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Fine-scale effects of sedentary urchins on canopy and understory algae

Juan P. Livore, Sean D. Connell *

Southern Seas Ecology Laboratories, School of Earth and Environmental Sciences, DX 650 418, The University of Adelaide, South Australia 5005, Australia

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ABSTRACT

The effect of sea urchins on algae has often been studied when sea urchins forage over areas to create or maintain urchin barrens. The effect of sea urchins that are not associated with barrens, however, is not so clear. This study tested the hypothesis that sedentary and largely site attached sea urchins (*Heliocidaris erythrogramma*) have detectable effects on the covers of canopy-forming and understory algae, whether that be due to their mere presence or grazing. Algal cover was estimated beneath and immediately surrounding urchins in a location where they do not create barrens but attain densities at the upper end of their local range. The area immediately beneath the urchins was mostly devoid of visible algae. Experimental removal of urchins over 3 years revealed that canopy-forming algae were able to develop in more extensive covers to match those in areas naturally lacking urchins. In the presence of urchins, the immediate area (i.e. first 5–6 cm from urchins) was primarily comprised of turf-forming algae, thereafter the cover of canopy-forming algae sharply increased until at ~8 cm their cover matched areas without urchins. These data support the model that composition and cover of algae can be altered in the presence of non-barren forming urchins, albeit only within a few centimetres of individual urchins. Where populations of sedentary urchins are dense and widespread (e.g. sheltered coasts for *H. erythrogramma*) such fine-scale effects may repeat over large areas such that urchins do not need to be associated with barrens before their effects are detectable.

1. Introduction

Canopy-forming algae are one of the most productive of all marine ecosystems (Valiela, 1995) and understanding variation in its cover is a persistent area of ecological research. Variation in the generation and maintenance of canopy cover may reflect a number of physical processes (e.g. storm-driven loss of canopies) and biological processes, including herbivory. Indeed, the effects of herbivory on cover of canopy and understorey algae are widely reported (review: Bigger and Marvier, 1998) and variation in the abundance of herbivores is often associated with the presence or absence of canopies (Andrew and Underwood, 1989).

Sea urchins are renown for their intense herbivory on attached algae and capacity to transform complex algal habitat into more simple sea urchin barrens (review: Pinnegar et al., 2000). Much attention has been given to the creation of sea urchin barrens and the mechanisms that drive this process (Andrew, 1993; Estes and Palmisano, 1974; Sala et al., 1998; Shears and Babcock, 2002). The grazing of canopy-forming algae is often thought to centre on a process that involves urchins abandoning shelter and then scrapping virtually all algae from rock (Andrew, 1993; Dean et al., 1984; Harrold and Reed, 1985). Less emphasis, however, has been placed on the effect of sea urchins when barren creation does not occur and urchins adopt a sit-and-wait feeding behaviour that relies on trapping drifting algae with their spines, pedicellaria and tube feet. At experimentally elevated densities such feeding can trap elevated amounts of drift algae and cause weak and ephemeral effects to attached algae (Vanderklift and Kendrick, 2005). There are many coastal areas where such sea urchins are abundant but do not create sea urchin barrens (Vanderklift and Kendrick, 2004), yet it is largely unknown whether they may affect the surrounding assemblage of algae.

The shallow subtidal rocky coast of the Leeuwin Current (i.e. South and Western Australia) is characterised by extensive forests of canopy-forming algae that lack sea urchin barrens (Connell and Irving, 2008). This absence of barrens is not due to a lack of urchins as the purple sea urchin, *Heliocidaris erythrogramma* (Valenciennes, 1846), is widely distributed across the temperate Australian coast. Their densities tend to be greater on the eastern coast of Australia compared with the southern and western coasts (Connell and Irving, 2008), except on some sheltered coasts of southern Australia (Livore, 2011; Vanderklift and Kendrick, 2004; Vanderklift and Wernberg, 2008). Although it has been observed to actively forage by scrapping algae from the rock in eastern Australian waters (Ling et al., 2010; Wright et al., 2005), this behaviour appears rare across the coasts of the Leeuwin Current (Livore and Connell, pers. obs.). Instead these latter coasts appear to be associated with passive drift-feeding mode, even when attached algae are readily available (Vanderklift and Wernberg, 2008). Whilst the relatively weak effects

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* Corresponding author. Tel.: +61 8 8303 6125; fax: +61 8 8303 4364.
E-mail address: sean.connell@adelaide.edu.au (S.D. Connell).

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of drift-feeding urchins on canopy-forming algae is largely accepted for broad parts of Australia's Leeuwin Current (Connell and Irving, 2008; Vanderklift and Wernberg, 2008), there remains little to no recognition of their potential effects where populations are unusually dense (i.e. sheltered bays) within this broad east–west coastline.

We quantified the cover of algae directly underneath and with increasing distance from sea urchins in a sheltered bay in South Australia that lacked obvious sea urchin barrens. The present study observed that the area immediately beneath urchins was devoid of algae in all cases. Potential models that account for this pattern centre on either the direct effects of urchins on algae or by the preference of urchins for areas devoid of algae. We tested the hypothesis that the removal of sea urchins will result in (i) an increase in algal cover in the area previously occupied by the urchin; and (ii) canopy cover would increase to match that observed in areas where urchins were naturally absent. We accepted the model of urchin driven effects and then assessed the scale of their influence by estimating the distance at which algal cover returned to match that of areas without urchins.

2. Materials and methods

The experiment was carried out on X-mark reef in Encounter Bay, South Australia chosen for its unusually high density of *Heliocidaris erythrogramma* ($\bar{x} = 5.46 \pm 0.24$ SE urchins m^{-2}). The limestone reef extends parallel to the shore and has an approximate depth of 2–3 m. The reef supports stands of canopy-forming algae predominantly dominated by fucoids (i.e. *Cystophora* spp and *Sargassum* spp). We classed the algae into four morphological groups: (i) canopy-forming: algae that reached >30 cm height; (ii) foliose: algae with a height range between 5 and 30 cm, (iii) turfs: non-crustose algae that developed to <2 cm and (iv) articulated corallines. Manipulative experiments to test the effects of urchin removal on algae began 1st April 2008 and finished 26th July 2011 (3.3 years). Three sites separated by no less than 100 m were randomly chosen within the reef. Urchins were removed and a steel peg with an identifying plastic tag was hammered into the rock immediately beside the bare plot where the urchin had sat (i.e. present) and in areas where sea urchins were absent ($n = 8$ plots treatment^{-1} site^{-1}). Sites were periodically monitored to ensure that removal plots were not re-occupied. Percentage primary cover of algal species was recorded at the 0, 8, 16, 24 and 40 months of the experiment in each plot with a 25 point quadrat (5 × 5 cm) which fitted well within the bare area found upon removal of individual urchins. In other words, this size of quadrat was chosen so that it was of similar size of the urchins themselves.

Before (0 months) and after (40 months) removal data was analysed using a three factor ANOVA that treated Time (before v. after removal) and Urchin (present v. absent) as fixed and orthogonal, whilst Sites were treated as random and orthogonal.

To quantify cover of algal groups with distance from sea urchins we sampled sea urchins' immediate surroundings. Fifteen centimetre transects from the edge of the urchin's test ($n = 90$ urchins) were used. Transects radiated in a random direction that avoided the presence of other urchins within 50 cm. Only one transect per urchin was used in order to obtain independent data. Cover of algal species was recorded within each centimetre. To test for a serial correlation in algal assemblage structure with increasing distance from urchins the RELATE routine was used. Cover data for each cm section of transects were square root transformed. The procedures reported here were performed in the PRIMER 6 software (Clarke and Warwick, 2001) with the PERMANOVA add-on (Anderson et al., 2007).

3. Results

The area directly under the urchins was consistently devoid of visible algae. Urchin removal had a positive effect on algal cover with plots previously occupied by urchins reaching 100% algal cover in all plots within the first eight months. Forty months into the experiment covers of all algal groups were indistinguishable between treatments (Fig. 1). Canopy-forming algal cover was affected by a time × urchin interaction (Table 1a). Greater cover was observed after than before manipulation in both urchin present and absent plots. No differences in canopy cover between urchin present and absent plots at the end of the experiment were detected (Table 1b). Foliose algal cover was marginally affected by a Time × Urchin interaction (Table 1a), no differences were detected at the end of the experiment between urchin present and absent plots (Table 1b, Fig. 1). The ANOVA also detected time and urchin effects on articulated coralline algae, with greater cover after the experiment and in urchin absent than present plots (Table 1a, Fig. 1). The ANOVA was not able to detect differences in percentage cover of turf-forming algae (Table 1a).

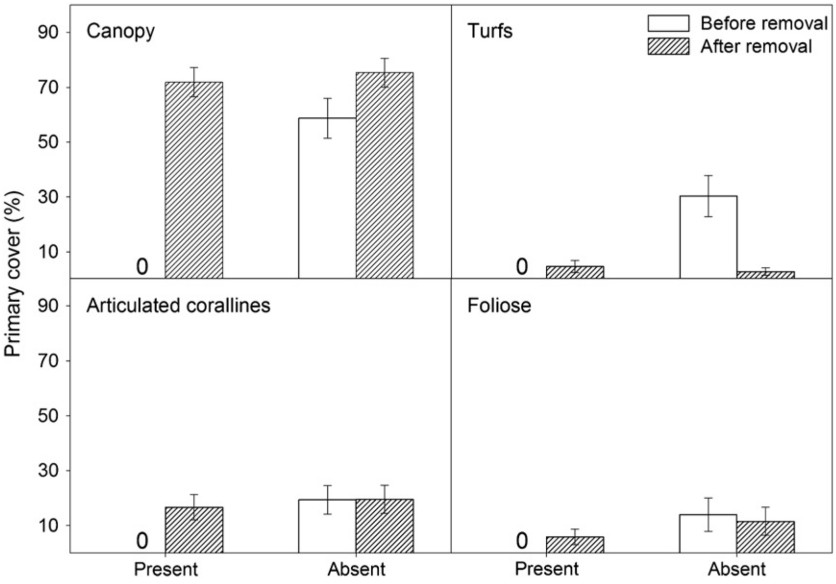

Fig. 1. Effects of time (before v. after urchin removal, 3.3 years) and urchin (presence v. absence) on mean (±SE) percentage cover of canopy-forming, turf-forming, articulated coralline and foliose algae.