COMMUNITY ECOLOGY – ORIGINAL RESEARCH

Drift-kelp suppresses foraging movement of overgrazing sea urchins

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Abstract

Sea urchins have the capacity to destructively overgraze kelp beds and cause a wholesale shift to an alternative and stable 'urchin barren' reef state. However, destructive grazing appears labile and contingent on behavioural shift. Changes in supply of allochthonous 'drift-kelp' food are hypothesised as a trigger of change in urchin grazing behaviour, yet field tests are lacking. Here we conduct a suite of in situ behavioural surveys and manipulative experiments within kelp beds and on urchin barrens to examine foraging movements and evidence for a behavioural switch to an 'overgrazing mode' by the Australian urchin *Heliocidaris erythrogramma* (Echinometridae). Tracking urchins using time-lapse photography revealed urchin foraging to conform to a random walk model within kelp beds and on barrens. However, many individuals tended towards local movement within proximal crevices and movement was reduced in kelp beds compared to barrens. Directional movement of urchins toward newly available kelp was experimentally inducible, consistent with locally observed 'mobile-feeding-fronts' that develop at barrens-kelp interfaces. Habitat-specific feeding modes were also evidenced by herbivory assays which revealed urchin grazing rates to be high on both drift-kelp and standing kelp on barren grounds, while drift-kelp but not standing kelp was consumed at high rates within kelp beds. Time-lapse tracking of urchin foraging before/after addition of drift-kelp revealed a reduction in foraging across the reef surface after drift-kelp capture. Collectively, results indicate that the availability of drift-kelp is a pivotal trigger in determining urchin feeding modes which thus mediates the shift between alternative stable states for rocky reef ecosystems.

Keywords Kelp beds · Urchin barrens · Regime-shift · Foraging behaviour · Movement

Introduction

Herbivory can be a pivotal 'top-down' process controlling the abundance of primary producers and consequently the diversity of plants and animals within an ecosystem (Lubchenco and Gaines 1981). The behaviour of herbivorous animals can, therefore, be a highly important determinant of ecosystem structure and can be locally diverse and species-specific (Ogden and Lobel 1978; Preen 1995; Fox

and Bellwood 2013; Tennant and MacLeod 2014). Typically, feeding behaviour shows plasticity, enabling species to cope with spatiotemporal variability in their environment arising from seasonality (Fehmi et al. 2002; Sokos et al. 2015), geographic variability (Lundberg and Golani 1995), and local environmental conditions (Berner et al. 2005).

In sub-tidal marine environments, sea urchins can display plasticity in foraging behaviour, sometimes actively foraging and overgrazing kelp beds (reviewed by Ling et al. 2015). However, at other times and places sea urchins inhabit kelp beds at densities sufficient to cause destructive grazing and yet coexist with standing kelps without deleterious effects (Harrold and Reed 1985; Contreras and Castilla 1987; Vanderklift and Kendrick 2004). In instances where high sea urchin density does not result in overgrazing, a high prevalence of 'passive' feeding by urchins on detached 'drift-kelp', either generated from the natal kelp bed (autochthonous) or from distant allochthonous sources (Vanderklift and Wernberg 2008), has long been suggested as a proximate driver of sea urchin behaviour mediating the overgrazing

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collapse and/or alternatively the recovery of kelp beds (Harrold and Reed 1985). Despite observational studies describing modes of 'active foraging' on standing kelp vs. 'passive feeding' on detached drift-kelp (Dean et al. 1984; Harrold and Reed 1985; Andrew 1993), the mechanisms involved in triggering the switch between 'active' and 'passive' modes has not been critically appraised.

The behaviourally complex 'barrens-forming' sea urchin *Heliocidaris erythrogramma* (Valenciennes, 1846; Family: Echinometridae) represents one of the most wide-spread and ecologically important species in temperate Australia, occurring from Shark Bay, Western Australia, through to the central coast of New South Wales and throughout Tasmania (Edgar 1997). Across its range, *H. erythrogramma* is variably associated with overgrazed urchin barrens and experimental studies examining the grazing impact of this species have revealed conflicting results regarding the capacity of this species to form and maintain barrens, such that this urchin has been referred to as an enigmatic grazer (Ling et al. 2010). In experimental studies, *H. erythrogramma* has been observed to display two contrasting foraging modes: (1) 'passive' feeding on drift-kelp predominately captured from within crevices (Vanderklift and Kendrick 2005; Valentine and Johnson 2005); (2) 'active' overgrazing of standing kelps across the reef surface (Constable 1989; Ling et al. 2010; Kriegisch et al. 2016, 2019; Reeves et al. 2018).

Here we use a combination of survey and manipulative field experiments to explore foraging patterns and processes underlying passive and active foraging and the switch between these modes. Specifically, we address the role of drift-kelp supply in modulating destructive sea urchin grazing by tracking urchin foraging using time-lapse monitoring in combination with a suite of manipulative experiments to address the sub-questions: (1) does urchin movement differ spatially and between barren grounds and kelp bed habitats?; (2) does *H. erythrogramma* detect and actively move towards kelp when available?; (3) do feeding rates on drift-kelp vs. standing kelp differ between barren grounds and kelp bed habitats?; and (4) does a critical change in urchin foraging behaviour occur once drift-kelp has been captured?

Materials and methods

Study location

The study was carried out in the semi-enclosed coastal environment of Port Phillip Bay (PPB) in SE Australia (Fig. 1), where *H. erythrogramma* is the most influential herbivore on shallow rocky reefs and demonstrates both 'passive' (feeding on drift-kelp) and 'active' (feeding on standing kelp) forms of foraging. To assess urchin foraging

Fig. 1 **a** Map of Port Phillip Bay Victoria, southeast Australia. Dotted lines in expanded view indicate distinct zonation of PPB reefs into the west, north, southeast and southwest (after Johnson et al. 2015); presence of kelp beds and/ or sea urchin barren grounds is indicated. Study reefs were located at Kirk's Point—western zone (S38°1′35.742″, E144°34′58.5516″), Williamstown—northern zone (S37°52′10.5564″, E144°53′36.4884″), Schnapper Point—southeast zone (S38°12′47.8836″, E145°1′56.517″) and Governor Reef—southwest zone (S38°9′8.6106″, E144°143′39.5076″). **b** Example images of time-lapse plots in kelp beds and urchin barrens in northern PPB, both images zoomed to a width of 60 cm
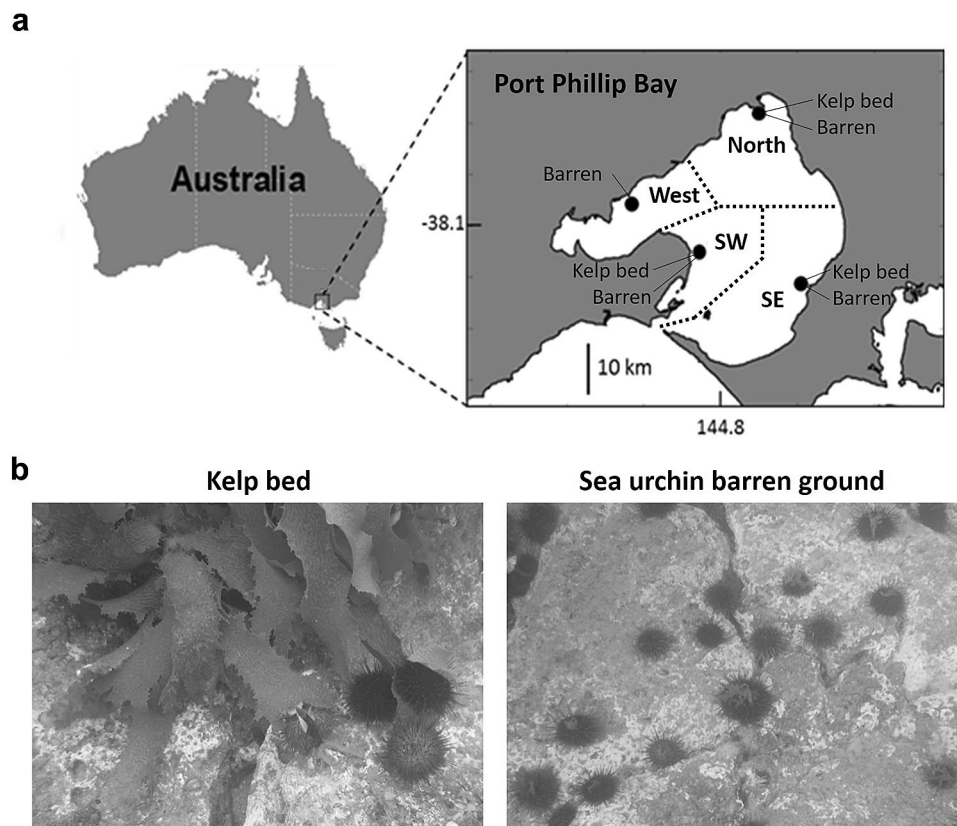
dynamics, movement was examined across four zones of PPB with distinct reef environments (Fig. 1). The zones represented a gradient in urchin overgrazing impacts from relatively small barrens patches of 10–100 s m^2 within kelp beds typical of southern zones, to extensive 'continuous' barrens stretching over 100,000 s m^2 of sub-tidal reef in northern and western zones (Johnson et al. 2015). In the west, kelp beds are essentially absent except for the occasional local presence of the ephemeral introduced Japanese kelp *Undaria pinnatifida*. In the north, kelp beds predominantly feature *Ecklonia radiata* and *U. pinnatifida* with only sparse growth of fucoid species (*Sargassum* spp. and *Cystophora* spp.) whereas in the southern zones kelp beds show more fucoid algae and a rich understory. The underlying reef substratum was consistent across all zones, occurring as mixed boulder/flat rock reef interspersed by sand patches to a depth of 5.5 m.

Time-lapse tracking of urchin movement in different zones and habitats

Movement of *H. erythrogramma* was assessed using time-lapse photography. Initial pilot studies were conducted during both day and night in the north and southeast to assess evidence for diel shifts in movement activity. Four Panasonic Lumix cameras (model FT4 with underwater housing) were attached to 1.5 m tall tripods and held square over the reef surface achieving approximately ~1.0 m by ~0.7 m field-of-view (FOV). Cameras were set to "time-lapse shot" mode with auto flash on. Images taken under low light conditions and at night were exposed to the cameras' flash which, at a frequency of 15 min, has previously been shown to have no measurable effect on propensity for urchin movement (Flukes et al. 2012). Time-lapse photography conducted on urchins during the day and night (night: 4 replicates; day: 5 replicates) revealed no significant differences in urchin movement between day and night across zones (Table 1a). Therefore, all subsequent monitoring of urchins was performed during daylight hours, which increased ease of camera deployments and retrievals.

To examine movement of urchins across zones and between kelp beds and extensive barren grounds, time-lapse cameras were deployed during the period summer 2012 to summer 2014 in the western, northern and southeastern zones of PPB (Fig. 1). In this experiment, the frequency of photographs for each monitored field-of-view (FOV) was increased to every 5 min and each sequence was 5 h in total duration (i.e., 60 images for each sequence). This was done to capture finer scale temporal changes in direction and speed of individual urchins between habitats. Sequences were captured in each zone, and in both kelp bed and barrens habitat if both habitats were present within each zone. Six replicate time-lapse sequences (i.e., experimental 'plots') were obtained for each habitat and in each zone during the 2 years (i.e., $n = 30$

Table 1 ANOVA tests comparing *Heliocidaris erythrogramma* movement speed (i) and displacement (ii) for (a) day vs. night (speed only), (b) barren grounds across different zones of Port Phillip Bay (day only), and (c) kelp bed vs. barren grounds across zones where both habitats occurred (day only)

	df	MS	Denominator for *F*-ratio	F	p
(a) Diel comparison (speed only)					
Zone (Z)	1	1.15	Plot (Z×T)	3.01	0.14
Time (T)	1	0.44	Plot (Z×T)	1.27	0.35
Zone×time	1	0.02	Plot (Z×T)	0.04	0.85
Plot (Z×T)	**5**	**0.19**	**Error**	**3.39**	**< 0.05**
Error	54	0.05			
(b) Zone comparison (barrens only)					
(i) Speed					
Zone	**2**	**415.48**	**Plot (Zone)**	**10.62**	**< 0.01**
Plot (Zone)	**15**	**39.11**	**Error**	**4.49**	**< 0.001**
Error	257	8.27			
(ii) Displacement					
Zone	**2**	**35.76**	**Plot (Zone)**	**20.60**	**< 0.001**
Plot (Zone)	**15**	**1.73**	**Error**	**1.73**	**< 0.05**
Error	241	0.01			
(c) Zone by Habitat (kelp beds vs. barrens)					
(i) Speed					
Zone (Z)	1	18.25	Plot (Z×H)	1.99	0.17
Habitat (H)	**1**	**136.05**	**Plot (Z×H)**	**14.87**	**< 0.001**
Zone×Habitat	1	13.58	Plot (Z×H)	1.48	0.24
Plot (Z×H)	**20**	**9.15**	**Error**	**3.39**	**< 0.001**
Error	160	2.70			
(ii) Displacement					
Zone (Z)	1	6.80	Plot (Z×H)	4.29	0.05
Habitat (H)	**1**	**1.86**	**Plot (Z×H)**	**11.83**	**< 0.01**
Zone×Habitat	1	0.11	Plot (Z×H)	0.70	0.41
Plot (Z×H)	**20**	**0.16**	**Error**	**0.16**	**< 0.01**
Error	152	0.07			

Transformations used were (a) speed: $Y^{0.5}$, (b) speed: $Y^{-1.3}$, displacement: $Y^{-0.1}$, and (c) speed: Y^{-1}, displacement: $Y^{0.4}$; values in bold indicate significant effects at $\alpha = 0.05$

sequences in total for the experiment). Each experimental 'plot' was photographed on a unique patch of reef to maintain independence of replicate samples. The criteria for identifying suitable plots for time-lapse sequences were that the reef had low topographic relief with high densities of urchins that could be squarely framed within the camera's FOV. For kelp bed plots, a kelp cover of > 25% (i.e., *Ecklonia radiata*) was required, whereas barren ground plots were composed of 0% cover of standing kelp or other macroalgae. Within suitable habitat, random fin kicks (ranging 5–25) were used to randomise plot positions. For each plot, an object of known dimensions was photographed to enable calibration of the dimensions of the FOV for each image sequence.

Time-lapse image sequences were imported to *ImageJ* (v1.47, National Institutes of Health, USA) and the FOV was calibrated for each sequence. The 'Manual Tracking' plugin for *ImageJ* was used to track the position of urchins through time. Individual paths were divided into a series of steps, stops and moves. A step was defined as the vector connecting successive positions (5 min apart), a stop as an interval in which an individual remained stationary for at least two frames (10 min) and a move as the vector between two 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 (after Flukes et al. 2012).

The moving speed (cm min^{-1}) and net displacement from start to end of each time-lapse sequence (cm 3.75 h^{-1}) was calculated for individual urchins within each independent plot, i.e., FOV. Moving speed was taken as the average speed of an individual over the 3.75 h, while displacement was calculated as the straight-line distance displaced from start to end of an individual urchin's track during this time. The time period of 3.75 h was chosen as it was the maximal duration for which 95% of all tracked urchins remained within the camera FOV. The number of urchins trackable within this time period within each FOV (i.e., time-lapse plot) ranged from two (southeast, kelp) to 45 individuals (west, barrens). To assess variability in urchin movement rates (average speed, displacement) on barren grounds across zones within PPB, a one-way nested analysis of variance (ANOVA) was undertaken with factors 'Zone' (fixed, 3 levels: west, north, southeast) and random effect of 'Plot' (nested within 'Zone').

The effect of habitat type on urchin movement was analysed across north and southeast zones (where both barrens and kelp habitat were present). Urchin speed and displacement were tested using a two-way nested ANOVA on the factors 'Habitat' (fixed, 2 levels: barrens vs. kelp), 'Zone' (fixed, 2 levels: north vs. southeast), and the 'Habitat' by 'Zone' interaction, plus additional exploration of the random effect of 'Plot' (nested within 'Habitat' × 'Zone'). Where data were heteroscedastic, the transformation used to stabilise variances was determined using the Box-Cox procedure (available in the MASS package). Note that the potential effect of seasonal timing on urchin movement was unimportant as water temperature (over range of 11.3–23.4 °C) had no detectable effect on urchin movement rate across habitats and zones (linear regression of urchin speed vs. temperature: $R^2 < 0.01$, $F_{1,28} = 0.034$, $p = 0.99$; with nil interactive effects between temperature and zone, temperature and habitat, or temperature by habitat by zone; min. p value = 0.55).

Testing movement patterns against a random walk model

To characterise movement types of *Heliocidaris erythro-gramma*, observed movement paths within daylight hours were compared with paths simulated by an established walk model. Here we initially explored movement using the saturated correlated random walk model of Kareiva and Shigesada (1983) but found the distribution of observed *H. erythrogramma* turning angles to be uniform (i.e., the mean cosine of angles was not significantly different from 0). Therefore, the model used for analysis was by definition reduced to a simple random walk (RW) equation:

$$R_n^2 = nm_2$$

where R_n^2 is the net-squared-displacement of an urchin path composed of n moves, and m_2 is the mean of the squared move length. Given 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 (see Turchin 1998; Conradt and Roper 2006). The presence of first-order autocorrelation between successive move lengths was also tested by Spearman rank tests (Zar 1999; Dumont et al. 2007).

Observed paths from within each habitat (pooling across zones was necessary to obtain sufficient number of individual movement paths with multiple steps) were compared with 1000 paths simulated by the RW model using the software MATLAB (v. 7.3.0) as described by Flukes et al. (2012). A sample size (n) of eight individuals was chosen as the minimum threshold for simulating the RWM. This meant that individual paths simulated by the RWM could have a maximum of eight moves per path (i.e., when data was pooled for barrens and kelp beds habitat, or 7 and 6 moves per path when barrens and kelp beds were simulated, respectively). 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; Turchin 1998; Manly 2006). The net squared-displacement ($\bar{R}_n^2$) 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 $\bar{R}_n^2$ fell outside the confidence intervals for at least half of all moves (Dumont et al. 2007).

Directionality of urchin movement towards newly available kelp

To examine whether *H. erythrogramma* moves directionally towards kelp (*Ecklonia radiata*), a 'choice' experiment was conducted in situ on barrens habitat (depth range 3–4 m) in the north of PPB during April 2014 (see Fig. 1, zone 2). Single urchins, situated on the top of large flat boulders (diam. > 2 m) were randomly chosen for use in the trials. Six dive weights were placed equidistantly at a radius of 200 mm around each selected urchin as it lay, i.e., the urchin was neither touched nor moved. The dive weights alternatingly held down pieces of kelp (*E. radiata*) and surrogate kelp (brown cloth) folded in half in such a way that the two free ends faced the urchin (Supplementary Information, Fig. S1). The cloth surrogate was similar in structure, colour and size to the *E. radiata* pieces. The dive weights were coated in epoxy and both the weights and surrogate cloth were pre-conditioned on the sea floor for 2 months prior to start of the experiment to mitigate potential effects of any unknown leachates. Hydrodynamic conditions were monitored with an additional dive weight holding a flexible piece of plastic tape 10 cm in length which was positioned just within the FOV of the camera. During all trials water movement was slightly tidal (< 1 m tidal range) either towards or away from shore, thus current flow was weak with maximal flow < 0.20 m s^{-1}.

To differentiate directional choice between natural vs. surrogate kelp, individual trials were monitored with time-lapse photography capturing images every 15 min. A monitoring period of 15 h per trial was chosen to ensure that any choice made by the urchin was recorded. A total of 11 replicate trials of different urchin individuals were conducted, all of which were started at midday. A 'choice' was recorded when the urchin moved to the kelp or to the surrogate and stayed at that position for more than 30 min (2 consecutive time-lapse images) or alternatively moved entirely out of the field-of-view, at which point the trial was deemed to have resulted in 'nil choice'. If kelp was chosen, the kelp was inspected for signs of urchin bite marks on the lamina to confirm that urchins were feeding on chosen kelp. Directionality of movement was assessable by visually tracking the movement of urchins between subsequent images. Typically, when kelp was chosen a period of stasis was followed by directional movement towards the kelp piece that was ultimately chosen. That is, urchins choosing kelp were observed to progress towards the kelp, albeit sometimes along a jittery path, but along a path that ultimately progressed towards the kelp over consecutive images. The kelp *E. radiata* was used as it is the dominant canopy-forming species across the range of *H. erythrogramma* and has been shown to be the urchins' preferred food (Hill et al. 2003; Vanderklift and Kendrick 2005; Kriegisch et al. 2019).

A Chi-square test was used to test the 'observed' vs. 'expected' frequency of directional movement towards and choice of 'kelp' vs. 'surrogate'. Statistical analysis for all experiments run in this study were undertaken using R (The R Foundation for Statistical Computing, Version 2.15.1, © 2012).

Consumption of drift-kelp vs. standing kelp in different habitats

A standardised assay of sea urchin herbivory over a 3-day period was used to compare rates and types of feeding behaviour of urchins on different types of kelp food sources on barrens and in *Ecklonia radiata* kelp beds, across the four different zones of PPB during March 2014. Following the protocol of Vanderklift and Wernberg (2008), assays in kelp beds and on barrens in the same zone occurred at a minimum separation distance of 50 m to ensure the urchin populations were independent based on maximum individual urchin movement over the assay period (i.e., max. movement speed observed in time-lapse indicates *H. erythrogramma* would move < 20 m over a 3-day assay period). Prior to the start of the assays, urchin population densities and biomass (m^{-2}) were defined for each habitat (Table S1) from a sample of eight randomly chosen replicate quadrats (1 m^2). Mean test diameter was estimated from $n = 10$ urchins in each zone and habitat and converted to biomass based on the relationship between test diameter and weight calculated for each zone/habitat (this relationship was determined from 48 to 90 urchins sampled randomly for each habitat/zone combination). Pieces of kelp were tethered to metal chains to simulate the 4 different types of kelp food sources (standing kelp on the benthos, drift-kelp on the benthos, the canopy of standing kelp elevated away from the substratum, and caged kelp as a control). To mimic standing kelp on the benthos accessible to sea urchins (and any other benthic herbivores), kelp pieces were fastened directly to the chain with clothes pegs. For simulation of drift-kelp, light nylon monofilament fishing line was attached to the chain and a piece of kelp was held in place by a clothes peg at the other end of the fishing line. To quantify the grazing impact of fish on kelp, pieces of kelp were fastened as per mimicking drift-kelp, but additionally with a float so that the kelp lamina floated at canopy height and was not accessible to urchins. To account for loss of algae due to tissue degradation and erosion (i.e., the 'control' treatment), another set of kelp pieces were fastened directly to the chain and protected with small plastic cages of mesh size 5 mm. Given the short duration of the experiment it was assumed that the lightweight cages had no effect on the kelp pieces within them. Each treatment had 12 replicate assay units, i.e., 48 pieces of algae in total per habitat/site combination.

The standardised kelp pieces used in the assays, i.e., 50 mm lengths of clean healthy lateral frond tissue of *E. radiata* with no visible epiphytes, were freshly harvested on the day of the experiment. To determine kelp loss over the 3-day duration of the assay, kelp pieces were photographed both prior to and at the conclusion of the assay. Kelp pieces were held flat by pressing the sample between a clear Perspex sheet and an opaque sheet and photographed. The change in kelp area was calculated using the software *ImageJ* as a proxy to estimate rates of consumption (the area of the 'control' pieces did not change over the course of the experiment). To convert consumption rates as planar area to biomass, ten standard 50 mm length kelp sections were taken to the laboratory, photographed and wet weights measured to calculate biomass per unit area. Since residual amounts of the kelp pieces remained clamped between the jaws of the clothes pegs (i.e., where grazers could not access), this small area (defined by the peg jaws) was subtracted from the overall area of the standard kelp piece for calculation of consumption.

Consumption rates of standing versus drift-kelp treatments were compared between habitat using the mean consumption of kelp pieces for three replicate kelp beds (in northern, southeast and southwest zones of PPB) and four replicate barrens (i.e., north, west, southeast and southwest zones). There was no detectable change in the area of the kelp pieces in cages (controls) or those elevated off the substratum in the canopy (where they were exposed only to herbivorous fishes), therefore, these treatments were excluded from the overall analysis. A two-way ANOVA was used to determine the effects of 'Treatment' (fixed, two levels: drift- kelp vs. standing kelp) and 'Habitat' (fixed, two levels: kelp, barrens) on the loss of kelp biomass (wet weight day^{-1}) through grazing.

Sea urchin behavioural switch upon capture of drift-kelp

The change in activity of *Heliocidaris erythrogramma* associated with the presence of drift-kelp was monitored using time-lapse photography. The experiment was implemented as a before–after control-impact (BACI) design, whereby urchin movement within a total of eight plots of ~ 0.6 m^2 on barrens habitat (Fig. 1, zone 2) was monitored before and after the addition of drift-kelp to treatment plots ($n = 4$). There were an identical number of control plots to which no drift-kelp was added. The number of urchins within each plot was similar, ranging from 8 to 13 individuals. The experiment was conducted during October 2014, with the BACI design involving an initial 4 h of tracking before the drift-kelp treatment was added and then a subsequent 4 h of tracking following the

application of kelp. The treatment involved gently placing drift-kelp so that it touched sea urchins within the FOV of the camera and within a 0.5 m buffer zone surrounding the camera FOV. Upon detection of the drift-kelp (a fresh cut lateral of *E. radiata*), urchins invariably extended their tube feet and seized the piece, which typically took on the order of 10 s. Speed of sea urchins was calculated from time-lapse imagery (see above sections) and used for analysis. While net displacement was also calculated it was highly correlated with speed ($R^2 = 0.76$, $F_{1,27} = 87.45$, $p < 0.001$, transformation: $Y^{0.3}$) and thus provided no additional information.

The experiment tested the effect of 'Treatment' (control and drift-kelp treatment groups) and 'Period' (before vs. after addition of drift-kelp) on speed of urchin movement (cm min^{-1}). Data were subject to a two-way nested ANOVA with the factors 'Treatment' (fixed, 2 levels: treatment vs. control), 'Period' (fixed, 2 levels: before vs. after), the 'Treatment' by 'Period' interaction; variability at the 'Plot' level (random effect nested within 'Treatment' by 'Period') was also examined. Where data were heteroscedastic, the transformation used to stabilise variances was determined using the *Box-Cox* procedure (available in the MASS package). Multiple comparisons (Tukey's HSD) were conducted using the means of each plot.

Results

Time-lapse tracking of urchin movement in different zones and habitats

A total of 367 sea urchins were tracked using time-lapse photography across three barrens and within two kelp beds (Table 1). Time-lapse monitoring of sea urchins on barren grounds revealed significant differences between the three PPB 'zones' in terms of average speed and net displacement (Table 1b, Fig. 2a). Urchins in the northern zone of PPB showed the highest average speeds and net displacements, followed by those in the southeast and then the western zone (Table 1b, Fig. 2a). Scaling to daily rates, mean urchin speed on barren grounds was 0.7, 1.1 and 2.4 m day^{-1} across western, southeast and northern barrens, respectively. Following the same rank, daily displacement of urchins on barren grounds was 0.14, 0.20 and 0.79 m day^{-1} for western, southeast and northern barren grounds, respectively. There were also significant differences in both speed and displacement among plots within the same zone, indicating that urchin movement varies on a small spatial scale (10 s of meters) across individual barren grounds.

Time-lapse monitoring also revealed a significant effect of habitat on sea urchin movement, with urchins showing
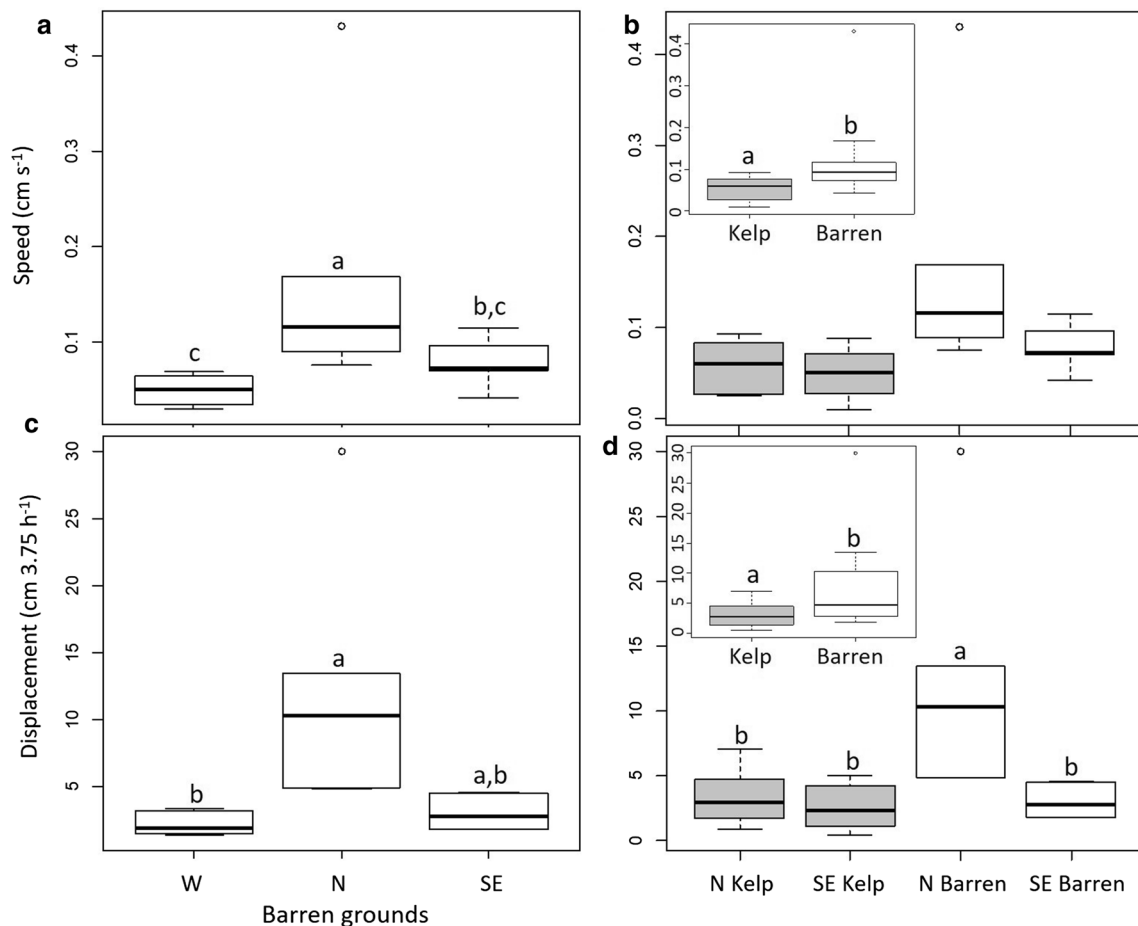
Fig. 2 Comparison of mean sea urchin movement speed (cm min^{-1}) as measured by time-lapse photography across **a** three zones of PPB (barren grounds only) and **b** kelp bed (grey-filled boxes) vs. urchin barrens (open boxes); and mean displacement (cm 3.75 h^{-1}) for **c** three zones of PPB (barren grounds only), and **d** kelp bed (grey-filled boxes) vs. urchin barrens (open boxes). Inset plots in **b** and **d** show differences between habitats pooled across zones given a lack of significant zone by habitat interactions. Boxplots were generated from mean sea urchin movement within $N=6$ time-lapse sequence plots per zone/habitat combination. Boxes sharing the same letters are not significantly different (Tukey's HSD, $\alpha = 0.05$)

significantly greater speed and displacement on barrens than within kelp beds (Table 1c, 'Habitat comparison', Fig. 2b). Furthermore, this effect was consistent across the north and southeast zones (where both kelp and barrens habitats were available), and significant differences in speed and displacement also occurred among plots within the same habitat and zone (Table 1c). Calculating daily averages, *H. erythrogramma* on barrens moved at a speed of ~1.8 m day^{-1} compared to a speed of ~0.8 m day^{-1} within kelp beds. Urchins on barrens also displaced further from their starting location approx. ~0.5 m day^{-1} compared to reduced displacement on kelp beds at ~0.2 m day^{-1}.

Indicating the relative intensity of grazing across the reef, the sum total of displacement of all urchins within a time-lapse monitored plot was positively correlated with increasing density of urchins within each habitat/zone of PPB (Figure S2a–e); while the overall relationship across all habitats and zones was suggestive of a hump-shaped distribution (Figure S2f). In contrast to patterns in displacement, trends in the speed of urchin movement were less clear with increasing urchin density; with generally nil apparent trends with increasing urchin density on barrens (Figure S3a, c, e), but a trend of increasing speed with increasing urchin density within kelp beds (Figure S3b, d) and again evidence for a humped shape trend in speed versus density when all habitats and zones were combined (Figure S3f).

Testing movement patterns against random walk model

Of all the sea urchins tracked across different habitats and zones, 96 paths (28 from kelp beds and 68 from barrens) were composed of at least three moves and were thus appropriate for use in the random walk analysis. Despite a high level of variability in movement parameters between individuals, relationships between the mean observed net-squared-displacement and the predicted net squared-displacement

of the random walk model (RWM) were broadly similar across habitats (Fig. 3). At the individual level, more urchins showed a tendency towards localised movement (i.e., intentionally staying close to home crevice) as opposed to directional movement (Table 2), but when averaged across multiple individuals this collectively conformed to the RWM
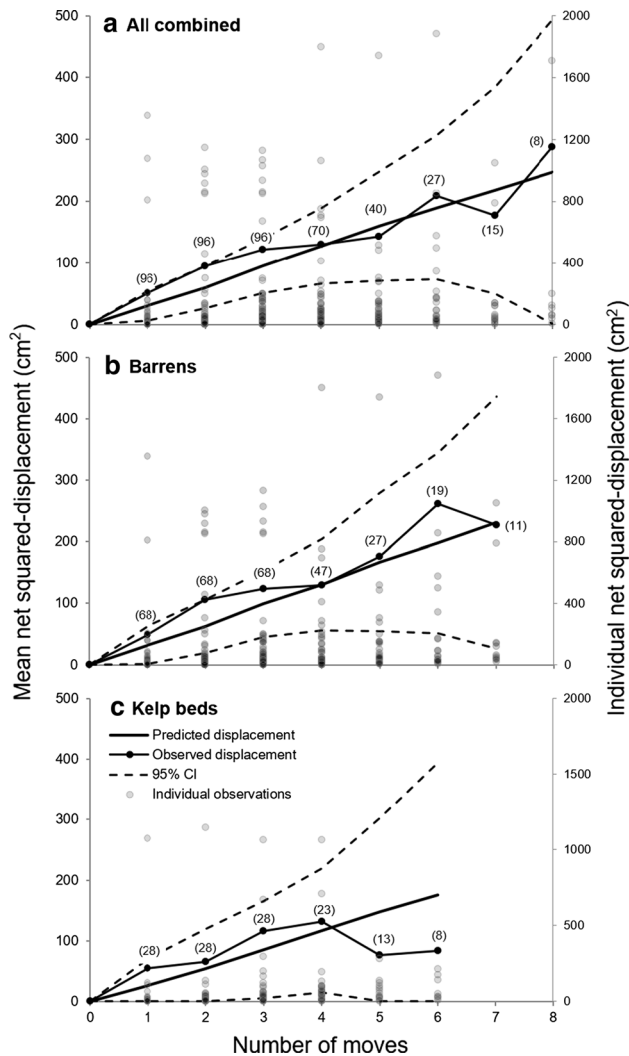
Table 2 Relative frequency of *Heliocidaris erythrogramma* individual movement types in kelp beds and barrens, plus both habitats combined

Habitat	n	Random (%)	Directional (%)	Local (%)	Undetermined (%)
All combined	96	14	17	59	10
Barrens	68	26	12	51	10
Kelp beds	28	89	7	0*	4

The number of tracks observed overall or in each habitat is given by (*n*). Movement type of a given track is classified depending on the proportion of moves within the track that fall above, below or within the confidence limits of random walk model predictions. Sea urchins are classified as directional, local or random movers for tracks where at least half of all moves fall above, below, or within model confidence limits, respectively. Paths were classified as undetermined where the same number of moves were assigned to multiple movement types (e.g., 4:4 for a path of 8 moves)

*Note that given the breadth of lower confidence interval for kelp beds, classification of local movement for this habitat (i.e., moves occurring below lower confidence limit) was not possible

Fig. 3 Examination of *Heliocidaris erythrogramma* movement relative to predictions of a random walk model for populations from **a** all combined, **b** barrens, and **c** kelp beds. Mean net squared-displacement is calculated over a minimum of 8, 7, and 6 consecutive moves for (**a–c**), respectively, from predicted (solid line) and observed (closed circles) movement paths. Paths were only simulated where at least *N*=8 urchins were observed to make that many moves [numbers in parentheses above the closed circles indicate the number (*N*) of observed individuals making the specified number of moves; note for 'all combined' 8 individuals made 8 moves: 5 from barrens and 3 from kelp beds]. Grey semi-transparent symbols represent individuals which are plotted relative to the extended secondary *y*-axis. Dashed lines are 95% confidence limits for the predicted net squared-displacement based on a random walk

predictions of 'random' movement (Fig. 3). Due to the low sample size of urchins in kelp beds (caused largely by the FOV being obscured by kelp), the confidence intervals were large and as a result local movement behaviour of individuals could not be statistically detected (as the lower CI is effectively zero; Table 2; Fig. 3c). However, urchins in kelp beds (Fig. 3c) did, on average, remain in closer proximity to a home crevice than those on barren grounds (Fig. 3b).

Directionality of urchin movement in the presence of newly available kelp

In 10 out of 11 instances, individual sea urchins moved directly towards the kelp pieces. Only one urchin was observed to move past available kelp pieces and out of the FOV entirely 2 h after the trial commenced. Typically, urchins choosing kelp showed a period of initial stasis followed by directional movement towards the kelp piece that was ultimately chosen. That is, urchins choosing kelp were observed to progress towards the kelp, albeit sometimes along a jittery path, but along a path that ultimately progressed towards the kelp over consecutive images. The duration of time before kelp pieces were actively intercepted by urchins choosing kelp varied from 0:59 to 15:02 h (average 4:26 ± 1:24 SE h). This highly significant choice (x^2 test: $F_1 = 7.36$, $p = 0.007$) indicates that *H. erythrogramma* can sense *E. radiata* and will move directionally towards it and consume it. That is, in seven of ten trials where urchins chose kelp, graze marks were observed on the kelp pieces when the urchin was removed from the kelp post-trial.

Consumption of drift-kelp vs. standing kelp in different habitats

Consumption rate was significantly higher for the drift-kelp than standing kelp and there was significantly greater over-all consumption of kelp on barrens than within kelp beds (Fig. 4a). Both standing kelp and drift-kelp were heavily consumed on urchin barrens, whereas drift-kelp pieces were preferentially consumed over standing kelp within kelp beds (Fig. 4a). Factoring for local urchin biomass (Table S1), there was still greater consumption of standing kelp and

drift-kelp per biomass of urchins on barrens than within kelp beds (Fig. 4b).

Sea urchin behavioural switch upon capture of drift-kelp

The speed of sea urchin movement in the control and drift-kelp addition treatment fields-of-view were similar before capture of drift-kelp (Fig. 5 "before drift-kelp addition"), whereas the speed of urchins in the treatment group after drift-kelp capture was significantly lower than the other periods/treatments (Fig. 5 "after drift-kelp addition").

Discussion

Movement patterns of urchins in different diel periods, zones and habitats

Initial exploration of *Heliocidaris erythrogramma* movement from time-lapse sequences revealed high variability in individual movement rates among local reef plots and a lack of distinct shift in activity between day and night as is frequently reported for diadematid urchin species (e.g., Flukes
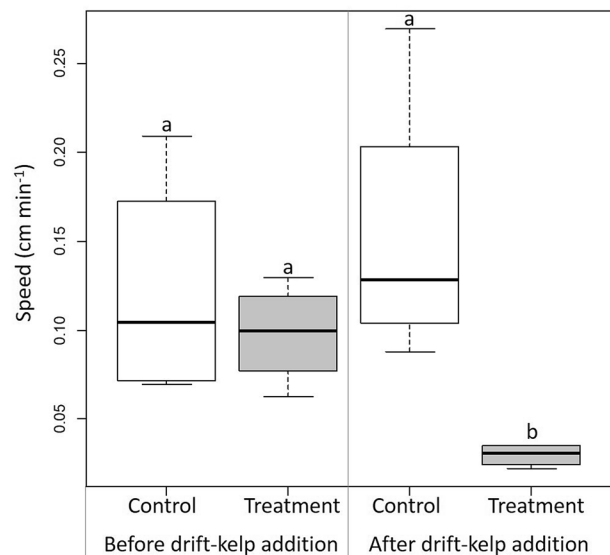

Fig. 4 **a** Consumption rate of kelp (g wet weight day^{-1}) after 3 days by treatment (standing kelp vs. drift-kelp) and habitat (kelp beds [grey-filled boxes] vs. barrens; two-way fixed-effects ANOVA (kelp beds $N=3$; barrens $N=4$), transformation: $Y^{-0.3}$, "Treatment", $F_{1,10}=6.38$, $p<0.05$; "Habitat", $F_{1,10}=36.54$, $p<0.001$; "Habitat by Treatment", $F_{1,10}=4.62$, $p=0.06$, different letters above box-whiskers indicate significant differences Tukey's HSD, $p<0.05$. **b** Consumption rates of kelp biomass by treatment and habitat expressed per local biomass of urchins (g wet weight kelp/g wet weight urchin day^{-1})

Fig. 5 Speed (cm min^{-1}) of sea urchins before and after capture of drift-kelp. Bars left-of-centre show the speed of the control group (open bar) and treatment group (grey bar) without drift-kelp, while bars right-of-centre show mean urchin speed in the control (no drift-kelp captured) and treatment groups in the period after addition of drift-kelp to the treatment urchins ($N=4$). ANOVA (transformation Y^{-1}) revealed a significant 'Treatment' by 'Period' interaction ($F_{1,12}=14.2$, $p<0.01$), and significant variation among plots within the same 'Treatment' and 'Period' ($F_{12,103}=2.45$, $p<0.01$). Boxes sharing the same letters are not significantly different (Tukey's HSD, $\alpha=0.05$)

et al. 2012). Despite inherently high variability in movement across local reefs, *H. erythrogramma* movement speed and displacement was observed to vary by a factor of ~3.3 and ~5.5 times across western, southeast and northern barren grounds. Examination of urchin movement for alternative kelp and barrens reef states revealed *H. erythrogramma* to move approximately half as much within kelp beds as on barren grounds. Similar contrasts in movement between these alternative states has been also reported for strongylocentrotid urchins on east and west coasts of North America (e.g., Harrold and Reed 1985; Dumont et al. 2007). On average, *H. erythrogramma* on barrens moved more rapidly and further from their starting location (i.e., greater net displacement) than within kelp beds, indicating enhanced foraging potential per unit area by urchins on barren grounds.

The reduced movement of urchins within kelp beds appears to be a response to rich local sources of food occurring in closer proximity, and/or the presence of drift-kelp facilitating increased stasis within crevices and catch drift with their tube feet (Harrold and Reed 1985; Konar and Estes 2003; Ling et al. 2019). However, urchins may also be prone to move less in kelp beds in response to the physical barrier provided by the kelp itself and/or the whip-lash effect of the kelp sweeping the substratum with their laminae under the action of ocean swell (Konar 2000), or because increased presence of predators within kelp beds causes urchins to seek and remain in crevices for longer periods (e.g., crustaceans and fish; Pederson and Johnson 2006; Ling et al. 2019). Ultimately, there is inherent risk of predation for exposed sea urchins and thus emergence from crevices to forage across the reef surface comes at a cost, even in the presence of relatively low predator abundance (Pederson and Johnson 2006; Ling et al. 2019). In the presence of high abundances of large predators and particularly in the absence of other prey items, sea urchins are rarely emergent on the surface of the reef and such emergent urchins are typically large and afford size-refuge (Ling and Johnson 2012, 2019).

Examination of *H. erythrogramma* movement with respect to local urchin density within time-lapse plots revealed a trend of increasing urchin speed and displacement with increasing urchin density. This suggests that not only will increasing density cause increased grazing, but that foraging movement of urchins on highly populated reefs will also accelerate with increasing density. However, limits to this relationship were suggested when data from all habitats and zones was examined together. That is, there was weak evidence for a hump-shaped trend whereby movement at extremely high urchin densities (>20 individuals m^{-2}, i.e., on the western zone barren ground) was reduced (Fig. S2f), likely due to local overcrowding as urchins were observed to frequently bump together in high density time-lapse sequences. Notably, such a decline in sea urchin movement at extreme densities has also been reported for *Strongylocentrotus droebachiensis* in Canada, where movement became increasingly reduced over the range from 30 to ~270 individuals m^{-2} (Dumont et al. 2007; Lauzon-Guay and Scheibling 2007).

Movement patterns of *H. erythrogramma* was examined relative to three modes: (1) random movement, fitting to a random walk model (RWM); (2) local movement characterized by outward and inward trips; and (3) long-distance directional movement away from a starting position, possibly guided by some chemosensory stimulus of kelp. On average, movement of *H. erythrogramma* conformed to the RWM when all movement paths were pooled or when analysed separately for barrens and kelp beds. Thus, at the scale of ~1 m^2 reef plots, the behaviour of *H. erythrogramma* is consistent with the predominantly random movement described for the northern hemisphere *Strongylocentrotus* species (Lauzon-Guay et al. 2006; Dumont et al. 2007). Similarly, *H. erythrogramma* also shares the same highly labile behavioural characteristics of the *Strongylocentrotus* genus by forming destructive and highly mobile-feeding aggregations that can sweep through kelp beds (Mattison et al. 1977; Lauzon-Guay et al. 2006; Dumont et al. 2007). Conversely, movement by *H. erythrogramma* contrasts strongly with the sympatric Australian sea urchin *Centrostephanus rodgersii* which exhibits highly nocturnal 'homing' movement (Flukes et al. 2012).

Examination of individual movement paths revealed a greater proportion of *H. erythrogramma* moved in a localized manner (although this was not detected when collectively averaged across multiple individuals; see above). Local movement suggests that *H. erythrogramma* either move in a restricted fashion in close proximity to particular focal points (i.e., 'home sites') or alternatively, demonstrate distinct outward and inward phases of movement, i.e., true homing behaviour. The broad conformance of observed movement with the predictions of the random walk model, in combination with observations of *H. erythrogramma* displaying erratic jittering movements around crevice 'home sites' in time-lapse sequences, suggests that *H. erythrogramma* foraging movements are loosely centred around 'home sites' as opposed to representing true homing behaviour. Homing behaviour among sea urchins is most typically observed among highly nocturnal diadematid sea urchin species that display en masse nocturnal emergence (Ogden et al. 1973; Nelson and Vance 1979; Bernstein et al. 1981; Flukes et al. 2012). In contrast, time-lapse monitoring showed *H. erythrogramma* to move consistently throughout the day with little apparent co-ordination between individuals. A movement mode centered on localised crevices is further supported by moderate levels of site fidelity over longer periods whereby rates of recovery for chemically tagged *H. erythrogramma* ranged from 6 to 16% after tagged individuals experienced 12 months of liberty on unfenced 30–60 m^2

plots across contiguous reef (> 100 s metres in length) where emigration could easily occur (Ling et al. 2019; see also Pederson and Johnson 2008).

Directional movement of urchins towards kelp

Time-lapse monitoring of *Heliocidaris erythrogramma* revealed evidence for random movement around crevice 'home sites', while manipulation of kelp presence demonstrated that urchins can show strong directionality in movement towards kelp. That is, over sub-metre scales *H. erythrogramma* can clearly sense kelp *Ecklonia radiata* as a food source and will actively move towards kelp to consume it. Few studies have distinguished between whether urchins can sense algae or whether they move randomly until they encounter food. Rodriguez and Farina (2001) manipulated drift-algae and observed the urchin *Tetrapygus niger* to form aggregations around drift-algae, suggesting that this species can also sense algal food sources and direct movement towards it. For *Centrostephanus rodgersii*, Y-maze experiments have indicated no directed movement towards *E. radiata* kelp, but rather a tendency for homing around any suitable crevice (Flukes et al. 2012). Thus, it would appear that the ability of sea urchins to sense food is species-specific and context-dependent, and in the case of *H. erythrogramma*, the capacity to sense and move towards kelp suggests that lack of available food near 'home sites' could trigger local-scale emergence from passive cryptic feeding to active foraging of standing kelps on the reef surface which was observed during time-lapse monitoring of urchins in kelp beds.

Kelp consumption rates in different habitats

The clear difference between consumption rates of standing kelp within kelp beds and on urchin barrens shown by our study supports the notion that in kelp beds, providing that drift-kelp is available, urchins will feed on drift without consuming standing kelp while on barrens the diminished food availability results in urchins feeding on any fleshy algae they encounter (Harrold and Reed 1985). Our finding is also consistent with that of Vanderklift et al. (2009) who conducted a similar experiment in kelp beds in Western Australia and found that *Heliocidaris erythrogramma* primarily consumed drift-kelp in kelp beds. However, it is possible that the higher kelp consumption rates on barrens may simply reflect higher local urchin biomass, but this was not the case in the current study as consumption rates of kelp were observed to be higher per unit biomass of urchin on barren grounds. Thus, the availability of drift-kelp within kelp beds and on barren grounds emerges as a key factor in understanding the spectrum of urchin feeding behaviours from benign foraging to destructive overgrazing.

Sea urchin behavioural switch upon capture of drift-kelp

The notion that decreased feeding on standing kelp is dependent on the availability of drift (Harrold and Reed 1985; Vanderklift and Kendrick 2005) was supported by the results of our manipulative field experiment whereby urchins became static and more cryptic upon the interception of drift-kelp. Similarly, in California Mattison et al. (1977) also observed *Strongylocentrotus franciscanus* feeding rates on drift-algae to decrease with increasing distance from kelp beds, whereas overall rates of movement increased with increasing distance from kelp beds. These authors postulated that decline in drift-kelp was the reason for increased movement because urchins would have to actively forage further to obtain food. Since then, various observational studies have described the relationship between movement and drift-kelp availability (e.g., Dean et al. 1984; Day and Branch 2002), however, studies manipulating drift-kelp are rare (but see Vanderklift and Wernberg 2008). The response we observed to manipulation of drift-kelp availability, in which urchins stopped upon capture of drift-kelp and retreated to local home sites, strengthens the notion that drift-kelp is a major determinate of foraging dynamics and thus a key controlling factor determining the propensity for destructive overgrazing by urchins.

Conclusions

The dynamic foraging traits of *Heliocidaris erythrogramma* evident in our experiments concord with patterns of grazing observed in this species across Australia (Vanderklift and Kendrick 2005; Wright et al. 2005; Vanderklift and Wernberg 2008; Ling et al. 2010). Our results support observations that *H. erythrogramma* shifts between distinct modes of movement, and only destructively overgrazes standing kelp on sheltered inshore reefs where drift-kelp supply is low (Ling et al. 2010), while the same densities of urchins are observed to have nil influence on the biomass of standing kelps on exposed offshore reefs with higher supply of drift-kelp (Vanderklift and Kendrick 2005; Vanderklift and Wernberg 2008). Our results are consistent with the notion that destructive grazing can be triggered by a decline in the availability of drift-kelp. We conclude that the presence of sufficient drift-kelp, either generated from autochthonous or allochthonous sources, can suppress urchin foraging movements and propensity for destructive grazing, thus ultimately increasing the resilience of local kelp beds to overgrazing. Conversely, as kelp beds undergo gradual decline, lower availability of drift-kelp will likely create a positive feedback accelerating the process of kelp bed overgrazing by sea urchins.

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