat-forming invasive species can elicit behavioural changes in native fauna. Although native species frequently co-occur with habitat-forming invasive species (Crooks 2002), there are many examples of native faunal species being less abundant within habitat-forming invasive species compared to uninvaded habitats (e.g. Trammell and Butler 1995; Valentine 2006). Habitat-choice experiments demonstrate that some native fauna avoid these invasive species, preferring native species as habitat (e.g. Valentine et al. 2007). Although such behaviour may be due to the native species responding to one or more of the changes in the abiotic environment following invasion, there is little information on the specific mechanism driving avoidance behaviour. Additionally, although implicit in such predictions of why native species avoid habitat-forming invasive species, the fitness consequences (i.e. survivorship) for native species in responding to the invader remain poorly understood.

Here, we document an important behavioural response in a native species to a habitat-forming invasive species and identify both the mechanism causing the response and the fitness benefit of changing behaviour. The invasive marine alga *Caulerpa taxifolia* (Vahl) C. Agardh (hereafter *Caulerpa*) forms dense stands in estuaries in southeastern Australia with anoxic sediment, low water flow and low water column dissolved oxygen (Wright 2005; Gribben et al. 2009a; McKinnon et al. 2009). The dominant native bivalve in this system, *Anadara trapezia* (Arcidae, Deshayes 1840, hereafter *Anadara*), recruits into *Caulerpa* but has poor post-recruitment and adult survivorship (Gribben and Wright 2006; Wright and Gribben 2008; Gribben et al. 2009a). Nonetheless, at least some adult *Anadara* present in sediment before *Caulerpa* invasion are able to persist for at least 5 years after invasion (J.T. Wright, P.E. Gribben, personal observations) despite the changes to the abiotic environment. In *Caulerpa*, adult densities can remain as high as 30/m² compared to seagrass (35–65/m²) and unvegetated sediment (35–90/m²; Wright et al. 2007). Thus, even though densities are lower in *Caulerpa*, the fact that *Anadara* do remain reasonably common suggests they may have a behavioural response to the abiotic changes caused by *Caulerpa* that mitigates its effects. Infaunal bivalves are often sedentary and unable to move far; however, an important behavioural response they have to poor quality habitat is to adjust their burrowing depth in the sediment (Byers 2002; Taylor and Eggleston 2000; Whitlow et al. 2003). To address how a native species responds to the creation of novel habitat by an invasive species, we determined: (1) differences in behaviour (burrowing depth) of *Anadara* between *Caulerpa* and uninvaded habitats; (2) the mechanism driving changes in behaviour of *Anadara* in *Caulerpa*; and (3) the survivorship consequences for *Anadara* of changing behaviour in the face of invasion by *Caulerpa*.

Materials and methods

Study system and sites

Caulerpa taxifolia has invaded several temperate regions worldwide (Lowe et al. 2000). In southeastern Australia, *Caulerpa* now occurs in 14 estuaries. Our study was conducted in three of those estuaries: St Georges Basin (35°12'S, 150°35'E), Lake Conjola (35°268'S, 150°508'E) and Burrill Lake (35°395'S, 150°447'E). *Caulerpa* was discovered in Lake Conjola in 2000, in Burrill Lake in 2001, and in St Georges Basin in 2004 (Creese et al. 2004). The three estuaries all have sites with thick infestations of *Caulerpa* which typically occurs in sheltered bays where there is little water flow (Gribben et al. 2009a). Large areas invaded by the alga, which would previously have been native seagrass or unvegetated habitats, contain *Anadara* (Wright et al. 2007). *Anadara* is a large (up to 70 mm shell length), thick-shelled bivalve occurring from the intertidal to shallow subtidal (0–3 m water depth) in sheltered mud, sand, seagrass and now *Caulerpa* habitats (Wright et al. 2007). *Anadara* are suspension feeders with short siphons, and in unvegetated sediment typically occur fully burrowed with only their siphons showing or approximately 80% burrowed within the sediment.

Differences in burrowing depth among habitats

The in situ burrowing depth of *Anadara* was measured in different habitats at depths between 1.5 and 2 m at two sites in St Georges Basin (Pats Bay and Smiths Bay) and one site each in both Burrill Lake (Broadwater) and Lake Conjola (Sponge Bay) between April and June 2006. We sampled the dominant habitats at each site (Wright et al. 2007): unvegetated sediment, *Halophila ovalis* (native seagrass), and *Caulerpa* in St Georges Basin; unvegetated sediment, *Zostera capricorni* (another native seagrass) and *Caulerpa* in Burrill Lake; and unvegetated sediment and *Caulerpa* in Lake Conjola. Individual *Anadara* were haphazardly selected in each habitat ($n = 18–25/\text{habitat}$) and a line marked with a pencil on the shell in situ denoting the sediment surface/water interface. Once marked, shells were removed from the sediment and the distance perpendicular from the line to the anterior edge measured to obtain burrowing depth. The total length of the shell was then measured along the same axis from the anterior edge to the posterior edge of the shell to obtain proportional burrowing depth. Differences in proportional burrowing depth among habitats were determined with a 1-factor analysis of covariance (ANCOVA) for each site separately with shell length as a covariate.

Dissolved oxygen in *Caulerpa* and unvegetated sediment and its effect on burrowing depth

Following our surveys of burrowing depth, we then compared how a key abiotic factor (water column dissolved oxygen, DO) differed between *Caulerpa* and unvegetated sediment and its effects on burrowing. We focused on differences between *Caulerpa* and unvegetated sediment because, in southeastern Australia, *Caulerpa* spreads primarily into unvegetated sediment where it forms dense patches, but does not readily invade seagrass beds (Glasby and Creese 2007). Differences in water column DO between *Caulerpa* and unvegetated sediment were determined in Sponge Bay, Lake Conjola, in January 2008. Water samples ($n = 10/\text{habitat}$) were collected during daylight 3–5 cm above the sediment surface using 20-ml syringes. Syringes were immediately wrapped in foil and kept in a cooler with ice, and water column DO was measured back on shore within 15 min of collection. Water column DO was measured using oxygen-sensing 100- μm optodes (Precision Sensing) calibrated linearly to 100% air saturation using methods outlined in Ulstrup et al. (2005). A t test (unequal variances) was used to determine differences in water column DO between habitats.

To distinguish the effects of low water column DO per se from other influences of *Caulerpa*—particularly anoxic sediment (Gribben et al. 2009a; McKinnon et al. 2009)—on the burrowing depth of *Anadara*, we tested the effects of sediment type (*Caulerpa* vs. unvegetated sediment) and water column DO (high vs. low) using an orthogonal experiment. Intact sediment cores were collected from *Caulerpa* and unvegetated sediment in Sponge Bay, Lake Conjola, on 10 February, 2008, and immediately placed into test containers (27 cm \times 12 cm \times 17 cm). *Caulerpa* cores included sediment and associated *Caulerpa*. Adult *Anadara* ($n = 480$) were collected from unvegetated sediment in St Georges Basin on the same day as the cores. All clams and cores were transported to the laboratory at the University of Technology, Sydney, and submerged in seawater for 24 h to recover. For the experiment, ten clams were added to each container and pushed into the sediment so that $\sim 20\%$ of the shell was exposed, their natural depth in unvegetated sediment. Single test containers were then placed into larger containers (32 cm \times 24 cm \times 15 cm) with seawater added to 6 cm above the sediment and sealed. The lid of each container had two small holes which we could uncover to allow us to remove oxygen and to measure water column DO.

To create the low water column DO treatment, nitrogen was bubbled into the seawater until water column DO reached ~ 2 mg/l. During the setting of the low water column DO levels, water column DO was measured continuously with an optode (described above) until the desired

concentration was reached and then the holes in the container lid were sealed. For the ambient water column DO treatments, air was bubbled continuously to ensure oxygenated water removed the low water column DO boundary layer but did not disturb sediments. For the treatments including *Caulerpa*, water column DO was measured under the canopy to ensure that the benthic boundary layer was broken down in the high water column DO treatments. Water column DO changed slightly during the experiment. Initial versus final water column DO (mean \pm SE) in the low water column DO treatments were: 1.97 (± 0.12) versus 1.22 (± 0.14) mg/l (unvegetated sediment) and 1.70 (± 0.22) versus 0.75 (± 0.01) mg/l (*Caulerpa*); and in the high water column DO treatments were: 7.69 (± 0.06) versus 7.94 (± 0.05) mg/l (unvegetated sediment) and 7.64 (± 0.04) versus 7.57 (± 0.11) mg/l (*Caulerpa*). Light was kept low so that photosynthesis and thus changes in water column DO was minimal. Water temperature was kept at a constant 23°C, within the range of summer water temperatures at our sites (SCC 2003). Replicate treatments ($n = 6$ for each treatment combination) were arranged randomly in the laboratory. After 36 h, we determined clam position (either burrowed or not burrowed, which we objectively defined as $>50\%$ of the shell exposed). Because such exposure represents a rapid movement to the surface, we refer to this clam behaviour as “pop-up”. A 2-factor ANOVA was used to determine the effect of sediment type (*Caulerpa* vs. unvegetated) and water column DO (high vs. low) on $\sqrt{\text{Arcsin}}$ -transformed proportions of *Anadara* popped-up in each container.

Changes in burrowing depth in *Caulerpa* and its consequences

To examine whether there were any benefits to *Anadara* in changing burrowing depth in *Caulerpa*, we determined the survivorship and pop-up rates of clams that were allowed to adjust burrowing depth ad libitum in caged tubs placed into *Caulerpa* and unvegetated sediment. In Sponge Bay, Lake Conjola, we created four blocks of paired 1.5 m \times 1.5 m habitat plots—*Caulerpa* and unvegetated sediment (created by removing *Caulerpa* by hand). On 11 October 2007, ten adult *Anadara* (40–60 mm shell length, collected from unvegetated sediment) were placed into tubs (10 cm deep \times 10 cm wide \times 25 cm long). Tub contained unvegetated sediment to initially ensure sediment quality was the same in both habitats to eliminate immediate potential effects of anoxic *Caulerpa* sediment on *Anadara*. We placed two tubs in each habitat type in each of the four blocks ($n = 8$ replicates per habitat). Tub were buried so that their sediment was level with the surrounding sediment. In *Caulerpa*, the canopy was gently pulled apart to allow tubs to be placed into the sediment and then carefully

replaced back over them. Tubs were caged with wire mesh (19 mm) that extended 5 cm in height over the tubs to allow space for clams to pop-up and to eliminate predation mortality to better isolate the effects of hypoxia. After 12 weeks, survivorship of each clam was determined and each surviving clam was identified as either burrowed or not burrowed (>50% of the shell exposed). Differences between *Caulerpa* and unvegetated sediment in clam survivorship and the proportion of surviving *Anadara* popped-up were determined with 2-factor ANOVAs with the factors habitat and block on $\sqrt{\text{Arcsin}}$ -transformed data.

Consequences of forced burial in *Caulerpa*

To determine what happens to clams that are not permitted to pop-up inside *Caulerpa*, we experimentally manipulated their burrowing depth in Sponge Bay, Lake Conjola. Adult *Anadara* were collected from unvegetated sediment and placed into four 0.046-m² plots (17.5 cm × 26 cm) in both *Caulerpa* and unvegetated sediment (created by removing the *Caulerpa* by hand, $n = 10$ clams/plot) on 10 January 2008. We pushed clams down into the sediment until only ~20% of the shell protruded and placed wire mesh cages (19 mm mesh size) over each plot. The sides of these cages extended down 6 cm into sediment to anchor them in place, with the mesh lid flush against the slightly protruded tips of the clams. The mesh both ensured that the clams could not pop up any further than they were initially set, and also pro-

tected the clams from predators. The clams were left for 1 month after which time we removed the mesh cage tops and assessed mortality. We compared the difference in clam survivorship between *Caulerpa* and bare habitats with a t test (unequal variances) on the $\sqrt{\text{Arcsin}}$ -transformed proportion of clams surviving in each plot.

Results

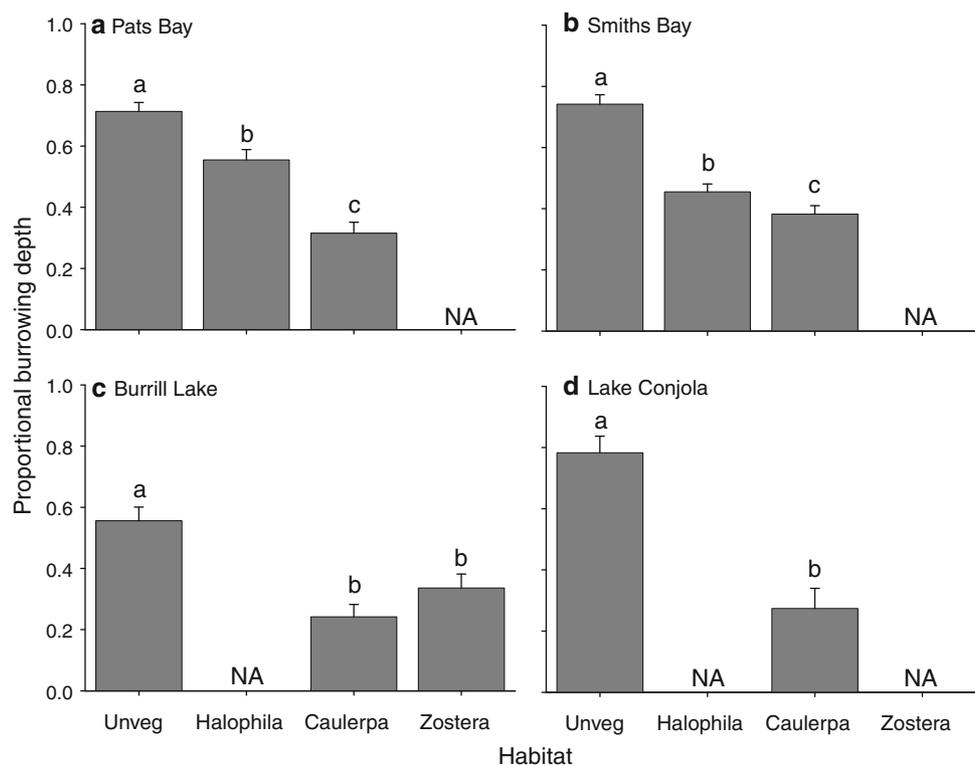
Differences in burrowing depth among habitats

Anadara burrowed significantly shallower in *Caulerpa* compared to unvegetated sediment at all four sites and significantly shallower in *Caulerpa* compared to the seagrass *H. ovalis* at both sites where they were compared (Fig. 1). There was no significant difference in burrowing depth between the seagrass *Z. capricorni* and *Caulerpa*. *Anadara* also burrowed significantly shallower in both seagrass species compared to unvegetated sediment (Fig. 1).

Dissolved oxygen in *Caulerpa* and unvegetated sediment and its effect on burrowing depth

In the field, dissolved oxygen was significantly lower within *Caulerpa* compared to unvegetated sediment ($t_{16} = 9.03$, $P < 0.001$), frequently reaching hypoxic levels <2.8 mg/l (Fig. 2a). In the laboratory, significantly more

Fig. 1 Proportional burrowing depth (mean + SE) of *Anadara trapezia* in unvegetated sediment (Unveg), *Halophila ovalis* (*Halophila*), *Zostera capricorni* (*Zostera*) and *Caulerpa taxifolia* (*Caulerpa*) habitats. ANCOVAs on untransformed data for the effect of habitat. **a** Pats Bay $F_{2,56} = 35.54$, $P < 0.001$; **b** Smiths Bay $F_{2,63} = 58.39$, $P < 0.001$; **c** Burrill Lake $F_{2,59} = 14.15$, $P < 0.001$; **d** Lake Conjola $F_{1,47} = 35.04$, $P < 0.001$. Shell length was a significant covariate only at Pats Bay ($F_{1,56} = 8.88$, $P < 0.004$). Habitats sharing a letter do not differ within sites at $P = 0.05$, Tukey's analysis. NA Habitat was not measured



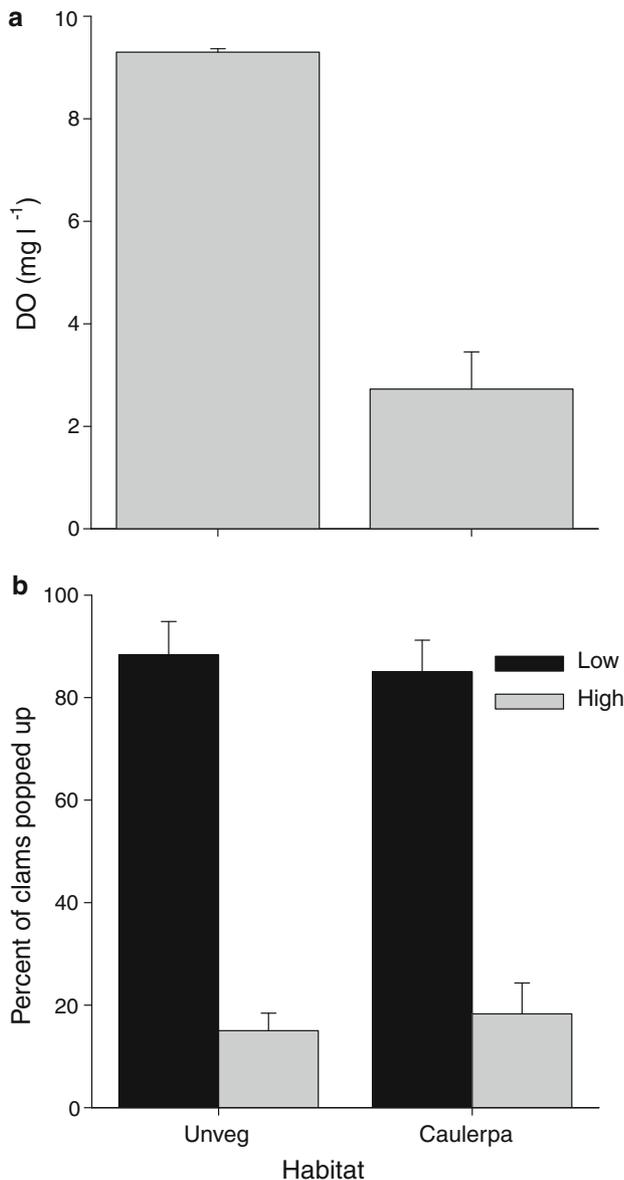


Fig. 2 **a** Water column dissolved oxygen, DO (mean + SE) in unvegetated (*unveg*) and *Caulerpa taxifolia* (*Caulerpa*) habitats in Sponge Bay, Lake Conjola ($n = 9$ samples/habitat). **b** Percent of clams popped up in unvegetated and *Caulerpa* sediments exposed to low water column DO (<2 mg/l) and high water column DO (>7.5 mg/l) after 36 h. $n = 6$ tubs per treatment combination with 10 clams in each tub

clams popped up when exposed to the low water column DO compared to the high water column DO ($F_{1,20} = 83.23$, $P < 0.001$; Fig. 2b). In the low water column DO treatment, $33.3 \pm 7.3\%$ of clams (mean \pm SE pooled across both sediment types) were gaping, indicating high levels of stress, compared to none in the high water column DO treatment. Although the *Caulerpa* sediment remained black and strongly anoxic throughout the experiment, sediment type had no effect on pop-up rate ($F_{1,20} = 0.13$, $P = 0.724$), and

the interaction term was non-significant ($F_{1,20} = 0.18$, $P = 0.673$).

Changes in burrowing depth in *Caulerpa* and its consequences

Anadara popped-up at more than double the rate in *Caulerpa* compared to unvegetated sediment (Table 1). These high rates of pop-up occurred despite tubs initially having the same sediment suggesting sediment within tubs in *Caulerpa* went anoxic relatively quickly and subsequently influenced hypoxia. There was no difference in the survivorship of *Anadara* between *Caulerpa* and unvegetated sediment after 12 weeks (Table 1).

Consequences of forced burial in *Caulerpa*

Clams died at significantly higher rates when forced to stay buried for 1 month in *Caulerpa* compared to unvegetated sediment (Table 1). As cage tops were removed in *Caulerpa* we observed that the sediment was mostly black (anoxic) and a white bacterial film was present.

Discussion

We have identified hypoxic water in the boundary layer beneath the canopy of invasive *Caulerpa* as a sufficient mechanism determining the behavioural pop-up response of the native bivalve *Anadara*. When *Anadara* are not able to surface in *Caulerpa* they have a high probability of mortality, presumably due to insufficient dissolved oxygen within the benthic boundary layer. This pop-up behaviour most likely allows *Anadara* to get above the hypoxic boundary layer into normoxic water. This behavioural response was not observed in the presence of *Caulerpa*

Table 1 Percent behavioural pop-up and natural survivorship of *Anadara* in cage protected plots over 3 months in unvegetated sediment and *Caulerpa*, and the percent that survived under forced burial for 1 month in each habitat

Comparison	Unvegetated (mean \pm SE)	<i>Caulerpa</i> (mean \pm SE)	Significance (of habitat effect)
Natural ^a			
Pop-up	32.3 \pm 6.6	71.6 \pm 7.1	$P = 0.005$
Survivorship	96.3 \pm 2.6	95.0 \pm 3.3	$P = 0.859$
Forced burial ^b			
Survivorship	90.0 \pm 4.1	42.5 \pm 8.5	$P = 0.002$

Tests comparing between habitats using $\sqrt{\text{Arcsin}}$ transformed proportions

^a Pop-up: $F_{1,13} = 11.10$ (Block: $F_{1,13} = 0.24$, $P = 0.631$); survivorship: $F_{1,13} = 0.03$ (Block: $F_{1,13} = 1.69$, $P = 0.296$)

^b $t_6 = 4.42$

rhizoids and the anoxic *Caulerpa* sediment as long as normoxic water was present, indicating that neither a physical barrier to burrowing nor anoxic sediments per se were responsible for the pop-up response. Nonetheless, *Caulerpa* sediment contains sulphide-reducing bacteria (Chisholm and Moulin 2003) which presumably drive microbial decomposition of organic matter and subsequent depletion of dissolved oxygen within the boundary layer. Importantly, when *Anadara* were able to adjust their burrowing depth, they had a similar survivorship in invaded and uninvaded areas indicating that *Anadara* mitigates the effects of hypoxia caused by *Caulerpa* on survivorship via this behavioural response.

Although habitat-forming invasive plants and sessile invertebrates often support many native fauna, the cues triggering behavioural responses (either positive or negative) of associated fauna remain poorly understood. For example, the avoidance of the leaf litter of an invasive vine by native lizards was suggested as being due to any of three potential mechanisms: changes in temperature, prey availability and camouflage (Valentine et al. 2007). Similarly, changes in the foraging behaviour of a native fish in response to an invasive aquatic macrophyte were due to either greater spatial complexity or reduced levels of light (Theel and Dibble 2008). Although the high densities of native epifauna often present in marine habitat-forming invasive species compared to bare substratum (e.g. Castilla et al. 2004) suggest positive behavioural cues may be important for larvae of epifauna, to our knowledge there have been no tests done to separate the effects of larval settlement and post-settlement survivorship on these patterns.

Our findings for *Anadara* highlight how existing adaptations of native species can ameliorate the effects of invasive species. For example, the shells of marine molluscs can become thicker and their refuge-seeking activity greater when exposed to cues from invasive crabs (Trussell et al. 2003; Freeman and Byers 2006)—both of which may decrease their susceptibility to crab predation. Marine invertebrates can respond to hypoxia by moving to water with higher DO or by reducing feeding activity (Diaz and Rosenberg 1995). In particular, under hypoxia, infaunal bivalves burrow shallower and extend their siphons further above the sediment in an attempt to access normoxic water above the boundary layer (Taylor and Eggleston 2000). Thus, the pop-up response of *Anadara* that allows them to tolerate the changes caused by *Caulerpa* appears a generalised response they already possess that is triggered by the proximate environmental conditions (hypoxia) created by *Caulerpa*.

In addition to identifying the mechanism causing the behavioural response of *Anadara* to the hypoxia caused by *Caulerpa*, our results emphasise that invasive habitat-forming macroalgae can create hypoxic conditions in shallow estuarine habitats. Hypoxia in estuaries is typically caused

by eutrophication which leads to increased microbial decomposition of organic matter and low dissolved oxygen (Kennish 2001). Such eutrophication-driven hypoxia can result in large-scale mortality of estuarine biota including bivalves (Diaz and Rosenberg 1995), although bivalves do vary in their tolerance (Altieri 2008) and behavioural responses to hypoxia (Taylor and Eggleston 2000; Seitz et al. 2003). Blooms of native macroalgae can similarly create hypoxic conditions and affect the burrowing behaviour of bivalves (Tallqvist 2001). The factors that contribute to low dissolved oxygen below canopies of blooms of native macroalgae include algal respiration, microbial decomposition of accumulated macroalgal detritus and low rates of photosynthesis (D'Avanzo and Kremer 1994; Deegan et al. 2002). However, for *Caulerpa*, two lines of evidence indicate that microbial decomposition of accumulated detritus within or on top of *Caulerpa* sediments is likely to be an important mechanism causing hypoxia within the *Caulerpa* canopy. First, there are very high densities of *Caulerpa* fragments in *Caulerpa* habitats (Wright 2005) suggesting high levels of detrital input. Second, sulphate-reducing bacteria are abundant in sediments underlying *Caulerpa* (Chisholm and Moulin 2003) and the white film frequently observed on sediment under the *Caulerpa* canopy is consistent with the presence of the sulphide-oxidising bacterium *Beggiatoa* (Preisler et al. 2007). We did not measure water column DO in native seagrass, but sediment redox potential and *Anadara* densities are both higher in native seagrass compared to *Caulerpa* (Wright et al. 2007; McKinnon et al. 2009) and pop-up was not as extreme, suggesting native seagrasses have different effects than *Caulerpa* on *Anadara* behaviour.

Given the declining number of adult *Anadara* and the very high post-recruitment mortality in *Caulerpa* (Gribben et al. 2009a), pop-up is an increasingly important behaviour that allows the persistence of shrinking *Anadara* populations. Moreover, the persistence of some adults for at least 5 years after *Caulerpa* invasion indicates that mitigation of the effects of *Caulerpa* via pop-up is likely to persist over longer time-scales than observed here. In a similar result to this study, Wright and Gribben (2008) showed that after 9 months, adult *Anadara* (40–60 mm shell length) that were reciprocally transplanted between *Caulerpa* and unvegetated sediment, left uncaged and allowed to adjust their burrowing depth naturally (patterns of burrowing in habitats were similar to those observed here) had no differences in survivorship. However, very low survivorship in *Caulerpa* was evident after 12 months but this only occurred following a very heavy rainfall event (Wright and Gribben 2008). Thus, under “normal” conditions, popping-up in *Caulerpa* provides a survivorship benefit as clams suffer 50% mortality within 1 month if they remain buried in the sediment. However, in *Caulerpa*, a long-term decline in fitness and condition can increase their mortality risk. Additionally,

unlike other infaunal bivalves (Whitlow et al. 2003; Meyer and Byers 2005), shallower burrowing of *Anadara* does not increase their risk of predation (Byers et al. 2010). Instead, there is a slight, but variable, reduction in predation in *Caulerpa* independent of burrowing depth (Byers et al. 2010). In contrast to the weak predation costs, there are strong sublethal fitness costs for *Anadara* that pop-up in *Caulerpa* (reduced condition, growth and reproduction; Wright and Gribben 2008; Gribben et al. 2009a). The reasons for these sublethal costs are not clear but may be due to the effects of hypoxia in reducing feeding activity or causing a shift to anaerobic respiration (Wu 2002) or to *Anadara* feeding outside the boundary layer where there may be less available food.

In addition to the benefits to survivorship described here, the behavioural pop-up response by *Anadara* results in important effects on the larger community. Pop-up of *Anadara* causes an increase in the shell surface above the sediment and thus greater hard substrata for colonisation by epibiota. Popped-up *Anadara* have a greater diversity and abundance of epifauna compared to deeply burrowed *Anadara* (Gribben et al. 2009b) and also greater recruitment of *Anadara* (Gribben and Wright 2006). This community-wide facilitation is driven by the invasion of *Caulerpa* which creates hypoxic conditions and causes the pop-up response in *Anadara*.

The impacts that invasive species have on native ecosystems can be complex, far reaching and occur on both ecological and evolutionary timescales (Strauss et al. 2006). Because they cause large changes to the abiotic environment, habitat-forming invasive species are likely to elicit extensive behavioural changes in native fauna, similar to the variety of behavioural responses observed in native fauna to invasive predators. The behavioural response of the dominant bivalve in this system to hypoxia associated with invasion by *Caulerpa* gives it an important survivorship benefit which has flow-on consequences for the epifaunal community in this system (Gribben et al. 2009b). These results highlight a crucial role for behaviour of native species in mitigating the impacts of habitat-forming invasive species by detecting and responding to cues associated with changes in the abiotic environment following invasion.

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