



Forming sea urchin barrens from the inside out: an alternative pattern of overgrazing

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ABSTRACT: Overgrazing by sea urchins on temperate reefs can affect a phase shift from macroalgal beds to 'barrens' habitat largely devoid of seaweeds. Existing models of barrens formation are derived largely from observations of stronglycentrotid urchins, which typically show a behavioural shift from cryptic feeding to exposed grazing fronts that move through and 'mow down' macroalgal beds. Foraging by the temperate diadematid urchin *Centrostephanus rodgersii* triggers a similar transition from intact macroalgal bed to widespread barren grounds but does not appear to involve a behavioural shift. Fine-scale foraging movements were observed using time-lapse photography across the urchin's range-extension region and described with respect to a random walk model. Foraging was highly nocturnal, with individuals homing strongly to available crevices. *In situ* monitoring of tagged individuals suggests strong fidelity to and thus high stability of barren patches, while similar behavioural patterns across habitat types representing a gradient of foraging intensities indicate no behavioural shift associated with overgrazing. Laboratory experiments showed that *C. rodgersii* lacks a directional chemosensory response to either macroalgae or conspecifics. Combined evidence suggests a model of barrens formation fundamentally different to the well-established 'feeding front' model, with formation of widespread barrens by *C. rodgersii* occurring from the 'inside out' via growth and coalescence of small barrens patches that form within macroalgal beds as a result of additive localised grazing radiating from crevice shelters. Regulation of urchin density at the spatial scale of individual barrens patches is proposed as a viable option to manage the formation of widespread barrens habitat within the urchin's recent range-extension to eastern Tasmania.

KEY WORDS: Phase shift · Kelp beds · Barrens · *Centrostephanus rodgersii* · Foraging ecology · Movement · Grazing effect · Range extension

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INTRODUCTION

Marine ecosystems worldwide are subject to increasing anthropogenic stress, lowering their resilience to 'catastrophic shifts' (after Scheffer et al. 2001) in ecological structure and function (Beisner et al. 2003). Grazing by herbivores is frequently implicated as a driver of phase shifts in marine environments via the removal of primary producers and biogenic habitat. In shallow temperate waters, sea urchins are one of the most dominant and conspicuous habitat-structuring taxa on rocky reefs, particularly through their propensity for intensive grazing

that triggers a shift from dense macroalgal beds to 'barrens' habitat largely devoid of fleshy macroalgae (e.g. Lawrence 1975, Bernstein & Mann 1982, Harrold & Reed 1985, Andrew & Underwood 1989, Johnson et al. 2005, 2011). Sea urchin barrens are characterised by decreased habitat complexity, biodiversity and productivity relative to adjacent seaweed beds (Chapman 1981, Himmelman et al. 1983, Tuya et al. 2005, Ling 2008). Unlike terrestrial herbivores that frequently overgraze their food, sea urchins are capable of maintaining high density populations on barrens by switching to alternative food sources including microalgae, non-geniculate

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coralline algae, drift algae (Johnson et al. 1981) and invertebrate material (Ling 2008). The transition to barrens habitat is particularly problematic because it represents a catastrophic phase shift between alternative stable states with hysteresis (e.g. Ling et al. 2009a), requiring extensive reductions in sea urchin densities for kelp beds to recover (Harrold & Reed 1985, Carpenter 1990).

Few studies have employed an experimental approach to elucidate the mechanism of grazing dynamics leading to the creation of barrens habitat. Among these, most have focussed on species of sea urchins in the family Strongylocentrotidae (e.g. Mattison et al. 1977, Dean et al. 1984, Dumont et al. 2007, Lauzon-Guay & Scheibling 2007b, Feehan et al. 2012). This focus in research is due in part to the wide geographical distribution of strongylocentrotids and their close proximity to northern hemisphere researchers, in combination with a spectacular and highly conspicuous mode of overgrazing that involves the formation of 3-dimensional 'feeding fronts' at the interface between kelp bed and barren habitat. Manifestation of this phenomenon appears to coincide with a switch in behaviour from low-effect sedentary or cryptic foraging to destructive motile and exposed feeding aggregations (e.g. Harrold & Reed 1985). The likelihood of barrens formation is therefore usually associated with complex behaviour involving threshold densities, and this pattern has been widely accepted and generalised across sea urchin taxa (e.g. Mattison et al. 1977, Dean et al. 1984, Lauzon-Guay & Scheibling 2007a). Our casual observations over several thousand person-hours of diving across hundreds of kilometres of coastline in Tasmania indicate that *Centrostephanus rodgersii* does not form grazing fronts in creating extensive sea urchin barrens, but this species forms relatively small patches which can eventually become sufficiently numerous to grow, coalesce and form extensive areas of barrens habitat. In the present paper, we identify behaviour consistent with our general observation of forming barrens habitat from the 'inside out' without the formation of grazing fronts. These findings indicate that well-established models of barrens formation do not apply universally across all systems and sea urchin taxa.

The role played by the diadematid sea urchin *Centrostephanus rodgersii* in structuring shallow rocky reef communities is unparalleled by any other benthic herbivore in southeastern Australia (reviewed by Andrew & Byrne 2001, Johnson et al. 2005, 2011). Throughout the species' historical range in New South Wales (NSW), it maintains widespread

and persistent barrens habitat across ~50% of all near-shore rocky reef (Andrew & O'Neill 2000). In recent decades, the species has extended its range southward to Tasmania, driven primarily by increased poleward penetration of the East Australian Current (Johnson et al. 2005, Ling et al. 2009b), and the establishment of reproductively viable populations in Tasmanian waters has further facilitated its spread and establishment (Johnson et al. 2005, Ling et al. 2008, Banks et al. 2010). Widespread barrens are now found extensively in the northeast of Tasmania, with a gradient of decreasing grazing intensity with latitude manifesting as patchy barrens decreasing in size and frequency down the east coast of Tasmania (Johnson et al. 2005, 2011). Continued barrens formation throughout the range-extension region in Tasmania poses a major threat to local biodiversity (Ling 2008) and to the lucrative reef-based abalone and rock lobster fisheries dependent on macroalgal production and habitat (Johnson et al. 2011). Importantly, removal of predatory spiny lobsters from Tasmanian rocky reefs via commercial and recreational fishing has reduced the resilience of kelp beds, increasing the risk of catastrophic shift to widespread barren habitat (Ling et al. 2009a).

In common with other diadematid sea urchins (Nelson & Vance 1979, Lissner 1980, 1983), divers observe *Centrostephanus rodgersii* to shelter in crevices during the day and emerge to forage at night (reviewed by Andrew & Byrne 2001). In Tasmania, *C. rodgersii* within dense macroalgal beds graze discrete patches surrounding their crevices to form local barren patches, termed 'incipient barrens' (Johnson et al. 2005). Formation of widespread barrens occurs more frequently on boulder substratum where localised shelters are abundant, although barrens may also form on featureless flat-rock substrata (Johnson et al. 2005, Ling & Johnson 2012), which sea urchins will graze from nearby rudimentary 'shelter' when all available crevices are occupied or persist exposed on flat rock surfaces throughout the entire diel cycle (e.g. Andrew & O'Neill 2000). The availability of crevice structure has been shown to mitigate the vulnerability of *C. rodgersii* to predation (Ling & Johnson 2012), with such crevice dependency found to influence the sea urchins grazing patterns to the extent that Andrew (1993) suggested that availability of crevices for shelter within kelp beds is a pre-requisite condition for barren formation. Thus, the development from incipient through extensive barrens on boulder substratum and finally to widespread barrens habitat on extensive areas of flat rock represents an increasing gradient of forag-

ing intensity that is effectively spatially mapped along the urchin's recent range-extension region in eastern Tasmania. The prevalence of incipient barrens on this coast therefore represents a crucial point in the initial transition from kelp bed to widespread barren habitat (Johnson et al. 2005, Ling et al. 2009a). Thus, isolating the mechanisms underpinning the dynamics of these patches is likely to be of key importance in understanding the phase shift caused by *C. rodgersii*.

We explore the movement of *Centrostephanus rodgersii* and its patterns of habitation persistence within incipient barren patches to infer foraging dynamics and thus the likely mechanisms by which these small-scale features form, grow and ultimately develop into widespread barrens. We describe (1) spatial and temporal patterns in foraging behaviour on 3 different types of barrens habitat representing a gradient in foraging intensity across the sea urchins' range-extension region in eastern Tasmania, (2) the extent of fidelity of sea urchins to individual barren patches and how per capita grazing effect scales with increasing barrens patch size and (3) sea urchin responses to chemosensory stimuli characteristic of patch boundaries. We assess whether incipient barren patches represent a series of largely independent local patches in a seaweed bed or a mosaic of patches interconnected by widely ranging sea urchins routinely moving among patches, and thus, we assess whether targeted management of patches can be used to limit their further expansion and ultimately the formation of widespread and ecologically undesirable barrens habitat.

MATERIALS AND METHODS

Spatial and temporal patterns of movement across range extension region

Fine-scale movement of *Centrostephanus rodgersii* on rocky reefs in eastern Tasmania was assessed using time-lapse photography between November 2009 and February 2010 across a number of different sites with similar environmental and exposure regimes. These sites were chosen specifically for the type of barrens habitat they contained, with targeted monitoring carried out in 3 distinct habitat types: widespread barrens (grazed areas $>10^4$ m²) composed of flat rock; widespread barrens composed of boulders; and incipient barrens (grazed patches 1 to 10 m²) representing the north-to-south gradient of decreasing grazing intensity across the sea urchin's

range-extension region (Fig. 1). Each monitored reef was characterised by moderate topographic relief reaching a maximum depth of 12 to 16 m, with a macroalgal canopy (where present) dominated by the laminarian *Ecklonia radiata* and fucoid *Phyllospora comosa*. Movement was recorded over 15 different nights with time-lapse sequences using Nikon D200 digital SLR and Pentax Optio W80 digital compact cameras equipped with red lighting to minimise disturbance of sea urchins throughout the nocturnal cycle (see Millott 1968, Gras & Weber 1983). Each sampling occasion was spatially independent, with a different area of reef and different sea urchins monitored in each of the photographic sequences. Cameras were mounted on adjustable aluminium tripods and deployed by SCUBA divers. The field of view (FOV) photographed by the cameras varied from ~5 to 30 m² depending on both the camera system used and the adjusted height of the tripod (0.8 to 3 m from the substratum, depending on topography), but this variation in FOV occurred haphazardly across the different habitat types. FOV dimensions were determined from image calibration based on measurements taken between visible features on the benthos. Image sequences spanned a minimum of 12 h between 19:30 and 07:30 h, with a single photograph taken every 5 min and sea urchin coordinates recorded using the 'Manual Tracking' plugin for ImageJ (v. 1.42). The time frame over which individual sea urchins could be reliably tracked was estimated from pilot trials examining urchin velocity. A frequency of photographing at 5 min intervals permitted unambiguous tracking of each urchin in the view field (see supplementary video at www.int-res.com/articles/suppl/m464p179_supp/).

The path followed by an individual through time was reproduced and divided into a series of steps, stops and moves. A step was defined as the vector connecting 2 successive positions (5 min apart), a stop as an interval in which an individual remained stationary for at least 2 frames (10 min) and a move as the vector between 2 successive stops (see Dumont et al. 2007 for a detailed explanation). An arbitrary minimum step length of 10 mm was used, below which movement was considered to be measurement error or indicating local spine movement of otherwise stationary individuals.

Movement of *Centrostephanus rodgersii* was initially observed over the entire diel cycle (24 h) to properly quantify periods in which sea urchins were active. Preliminary analyses of these images indicated highly nocturnal foraging consistent with observations on mainland Australia, so all sub-

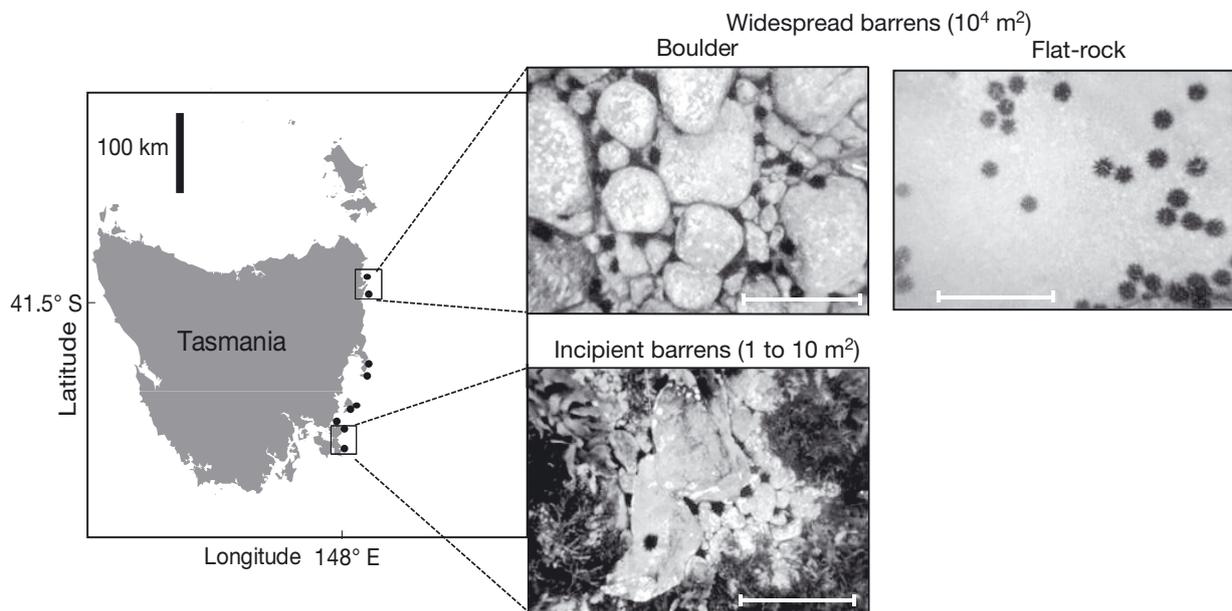


Fig. 1. Map of Tasmania (southeastern Australia). ●: sites where patch-size dynamics of *Centrostephanus rodgersii* was recorded using geo-referenced timed swims (November 2008 to June 2009). Ordered north to south: Sloop Rock, St. Helens Island, Wineglass Bay, Trumpeter Bay, Mistaken Cape, Bunker Bay, Cape Paul Lemanon, North Bay, Fortescue Bay. Abundance of *C. rodgersii* and prevalence of barrens declines with latitude southward along the eastern Tasmanian coast (Johnson et al. 2005, 2011, Ling et al. 2009a), with widespread barrens (10^4 m²) occurring in the northeastern (NE) region, while only small scale (1 to 10 m²) barrens are currently present in southeastern (SE) Tasmania. Expanded boxes indicate the 2 regions where movement was examined. NE: widespread flat-rock (minimal cracks and crevices) and widespread boulder barrens; SE: incipient barrens patches only. White scale bars = 1 m. Overgrazing progresses from incipient barrens centred on boulder habitat to widespread boulder barrens, and finally, where grazing is most intense, flat-rock habitats are stripped bare of kelp

sequent photography was from 19:30 to 07:30 h (overnight, daylight-to-daylight). Images from the different habitat types were examined separately for temporal patterns in speed of movement. The frequency of sea urchins moving faster than the nightly average within each hourly period was calculated to identify times throughout the night corresponding with peaks in activity. Quantitative comparisons between distributions from each habitat type were made using pair-wise Kolmogorov-Smirnov tests, with Bonferroni adjustments made to α to protect against compounding Type I error. Net displacement and total distance moved over the night were calculated for the subset of sea urchins within each habitat that remained in the FOV for the entire duration of nocturnal footage. Sea urchin density was estimated for each night of footage as the mean of 5 density measures taken at 3 h intervals between 19:30 and 07:30 h. All response variables were initially examined using 1-way nested ANOVA with sampling occasions (replicates) nested within habitats. Sampling occasion (night of camera footage) was non-significant ($p > 0.25$ for all response variables), so replicates were post-hoc pooled (removal of the factor

'sampling occasion' from the model) in accordance with Underwood (1997). One-way ANOVA with associated REGWQ *a posteriori* multiple range tests as appropriate were then performed on all response variables across 3 levels of barren habitat type using SAS[®] (v. 9.1).

To characterise movement in *Centrostephanus rodgersii*, observed movement paths were compared with paths simulated by an established walk model. Kareiva & Shigesada (1983) give an equation for a correlated random walk model that is frequently used to characterise the foraging behaviour of animals in homogenous environments (Byers 2001, Austin et al. 2004, Lauzon-Guay et al. 2006, Dumont et al. 2007):

$$R_n^2 = nm_2 + 2m_1^2 \frac{\psi}{1-\psi} \left(n - \frac{1-\psi^n}{1-\psi} \right) \quad (1)$$

where R_n^2 is the net squared-displacement of a path, n is the number of moves in a path, m_2 is the mean of the squared move length, m_1 is the mean move length, and ψ is the mean cosine of the turning angle. The distribution of observed *C. rodgersii* turning angles was initially analysed and found to be uniform

(i.e. the mean cosine of angles was not significantly different from 0); hence, the model was by definition reduced to a simple random walk (RW) equation:

$$R_n^2 = nm_2 \quad (2)$$

Because the RW model assumes no autocorrelation between either the length or direction of consecutive moves, turning angles were tested for first- and second-order autocorrelation within each habitat type using the method described by Conradt & Roper (2006) and Turchin (1998). The presence of first-order autocorrelation between successive move lengths was also tested for using Spearman rank tests (Zar 1999, Dumont et al. 2007).

Observed paths from within each habitat were compared with 1000 paths simulated by the RW model using the software MATLAB (v. 7.3.0). A maximum of 6 moves per path was used in the model simulation, as this was equal to the maximum number of moves made by at least 10 individuals within each habitat. For every iteration of the simulation, n move lengths and n turning angles were drawn randomly (with replacement) from the respective empirical distributions for each habitat, and a single path was generated (Bootstrap method, Turchin 1998). Once 1000 simulated paths were obtained for each habitat, the mean net squared-displacement (\bar{R}_n^2) was calculated for every value of n as the mean of these 1000 paths. Variation around the expected \bar{R}_n^2 was examined using the technique recommended by Turchin (1998), with 95% confidence intervals estimated using the percentile method (Crowley 1992, Manly 1997, Turchin 1998). The net squared-displacement (R_n^2) of individual sea urchins was classified as local, directional or random based on whether it fell below, above or within the confidence intervals of the walk model, respectively (Austin et al. 2004). An individual track was considered significantly different from the model when the observed R_n^2 fell outside the confidence intervals for at least half of all moves (Dumont et al. 2007).

Assessing fidelity to incipient barren patches

To assess the long-term stability of incipient barren patches, the fidelity of *Centrostephanus rodgersii* to individual patches was evaluated by measuring movement and dispersal of tagged sea urchins at Fortescue Bay, Tasman Peninsula. Three incipient barren patches in close proximity (~20 m from nearest adjacent barren) were selected haphazardly from within the kelp bed at depths of 6 to 8 m. The patches

varied in area (1.2 to 3.9 m²), perimeter (15 to 30 m) and the number of urchins they contained (6 to 22) and were broadly representative of the typical scale of patches in incipient barrens habitat. All *C. rodgersii* found within these patches ($n = 14, 22, 6$ ind. for Patches I to III, respectively) were tagged at the commencement of the experiment by drilling 2 small holes through the test with a hypodermic needle (100 mm long by 1.25 mm diameter), threading a 150 mm length of monofilament line (0.45 mm diameter) with a uniquely numbered spaghetti tag through the needle and crimping the line ends together with a leader sleeve (Ling et al. 2009a). Despite previous findings of minimal mortality and tag loss (<5%) associated with *ex situ* tagging in this way (Pederson & Johnson 2006, Ling et al. 2009a), all tagging was conducted *in situ* by SCUBA divers, and individuals were returned to within 10 cm of their initial position immediately following application of the tag. *In situ* tagging in this way avoided any risk of behavioural changes that might result from removal to the surface and subsequent release.

Patches were searched for tagged sea urchins 1 wk after tagging and again every 3 wk over a period of 90 d (total of 6 encounter occasions). The area of kelp immediately surrounding the patch was also searched on each occasion using a 5 m circular sweep around a central fixed point within the patch. Each time a tagged sea urchin was sighted, its identity was recorded, its test diameter was measured, and its location within the patch or surrounding kelp bed was triangulated with respect to 2 fixed pickets hammered into the reef. The position of each sea urchin was also recorded as 'shallow' or 'deep' depending on its location relative to the shore and pickets. These 3 measurements provided a unique set of coordinates, allowing calculation of the net distance moved since an individual's previous sighting and displacement from its initial tagging position for each individual. The relationship between the cumulative total distance moved (the sum of net movements between consecutive sightings) and overall displacement from the original position was examined for every resighting occasion and used to assess patch fidelity. Given evidence for a strong positive relationship between movement and body size in stronglycentrotid sea urchins (Dumont et al. 2004), size-specific movement was examined by quantile regressions of test diameter against net movement using the 'quantreg' package (Koenker 2009) for the 'R' software. To verify that fidelity and movement estimates were not biased by some sea urchins moving beyond the boundaries of the experimental area,

the daily survival and encounter probabilities of individuals were assessed using a Cormack-Jolly-Seber (CJS) mark-recapture model with the factors 'plot' and 'time' and a covariate of 'size'. Data were analysed using the CJS routine of the MARK (v. 6.1) software (White & Burnham 1999), whereby the saturated model was tested for goodness-of-fit and the most parsimonious model identified using the quasi-likelihood form of the Akaike information criterion, as per Ling et al. (2009a).

Role of chemosensory cues in determining patch dynamics

The potential role of food and conspecific chemosensory cues in stimulating movement of *Centrostephanus rodgersii* across the barren–macroalgal interface at the perimeter of patches were investigated in a series of laboratory choice experiments. Sea urchins were collected between February and March 2010 and housed in flowing seawater tanks without food for a minimum of 4 wk before trials commenced. Given an average gut passage time of 24 to 60 h under normal feeding regimes across a number of sea urchin taxa and a maximum food retention time of 1 to 2 wk in starved sea urchins (see De Ridder & Lawrence 1982 and references within), a 4 wk starvation period was assumed to be sufficient to ensure significant motivation to feed. Experiments were conducted in a 250 mm diameter Y-shaped maze constructed from PVC piping with section lengths of 0.5 m (arms) and 0.7 m (trunk). Each arm was connected to a header tank containing either a 'stimulus' or 'blank' seawater. A flow rate of 21 l min⁻¹ (velocity 0.24 m min⁻¹ in the main stem) was maintained throughout all trials, with dye experiments conducted regularly to verify minimal mixing of water upstream of the junction point. Initial trials indicated that large individuals (in which the lateral diameter of the spine canopy spanned the width of the experimental apparatus) tended not to move within the maze, so only sea urchins with spine canopies <250 mm were retained for analysis since they moved freely in the maze and were not impeded by the dimensions of the apparatus. The first 2 sets of trials tested the potential role of food cues in stimulating sea urchins to cross the barren–macroalgal boundary by using fresh *Ecklonia radiata* (simulating attached plants) and damaged or decomposing *E. radiata* (representing detached drift algae), both of which are known to be consumed by *C. rodgersii* (Andrew 1993, 1994, Hill et al. 2003). The third set of trials addressed the hypothesis that patch fidelity of

C. rodgersii is maintained by attraction to conspecifics, and in these trials, 15 to 20 sea urchins (depending on size, 0.3 to 0.4 urchins l⁻¹) were held in one of the header tanks. All trials were conducted at night between 21:00 and 05:00 h in complete darkness during the peak of *C. rodgersii* feeding activity.

Trials commenced with a single sea urchin placed in the centre of the main Y stem. Its location was monitored every 10 min for a period of 40 min, and a choice was considered to have been made when an individual moved either side of the junction and its centroid crossed the entrance to one arm of the maze. Each sea urchin response was scored as positive (toward stimulus), negative (away from stimulus) or no response (no choice made between either arm). Water inflows were swapped after every second trial to eliminate any potential bias in the apparatus. For trials in which sea urchins made a choice between arms of the apparatus, the exact probability of the observed outcomes was analysed using χ^2 tests.

Scaling per capita grazing effect with barrens patch size

The grazing effect of *Centrostephanus rodgersii* individuals at the forefront of the urchin's range-extension region was assessed by broad-scale diver surveys in incipient barrens habitat across 9 sites in eastern Tasmania (Fig. 1). Over a total of 20 geo-referenced timed swims (surface GPS towed by diver for 30 to 45 min, n = 4 swims per site for North Bay and n = 2 swims for all other sites) between 5 and 15 m depth, divers searched for incipient barrens patches and carried out *in situ* estimations of patch sizes using a 1 × 1 m quadrat for calibration. The abundance of *C. rodgersii* within each patch was estimated for patch sizes up to a maximum of 5 × 5 m (25 m²) in area; beyond this size, patches became too large to efficiently estimate urchin abundance (see Fig. 1 caption for more detail). The relationship between planar grazed area of each barrens patch and *C. rodgersii* abundance was assessed using linear regression analysis. To assess overall effects of urchin grazing on kelp beds (beyond individual patches considered above), diver belt-transect data from Johnson et al. (2005) was re-analysed by linear regression to determine the relationship between mean *C. rodgersii* density and mean percentage cover of barrens habitat for 13 sites across the sea urchins' range-extension region (means of n = 3 sub-sites per site, with sub-site estimates obtained from the mean of 4 belt transects) (see Johnson et al. 2005 for full method).

Table 1. *Centrostephanus rodgersii*. Sample sizes and movement characteristics on incipient (IB), widespread boulder (BB) and widespread flat-rock (FB) barrens. Means \pm SE. Where ANOVA results are presented, all numerator df = 2. *Significantly different from other means as indicated by 1-way ANOVA (for significant overall tests) and REGWQ multiple range tests

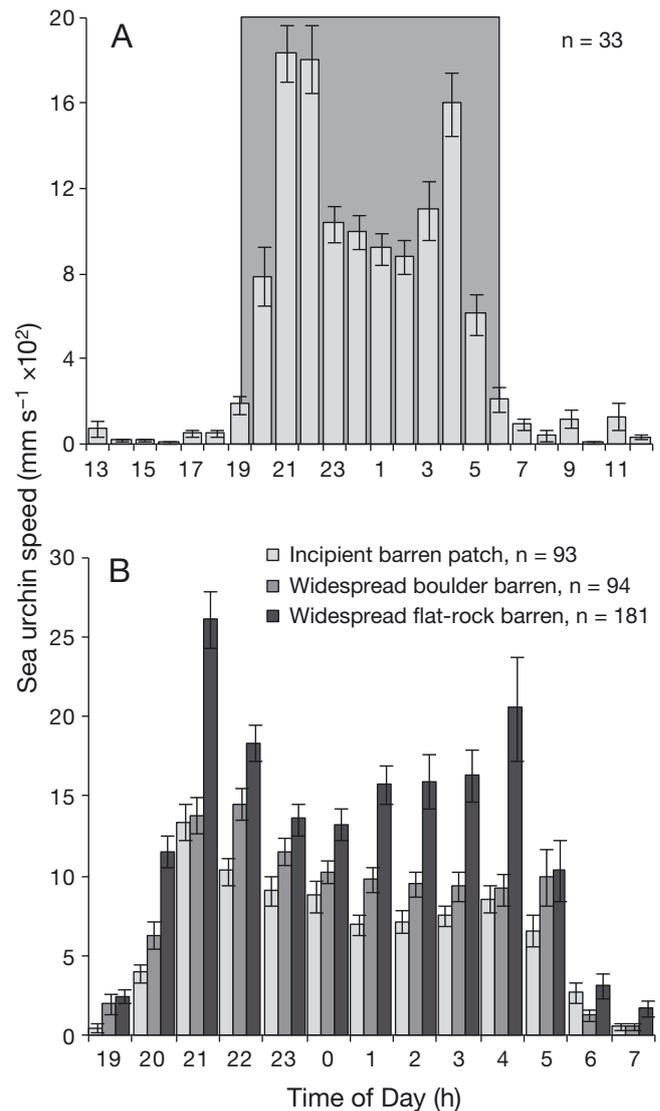
Characteristics	Barren habitat			ANOVA		
	IB	BB	FB	df	F	p
Sampling period	Dec 09–Feb 10	Nov 09–Dec 09	Dec 09	–	–	–
Nights of movement observations	7	4	4	–	–	–
Total no. of sea urchins tracked	93	94	181	–	–	–
No. of sea urchins in field of view all night	53	51	85	–	–	–
Sea urchin density (m^{-2})	1.99 \pm 0.11	1.88 \pm 0.28	1.93 \pm 0.33	14	0.06	0.946
Proportion of time spent moving (%)	49.9 \pm 1.7*	59.6 \pm 1.5	57.6 \pm 1.2	367	9.91	<0.001
Speed (mm s^{-1})	0.16 \pm 0.009	0.15 \pm 0.006	0.19 \pm 0.005*	367	22.0	<0.001
No. observed paths \geq 3 moves	54	60	99	–	–	–
Length of move ($\text{mm} \times 10^2$)	2.39 \pm 0.17*	3.37 \pm 0.27*	5.06 \pm 0.31*	291	25.6	<0.001
Cosine turning angle	0.08 \pm 0.07	0.06 \pm 0.06	0.05 \pm 0.06	291	0.05	0.955

RESULTS

Spatial and temporal patterns of movement

A total of 368 sea urchins were tracked across the 3 barren habitat types, each of which contained a similar density of sea urchins (Table 1). The movement of *Centrostephanus rodgersii* was strongly nocturnal, with peaks in speed occurring immediately following sunset and just before sunrise (Fig. 2A). This broad pattern was common to all habitat types, although sea urchins consistently moved fastest on flat-rock surfaces and slowest in incipient barrens patches on boulder habitat (Fig. 2B). The mean speed of individuals on widespread flat-rock barren was fastest from ~01:00 h relative to other habitats (see Fig. 2B); however, this was driven primarily by a small number of individuals returning late to shelter toward the end of the night. After standardising by the frequency of individuals moving faster than the nightly average (assessed across hourly bins), differences among habitat types in the distribution of movement patterns across hourly time intervals during the night were not significant (Bonferroni adjusted $\alpha = 0.017$, $p > 0.23$ for all pair-wise Kolmogorov-Smirnov comparisons).

Fig. 2. *Centrostephanus rodgersii*. Time-dependent velocity on incipient, widespread boulder and widespread flat-rock barrens as recorded using time-lapse photography (means \pm SE). Time is given in 24 h format. (A) Movement over entire diel cycle and pooled across habitat types. Background shading = twilight and nighttime based on the timing of sunset (20:38 h) and sunrise (05:27 h) averaged across recording dates. (B) Movement over nocturnal period separated into habitat types



A total of 189 sea urchins remained within the FOV of the camera for the entire duration of filming, and approximately equal proportions of the 179 excluded transitory individuals moved into (44%) and out of (56%) the FOV (χ^2 , $p = 0.12$). The total nightly distance (mean \pm SE) travelled by sea urchins on widespread flat-rock barrens (5.1 ± 0.3 m) was significantly greater than that of individuals on either widespread boulder (3.5 ± 0.2 m) or incipient (2.8 ± 0.2 m) barrens habitat on a boulder substratum ($F_{2,188} = 15.62$, $p < 0.001$) (Fig. 3A). Similarly, individuals on flat-rock were significantly further from their starting position at the end of the night ($F_{2,188} = 13.75$, $p < 0.001$), and their overall homing tendency to their site of origin at the beginning of the night was weaker relative to those on incipient or widespread boulder barren (Fig. 3B). The net displacement of sea urchins on incipient barrens was not significantly different to that of individuals on widespread boulder barrens; however, 98% returned to within 0.8 m of their starting position compared with 84% on widespread boulder barrens and just 24% on widespread flat-rock barren habitat. Sea urchins in incipient barrens also spent significantly less time moving ($F_{2,367} = 9.91$, $p < 0.001$) than their counterparts on widespread boulder or flat-rock barrens (Table 1). The total dis-

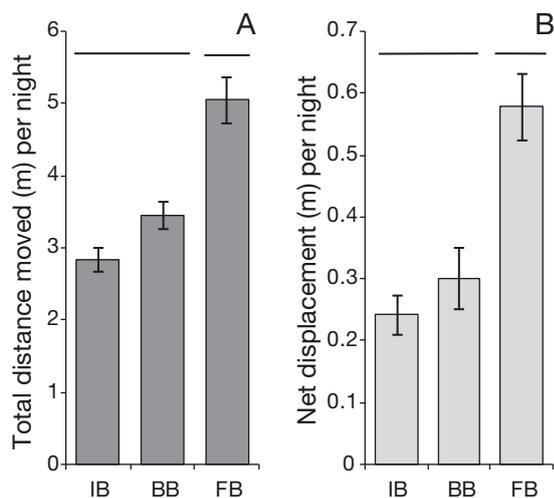


Fig. 3. *Centrostephanus rodgersii*. Movement on incipient (IB), widespread boulder (BB) and widespread flat-rock (FB) barrens between 19:30 and 07:30 h as determined by time-lapse photography (means \pm SE). Only sea urchins remaining within the field of view for the duration of filming were considered; $n = 54, 51, 85$ for IB, BB and FB barrens, respectively. Horizontal bars above columns indicate significant differences between habitat means determined by REGWQ tests after significant ANOVA. (A) Total distance moved throughout the recording period. (B) Net displacement (straight line distance) of sea urchins from their starting position after a night of foraging

tance moved by sea urchins within each habitat was generally less than the minimum FOV dimension for filming on that habitat. While many foraging species display classic Lévy flight movements (i.e. local random movement with occasional large 'jumps' to new sites), there is no evidence to suggest that *Centrostephanus rodgersii* exhibits this mode of behaviour, as indicated by high recovery of tagged urchins from circumscribed sites after 12 to 14 mo (Ling & Johnson 2009). Using this evidence, combined with a moderate to strong homing tendency across all habitats (average net displacement < 0.6 m) (Fig. 3B) (see 'Fidelity to incipient patches'), we are confident that exclusion of individuals leaving the camera FOV did not influence our estimates of the total distance moved and net displacement.

Of all the sea urchins tracked, 292 paths were composed of at least 3 moves and were thus appropriate for use in the random walk analysis. The average length of moves varied significantly among habitats ($F_{2,291} = 25.6$, $p < 0.001$), with sea urchins on flat-rock barren travelling $\sim 50\%$ further in a single move than those on widespread boulder barren and more than twice as far as the average length of move in incipient barren patches. A strong autocorrelation in the length of successive moves was detected for sea urchins on flat-rock barren (Spearman rank correlation, $r_s = 0.605$, $p < 0.001$) but not in either of the other 2 habitats ($p > 0.1$ for both incipient and widespread boulder barrens). This violates one of the assumptions of the RW model (Turchin 1998); however, it likely reflected the occurrence of distinct behavioural types (active and passive movers) that was evident only in sea urchins on flat-rock habitat. Also, no first- or second-order autocorrelation in turning angles was detected (χ^2 , $p > 0.07$ for all habitats), and hence, it was deemed reasonable to proceed with the RW analysis.

The RW model significantly overestimated the net squared-displacement of sea urchins in all habitats (Fig. 4). Despite variation in individual movement parameters (see Table 1), the relationship between observed and predicted net squared-displacement was similar across habitats. The observed net squared-displacements of pooled paths was within or close to the 95% confidence limits of model predictions for the first and second move of a path, but displacement increased very little beyond these 2 initial moves. The value at which the observed mean net squared-displacement (\bar{R}_n^2) stabilised varied from ~ 1 m² in flat-rock barrens to ~ 0.35 and ~ 0.15 m² in widespread boulder barrens and incipient barrens habitats, respectively (Fig. 4). A smaller stabilising

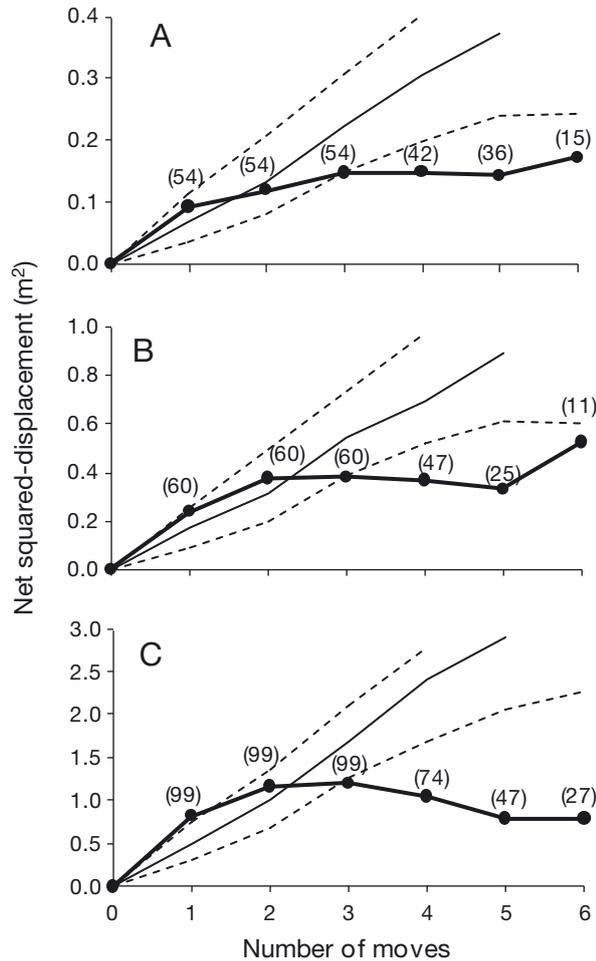


Fig. 4. *Centrostephanus rodgersii*. Examination of movement across habitats relative to predictions of a random walk model. Mean net squared-displacement is calculated over 6 consecutive moves from predicted (solid line) and observed (●) movement paths in 3 habitat types. Dashed lines: 95% CI for the predicted net squared-displacement based on a random walk. (number) = number of individuals observed. (A) Incipient barren, (B) wide-spread boulder barren, (C) widespread flat-rock barren

value of \bar{R}_n^2 for individuals in incipient barrens relative to widespread boulder barrens reflects a shorter average move length and less frequent movement overall (see Fig. 3, Table 1). The majority of movement within each habitat was local (displacement less than random) due to active homing or movement of short distances within a restricted area. A greater proportion of individuals in incipient barrens patches followed movement paths that fell within the predictions of the random walk. However, sea urchins exhibited directed movement less frequently in this habitat, indicating a greater tendency for homing or localised movement relative to that observed on widespread flat-rock or boulder barrens (Table 2).

Fidelity to incipient patches

Of the 42 sea urchins tagged, 71.4% were recovered from within or immediately adjacent to their respective incipient barren patches after 3 mo of monitoring. Every individual was resighted on at least 1 occasion (i.e. they 'disappeared and reappeared'), suggesting that the 12 urchins not recovered at the end of the study were likely present in the reef matrix but simply not found by divers. The cumulative distance moved by individuals between the 5 consecutive sampling periods was considerably greater than their net displacement (even with relatively infrequent sampling), indicating that while local movement and reshuffling of shelter sites continued to occur within patches over the monitoring period, most individuals remained within their particular patch over a period of 3 mo (Fig. 5A). Correspondingly, the mean net displacement of sea urchins over the monitoring period did not exceed 2.5 m from the position of initial tagging, although this metric was clearly influenced by the physical dimensions of the patch (Fig. 5B). No more than 6 individuals (14% of the total) were observed outside incipient patches on any one occasion, 5 of which were on the periphery of an incipient grazed patch following a seasonal flush of small ephemeral algae. After demonstrating satisfactory fit ($p = 0.469$) of the saturated mark recapture model [$\phi(\text{plot} \times \text{time} \text{ size}_{\text{cov}})P(\text{plot} \times \text{time} \times \text{size}_{\text{cov}})$], analysis of encounter rates of individually tagged sea urchins revealed that the best supported CJS model contained urchin survival (ϕ) as independent of plot, time or body size, while encounter probability (P) was dependent on sea urchin size only

Table 2. *Centrostephanus rodgersii*. Relative frequency of movement types (%) on incipient (IB), widespread boulder (BB) and widespread flat-rock (FB) barrens. n: number of tracks observed in each habitat. Movement type of a given track is classified depending on the proportion of moves within the track that fall above, below or within the CI of random walk model predictions. Individuals are classified as directional, local or random movers for tracks where at least half of all moves fall above, below, or within model CI, respectively. Given a maximum of 6 moves per path, paths are classified as undetermined where the same number of moves are assigned to 2 or more different movement types (e.g. 3:3, 2:2:2)

Habitat	n	Random	Directional	Local	Undetermined
IB	54	14.8	5.6	70.4	9.3
BB	60	6.7	13.3	70.0	10.0
FB	99	6.1	16.2	67.7	10.1

$[\phi(\cdot)P(\text{size}_{\text{cov}})]$ (Fig. 6A,B). Although large sea urchins had a greater potential for movement than smaller ones (75th quantile regression, $p = 0.037$) (Fig. 6C), the strong positive relationship between size and encounter probability (Fig. 6B) shows that large individuals consistently remained within or nearby their 'home' patches. Tagged individuals that were resighted less frequently were predominantly small ones that displayed restricted movement within

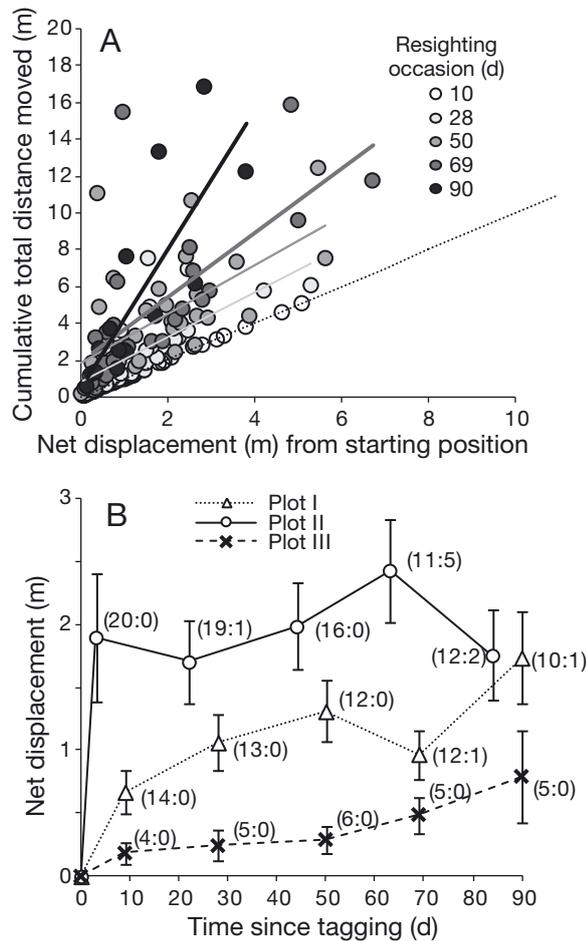


Fig. 5. *Centrostephanus rodgersii*. Movement of tagged individuals over a 3 mo monitoring period. (A) Cumulative total distance moved by individuals between sightings vs. net displacement from initial tagging position. Dashed line = perfect directional movement (1:1) away from the initial position. Vertical line passing through the origin = perfect homing. Grey scale of points and fitted lines darken with successive sighting occasions at 10, 28, 50, 69, 90 d since commencement of the experiment. Increasing slope of lines with successive sightings indicates persistent fidelity to incipient barren patches. (B) Displacement of sea urchins from initial tagging position over time across monitored plots (barren patch plus surrounding kelp area; means \pm SE). Numbers in () = number of individuals sighted on each monitoring occasion (inside patch: outside patch). Barren patch areas I to III are 2.41, 3.85 and 1.27 m², respectively

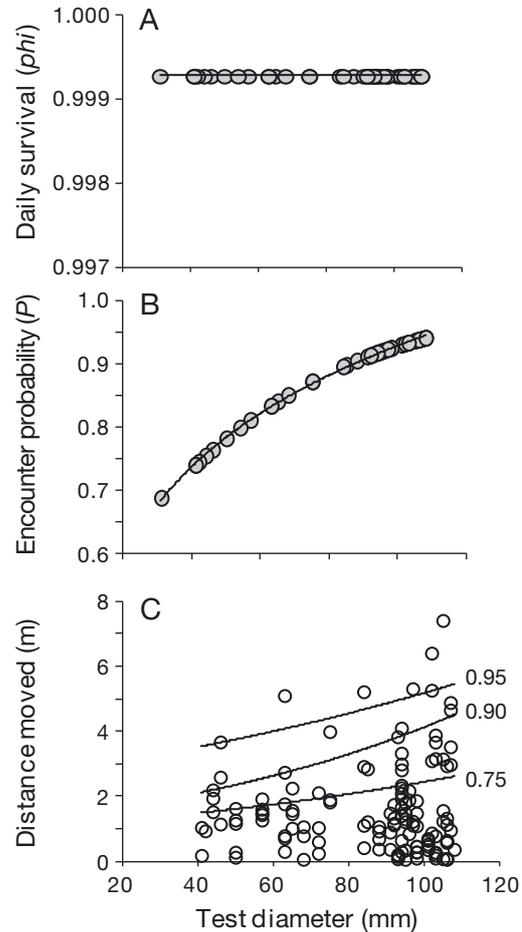


Fig. 6. *Centrostephanus rodgersii*. Size-specific characteristics of tagged individuals. Relationships between test diameter and (A) daily survival (ϕ); (B) encounter probability (P), as estimated from the most parsimonious CJS model (variance inflation factor $[\hat{\epsilon}]$ adjusted to account for overdispersion in sampling variation per Pollock et al. 1990); (C) net distance moved between consecutive sightings of individuals. 95th, 90th and 75th quantiles are given by $y = \exp(0.0065x + 0.9980)$, $p = 0.281$; $y = \exp(0.0113x + 0.2908)$, $p = 0.074$; and $y = \exp(0.0084x + 0.0573)$, $p = 0.037$, respectively

patches (Fig. 6C) but were less easily found by divers among the reef matrix (Fig. 6B).

Response to chemosensory cues

A choice, toward or away from either a food or conspecific stimulus, in Y-maze trials was made by ~70% of all sea urchins tested. However, there was no trend in the pattern of choices so that the number of reacting individuals did not differ significantly for any of the stimuli trialled ($p > 0.5$ for all sets of trials) (Table 3), indicating no directional response to olfactory stimuli.

Per capita grazing effect versus barrens patch size

The relationship between incipient barrens patch size and the number of sea urchins contained within each patch was well described by linear regression, with each individual maintaining a grazed area of $\sim 0.6 \text{ m}^2$ independent of the patch size and thus independent of the number of individuals per patch (Fig. 7A). Beyond individual barrens patches, the percentage cover of barrens across entire kelp beds also displayed a strong linear relationship with *Centrostephanus rodgersii* density, suggesting existence of a fixed grazing effect that is a simple function of the local density of *C. rodgersii* at a site absent of any density-triggered behavioural shift (Fig. 7B).

DISCUSSION

Patterns of foraging behaviour across barrens types

Our detailed observations of the nocturnal behaviour of *Centrostephanus rodgersii* were consistent with previous *in situ* observations (Jones & Andrew 1990) and evidence of light sensitivity in other diadematid sea urchins (Millott 1954, 1968, Gras & Weber 1983). Peaks in the velocity of their movement at the end of the night were most pronounced on widespread flat-rock barrens, where the dawn appeared to trigger a short burst of rapid and directional movement toward micro-crevices (the only available shelter on otherwise featureless flat-rock surfaces) in browsing individuals. This behaviour was observed less frequently in either of the boulder-based habitats and may be explained by the relative scarcity of crevices on flat-rock substratum. Aside from subtle

Table 3. *Centrostephanus rodgersii*. Movement responses to waterborne cues from food (*Ecklonia radiata*) or conspecifics in Y-maze trials. n: number of trials conducted for each stimulus set. C: choosing; NC: not choosing—individuals that did not move up the trunk of the maze and into either branch arm. p: probability indicating likelihood of choices differing from no choice (i.e. ratio of 1:1 responses to both stimuli) by chance, estimated using the χ^2 statistic

Pairs tested	n	No. of sea urchins		p
		C	NC	
Blank	24	9	8	0.617
<i>E. radiata</i> (fresh)		7		
Blank	24	9	7	0.808
<i>E. radiata</i> (decomposing)		8		
Blank	25	7	8	0.532
Conspecifics		10		

differences in the timing of peak velocity, time-related patterns in foraging were similar across habitats, indicating a common response to ambient light levels and an inherent circadian cycle (e.g. Ogden et al. 1973, Bernstein et al. 1981, Hereu 2005).

A dramatic shift in behaviour from sedentary low-effect grazing to motile feeding aggregations is a consistent feature in the formation of widespread barrens habitat by stronglycentrotid sea urchins (Dean et al. 1984, Lauzon-Guay & Scheibling 2007a, Scheibling & Hatcher 2007). If *Centrostephanus rodgersii* exhibited a similar behavioural shift, we

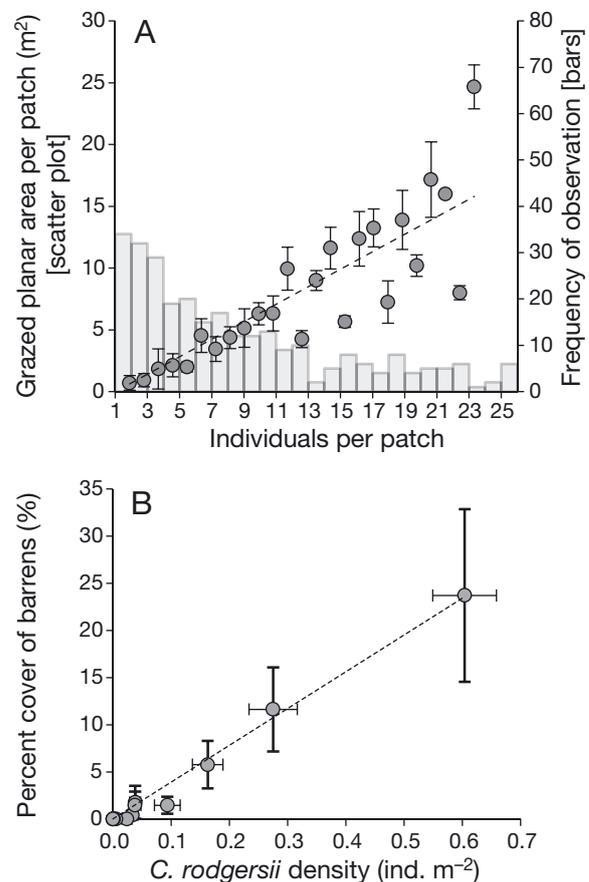


Fig. 7. *Centrostephanus rodgersii*. (A) Relationship between the grazed planar area of barren patches ($n = 284$) and number of individuals per patch (means \pm SE) as assessed by timed geo-referenced diver swims. Linear regression given by $y = 0.631x$, $R^2 = 0.901$, $t(24) = 15.1$, $p < 0.0001$. Grey bars = observed frequency of each data point. (B) Coverage (%) of sea urchin barrens and *C. rodgersii* density across sites spanning the range-extension region, as assessed by $n = 156$ diver belt-transects (data from Johnson et al. 2005). Means \pm SE. Linear regression given by $y = 39.2x$, $R^2 = 0.99$, $t(12) = 37.5$, $p < 0.0001$. Note: As sea urchin barrens on exposed eastern Tasmanian coast are caused by *C. rodgersii* with only negligible contributions from grazing by the native *Heliocidaris erythrogramma* (see Johnson et al. 2005), the intercept for the linear regression was set to 0

would expect it to occur between the progression from incipient 'developing' to widespread 'established' barrens and that it would manifest as measurable differences in nocturnal (when the individuals are active) foraging patterns among individuals on these different habitats. However, the pattern of foraging activity was similar across all 3 habitat types, and the subtle habitat-specific patterns observed can be attributed to features of the substratum rather than the extent of barrens formation. For example, sea urchins on widespread flat-rock barren moved faster and over greater distances than their counterparts on boulder substratum (whether widespread or incipient barrens) and had a greater net displacement over the nightly foraging period. This may be explained by more rapid locomotion of sea urchins across flat-rock substrata in the absence of crevices and vertical surfaces (Laur et al. 1986). However, we note also that a systematic underrepresentation of movement on boulder substratum is unavoidable when movement on a complex 3-dimensional landscape is converted to a 2-dimensional planar measurement; hence, the magnitude of the differences in movement parameters between flat-rock and boulder substrata would likely be somewhat reduced if rugosity was taken into account.

Homing behaviour: non-random movement

Movement of *Centrostephanus rodgersii* is highly localised relative to the predictions of the RW model. This suggests either that urchins move in a restricted fashion remaining in close proximity to a particular focal point (i.e. a 'home site') or, alternatively, that they move predominantly randomly but with the addition of a distinct 'outward' and 'inward' phase away from and returning to a home crevice (i.e. homing behaviour). A homing strategy is a more parsimonious explanation of the observed foraging behaviour, with the observed net-squared displacement only deviating from the predictions of the RW model following the second move of a path (only tracks with at least 3 moves were retained for analysis, so an increasing proportion of tracked individuals returned to a home crevice and 'ended' a foraging path for move numbers ≥ 3). Homing behaviour has been well documented in conspicuous marine invertebrates, such as limpets (e.g. Underwood 1977, Ruiz Sebastián et al. 2002), as has the alternation between random and homing 'phases' of movement (although with an overall strong homing pattern) (Mackay & Underwood 1977). The homing behaviour

of *C. rodgersii* observed here contrasts with the predominantly random movement observed in *Strongylocentrotus droebachiensis* (Lauzon-Guay et al. 2006, Dumont et al. 2007). While neither of these studies examined habitat-specific movement characteristics *per se*, movement was random on both barrens habitat and in grazing fronts, suggesting an inherent difference in foraging dynamics between *S. droebachiensis* and *C. rodgersii*.

Shelter-oriented homing behaviour has previously been observed and quantified in the diadematid sea urchins *Centrostephanus coronatus* (Nelson & Vance 1979) and *Diadema antillarum* (Carpenter 1984). In general, a homing strategy is thought to be advantageous when predation pressure is reduced by occupying a shelter site and when the availability of such sites is limited (Cook 1979, Nelson & Vance 1979). Shelter-centric homing behaviour is frequently observed in conjunction with nocturnal patterns of activity as a defence against predation during daylight hours (Ogden et al. 1973, Nelson & Vance 1979, Bernstein et al. 1981, Hereu 2005). The reasons for homing and nocturnal foraging observed in *C. rodgersii*, however, may be less clear. The principle predator of *C. rodgersii* in Tasmania is the rock lobster *Jasus edwardsii* (Johnson et al. 2005, Ling et al. 2009a), which is also a nocturnal forager, and thus a homing strategy and sheltering in crevices during the day is unlikely to confer any survival advantage against the threat of lobster predation. Importantly, the establishment of *C. rodgersii* in Tasmania is very recent (Johnson et al. 2005, 2011), and the sea urchins' behaviour may reflect that, historically at least, within its native NSW range, its major predator is the large diurnally foraging grouper *Achoerodus viridis* (Labridae) (see Andrew 1993). If so, then the persistence of nocturnal foraging and diurnal sheltering by *C. rodgersii* in Tasmania suggests that the behaviour is evolved and innate.

The only discernible differences in foraging patterns of *Centrostephanus rodgersii* between incipient and widespread barren habitats were in the absolute distance travelled in a time period (i.e. magnitude of net squared-displacement) and in the dominant movement 'type'. The 3 types of behaviour we considered were (1) random movement, fitting the RW model, (2) movement characterised by a return trip, i.e. the 'homers', and (3) those undertaking long-distance directional movement away from a starting position, possibly guided by some chemosensory stimulus. Directional movement was rare in incipient barren patches relative to in widespread barrens. Sea urchins within incipient barrens seem to adopt

local movement or random movement but within the boundaries of the patch, whereas urchins on wide-spread barrens habitat may adopt the full spectrum of movement types, including directional foraging. As with invariant nocturnal patterns in movement, there were no major differences in movement between incipient and widespread barrens, as might be expected if *C. rodgersii* exhibited the kinds of behavioural shifts demonstrated in strongylocentrotid sea urchins (Mattison et al. 1977, Dean et al. 1984, Lauzon-Guay & Scheibling 2007a, Scheibling & Hatcher 2007). Importantly, observations of homing tendency around localised shelter sites on wide-spread barrens over short time scales are consistent with our observations of high levels of site fidelity over much longer time scales, as evident from up to 45% recovery of chemically tagged individuals within unfenced 8 × 8 m areas on extensive barrens over a 14 mo time period (Ling & Johnson 2009).

Incipient barrens patches as 'isolated' systems

Most sea urchins monitored over 3 mo demonstrated high fidelity to incipient barrens patches, with their net dispersal over this entire period less than the mean distance travelled during a single night of foraging. Previous work has indicated that large sea urchins may be particularly motile in kelp bed habitats (Ling & Johnson 2009); however, the majority of tagged individuals that failed to be consistently re-located during our study were small, cryptic ones that persisted throughout the experiment but were less visible to divers. Net dispersal measurements are therefore biased toward larger and more motile sea urchins, and hence, our estimates of patch fidelity are likely to be conservative when considering the full range of cryptic and emergent size classes of the sea urchin. Observations of marked incipient barren patches in eastern Tasmania have indicated long-term persistence (2001 to 2011) of patches (S. Ling unpubl. data), but previously, it was unknown whether these patches were maintained by transitory individuals from the surrounding kelp bed and neighbouring patches or by sea urchins that largely remain resident within a given patch, as indicated by our results. Our observations reveal that individuals can cross the macroalgal boundary at the perimeter of patches, i.e. substratum discontinuities or abrasion by kelps sweeping the substratum (Andrew 1993, Konar 2000, Konar & Estes 2003) do not completely inhibit movement across the kelp–barrens interface. Hence, the ob-

served tendency of sea urchins to remain within patches suggests strong fidelity to patches rather than inhibition of movement beyond patch boundaries. Importantly, this fidelity effectively renders each incipient barren patch an isolated system independent of other patches.

Aggregative behaviour does not drive patch dynamics

The absence of locomotory responses of *Centrostephanus rodgersii* to food cues in the laboratory trials is consistent with *in situ* observations by divers and from time-lapse photography that urchins do not move toward or aggregate around attached kelps. Individuals may stop at a high-quality food patch whilst foraging, but they either appear not to detect chemosensory stimuli emitted from macroalgae or else do not respond to detected food cues with directional movement. This contrasts strongly with established models of strongylocentrotid foraging, which involves strong attraction to food and subsequent formation of aggregations, as has been demonstrated in both laboratory (Bernstein et al. 1983, Mann et al. 1984, Prince & LeBlanc 1992) and field (Mattison et al. 1977, Lauzon-Guay & Scheibling 2007a) experiments. Using a modelling approach, Lauzon-Guay et al. (2008) suggested that chemoreception may not be a necessary prerequisite to formation of strongylocentrotid urchin aggregations along the margins of kelp beds and that these aggregations could instead arise purely through random encounters. Using an extension of this model, Feehan et al. (2012) recently found that large stationary aggregations of urchins within cleared patches in kelp beds do not appreciably expand these patches, particularly on shallow or sheltered reefs, largely because they are supplied with drift algae and can access prostrate kelp fronds on the margins of patches. These findings contrast with an extensive body of literature on strongylocentrotid sea urchins based on both field observations (Breen & Mann 1976, Scheibling et al. 1999, Lauzon-Guay & Scheibling 2007a) and mathematical models (Lauzon-Guay et al. 2008, 2009) but, interestingly, appear to be more consistent with our own observations of *C. rodgersii* behaviour. A major difference, however, is the conspicuous absence of *C. rodgersii* feeding on drift algae, presumably because of an inability to effectively trap algae using tube feet on their aboral surface given their considerable spine length. The absence of a clear aggregation response of *C. rodgersii* to attached macroalgal food, in combi-

nation with their homing-like behaviour within patches and thus fidelity to particular patches, confers stability to incipient barren patches since feeding by sea urchins on macroalgae at the periphery of patches will only arise through random encounters.

Centrostephanus rodgersii was similarly unresponsive to stimuli from conspecifics despite a natural tendency to cluster and a contagious dispersion when translocated to seemingly homogenous reef habitat (S. Ling unpubl. data). Attraction to conspecifics as a potential mechanism by which formation of incipient barrens is initiated cannot be ruled out. However, chemosensory detection of conspecific cues does not appear to induce a locomotory response in *C. rodgersii*, and so the common observation of aggregated distributions around crevices in the field may instead be mediated via direct contact or, more likely, attraction to optimal local shelters (the importance of which has recently been demonstrated by Ling & Johnson 2012). The high frequency of sheltering behaviour of *C. rodgersii* in the field is consistent with the overriding tendency of large individuals in Y-maze experiments to remain stationary under laboratory conditions when their spine canopy spanned the diameter of the apparatus, mimicking a concave shelter (hence the decision to exclude these from analysis), and is indicative of the importance of crevice structure in determining local spatial patterns of sea urchin distribution (Andrew 1993).

An alternative model of sea urchin overgrazing

The behaviours of *Centrostephanus rodgersii* revealed in the present study, coupled with our general observations made over thousands of person hours of diving in the system, indicate the likely mechanisms of widespread barren formation. Broad similarities in foraging behaviour across the range-extension region and thus all stages of barren development, from incipient to widespread barren, on all substratum types suggest no evidence of a distinctive behavioural shift leading to overgrazing by exposed individuals as has been described in other barren-forming sea urchins (e.g. Dean et al. 1984, Harrold & Reed 1985, Vadas et al. 1986). The fidelity of individual *C. rodgersii* to their particular incipient patch is strong, macroalgal cues do not stimulate movement across the kelp-patch interface, and in particular, the aggregative behaviour thought to precipitate the formation of feeding fronts in strongylocentrotid sea urchins (Mann et al. 1984, Dumont et al. 2007, Lauzon-Guay & Scheibling 2007a) is conspicuously absent. As a result, individual

incipient barren patches are highly stable, and each patch effectively behaves independently. The detailed behavioural observations and patch size dynamics presented here are consistent with broad-scale data from our general observations over several 100 km of coastline which suggest that the size of individual barrens patches increase as a linear function of sea urchin abundance, that density within patches is remarkably consistent (at 1 urchin per ~0.6 m² of barrens area) and that eventual widespread barrens occur through the simple process of patch formation, expansion and eventual coalescence of multiple patches. Interestingly, this very mechanism has recently been suggested as a possible alternative behavioural model for *Strongylocentrotus droebachiensis* (Feehan et al. 2012); however, this is yet to be demonstrated experimentally in an unmanipulated strongylocentrotid system. The position and size of any particular *C. rodgersii* barrens patch is dictated by the individual grazing efforts of sea urchins contained within it, and for a given overall density, the local spatial distribution of the urchins is strongly influenced by the availability of shelter. Similarly, the likelihood of initial patch formation is also a direct consequence of local sea urchin density, and thus the distribution of sheltering sites, within a macroalgal bed (see Lauzon-Guay & Scheibling 2010). Thus, it appears that increases in population density of *C. rodgersii* across a reef manifest as an increased number of discrete incipient barren patches that, as they grow by the recruitment and grazing activity of additional urchins, eventually coalesce to form widespread barrens habitat from the 'inside out'. This pattern, underpinned by high fidelity to patches and a homing tendency irrespective of habitat, sea urchin density or stage of barrens formation across the range-extension region suggests that regulation of urchin density at the spatial scale of individual patches will reduce the likelihood of widespread barrens formation.

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