Density-dependent feedbacks, hysteresis, and demography of overgrazing sea urchins

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Abstract. Sea urchin grazing can result in regime shift from productive kelp beds to sea urchin barren grounds that represent an alternative and stable reef state. Here we examine the stability of urchin barrens by defining the demographics of the Australian urchin *Heliocidaris erythrogramma* during regime shift to, and maintenance of, barrens. Inverse-logistic modeling of calibrated *in situ* annual growth increments for five urchin populations, two from kelp beds and three from barrens, demonstrate slowing of urchin growth as availability and consumption of standing and/or drift kelp declines. Population age structures were predicted from observed sizes over four years (2012–2015, *n* = 5,864 individuals), which indicated stable age distributions for populations both maintaining barrens and actively grazing among kelp beds. Younger age distributions occurred on barrens whereas more mature populations existed within kelp beds, indicating that high recruitment facilitates maintenance of barrens while overgrazing appeared more reliant on adult urchins grazing from the edges of kelp beds, as opposed to juvenile recruitment among kelp. Leslie-matrix projections indicated potential for unchecked population growth for all study populations, but which varied depending on whether local or regional recruitment rates were modeled. Ultimately, strong density dependence was observed to check population growth; with high-recruitment/high-density populations offset by reduced growth rates and decreased longevity. Increasing disease rates among older urchins in high-density populations were consistent with observed density-dependent mortality, while tethering of healthy urchins revealed highest predation on small urchins within kelp beds, suggesting some remnant resilience of declining kelp habitat. Results demonstrate that the greatest opportunity for urchin population control is when reefs exist in the kelp bed state, at which point urchin populations are prone to negative feedback. Conversely, control of urchins on barrens is demonstrably difficult given positive density-dependent feedbacks that act to stabilize population size and which evidently underpin the hysteresis effect governing the persistence of this alternative stable state.

Key words: age; alternative stable states; catastrophic regime-shift; disease; growth; kelp beds; population dynamics; predation; sea urchin barrens; temperate reef ecology.

INTRODUCTION

Ecosystems are often conceptualized as stable configurations maintained by harmonic feedback cycles. In reality, such notions of the "balance of nature" appear noisy and highly dynamic as component species, and the biological checks-and-balances themselves, are prone to presses and pulses in environmental conditions. While this inherent noise challenges perceptions of ecosystem identity in space and time, biological communities appear to absorb perturbations and gravitate toward broad "basins of attraction" in configuration, at least until critical tipping points are exceeded (Holling 1973, May 1977).

Importantly, there is an emergence of examples from woodlands, arid lands, lakes, coral reefs, and oceans demonstrating persistence of reconfigured ecosystem states that appear to center on alternative "basins of attraction" even after environmental conditions are reversed to that observed during the existence of the original ecosystem state (Holling 1973, May 1977, Scheffer et al. 2001). Termed "catastrophic shifts," self-reinforcing feedback mechanism(s) of the reconfigured ecosystem state are thought to provide resilience to the new stable regime, with reversal back to the original state only possible if conditions are sufficiently reversed to a recovery tipping point (reviewed by Scheffer et al. 2001). Logically, it then follows that understanding the feedback mechanisms of altered unwanted stable states is central for attempts to overcome this inherent ecological hysteresis.

One of the most widespread and abrupt catastrophic shifts in nature is the transition from productive kelp

beds to an impoverished "barrens" reef state as a result of sea urchin overgrazing (reviewed by Filbee-Dexter and Scheibling 2014, Ling et al. 2015). Sea urchin barrens are characterized by decreased habitat complexity, biodiversity, and primary productivity relative to kelp beds (Lawrence 1975, Chapman 1981, Himmelman et al. 1983, Ling 2008). Shifts from kelp bed to barrens also causes decline in key reef fisheries, such as spiny lobsters and abalone, dependent on kelp habitat (Andrew and Underwood 1992, Strain and Johnson 2009, Johnson et al. 2011, 2013). Causes of sea urchin overgrazing varies across systems, but appears triggered by either environmental and/or trophic change (Tegner and Dayton 2000, Steneck et al. 2002, Ling et al. 2009a). Environmental change can facilitate large sea urchin recruitment events (e.g., Hart and Scheibling 1988, Ling et al. 2008, 2009b), while trophic change, observed to result via ecological overharvesting of sea urchin predators, can lead to urchin population increases in exceedance of overgrazing thresholds (reviewed by Steneck et al. 2002, Ling et al. 2015, Sheppard-Brennand et al. 2017).

Control measures to reduce sea urchin abundance and restore kelp beds and secondary productivity, have been pursued for as long as the urchin barrens phenomenon has been recognized (Leighton et al. 1966, Mann 1977). However, attempts to recover kelp following urchin overgrazing are challenging given the ecological hysteresis of this regime shift between alternative stable states (Filbee-Dexter and Scheibling 2014, Ling et al. 2015). That is, while many urchins may be required to overgraze in the first instance, very few are required to maintain the barrens once formed. The practicality of this hysteresis effect, estimated to be an order of magnitude in urchin biomass, is that nearly all urchins must be eradicated on barren grounds for kelp beds to recover (Ling et al. 2015). As a result, restoration efforts have typically only been successful when barrens occur at highly localized scales, i.e., tens to hundreds of square meters (Tracey et al. 2015, Sanderson et al. 2016, but see historical use of quicklime chemical control over thousands of square meters; Leighton et al. 1966).

While alternate collapse and recovery dynamics of kelp and barrens are now well documented (reviewed by Filbee-Dexter and Scheibling 2014, Ling et al. 2015), understanding the dynamics and feedback mechanisms of the urchin populations themselves during overgrazing and subsequent maintenance of barrens is less appreciated. The ability of urchins to persist on barren grounds has long intrigued ecologists and attracted much interest given the significant challenge it presents for population control (Lang and Mann 1976, Johnson and Mann 1988, Kenner 1992, Johnson et al. 2013). Two chief mechanisms are ostensibly capable of ensuring persistence of urchins on barrens, and govern the stability of this collapsed reef state: (1) diet switching, whereby urchin populations persist on barrens by shifting diet from nutritious kelp to filamentous and encrusting calcareous algal forms to effectively avoid "eating themselves out of house and home" (reviewed by Ling et al. 2015), and (2) increased recruitment of sea urchins on barrens whereby removal of kelp effectively "paves the way" for increase in population size by reducing predators existing within kelp beds and in removing mechanical whiplash by kelp on urchins under ocean swell, plus facilitation of ongoing recruitment due to high cover of encrusting calcareous algal substrates favored by settling urchin larvae (Breen and Mann 1976, Lang and Mann 1976, Konar and Estes 2003, Ling et al. 2009b, Hernández et al. 2010).

For both putative mechanisms of persistence, individual performance in terms of body condition, growth, survival, and per capita reproductive potential is predicted to decline due to density dependence; however, apparent persistence of urchin populations on barrens may emerge simply due to higher population turnover despite declines in individual performance.

Here we examine the mechanisms underpinning the stability of sea urchin barrens by defining the population dynamics of the overgrazing Australian sea urchin *Heliocidaris erythrogramma* (Echinometridae) during a shift to, and during maintenance of, barren grounds. This was achieved via the development of field-calibrated models of individual growth, which in combination with measurements of other critical life-history parameters including fecundity, recruitment, disease, and predation rates allowed the tracking/projecting of urchin demographics over multiple years at multiple sites. Scaling life-history parameters by population abundance, both negative and positive population-level feedbacks are revealed that respectively counteract or promote overgrazing, with positive feedback evidently acting to underpin the hysteresis effect of overgrazing which limits opportunities for urchin population control.

METHODS

Study populations

The temperate Australian sea urchin *Heliocidaris erythrogramma* can cause extensive overgrazing of kelp beds on southeastern Australian reefs (Wright et al. 2005, Ling et al. 2010, Kriegisch et al. 2016, Reeves et al. 2018). Across its range, highest population densities of *H. erythrogramma* occur within Australia's largest embayment, Port Philip Bay (Fig. 1a), where the urchin achieves densities on local rocky reefs up to ~60 individuals/m^2 and where it has caused catastrophic overgrazing (Fig. 1b) across 60% of all rocky reef by area (Johnson et al. 2015).

Population dynamics of *H. erythrogramma* were established for five populations in PPB, two occurring within kelp beds and three on urchin barrens, and were examined over a four-year period from 2012 to 2015, inclusive. Following initial scoping of PPB reefs based on 27 km of manta towed diver observations (January 2012), experimental sites were selected to ensure a gradient in population abundance and to also include
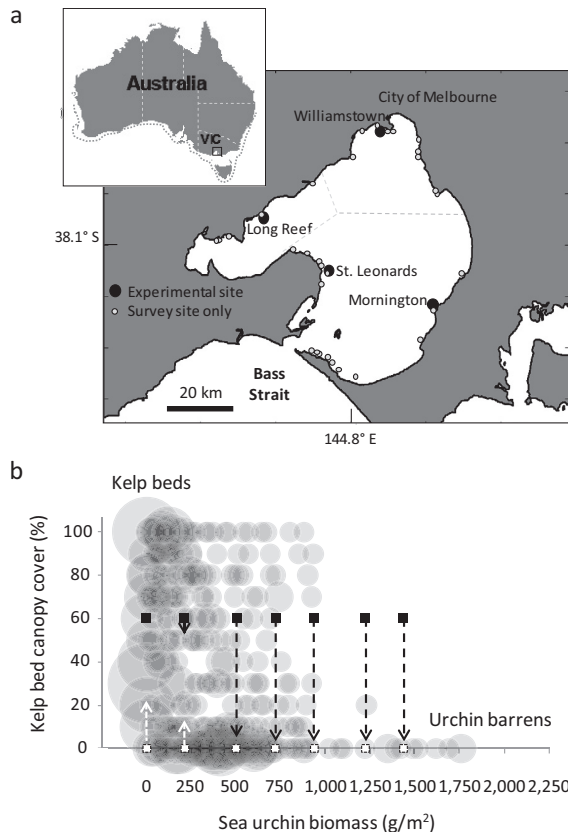
a

b

Fig. 1. (a) Map of Port Phillip Bay (PPB) in the State of Victoria, southeastern Australia. The sea urchin *Heliocidaris erythrogramma* is broadly distributed across the southern one-half of the Australian continent, including around Tasmania (dotted line); within PPB, dashed lines divide The Bay into the western, northern, and southern zones, which show distinctive reef community types and genetic connectedness (after Johnson et al. 2015). (b) Bubble plot showing frequency of particular combinations of canopy kelp bed cover (planar estimate to nearest 5%) and sea urchin biomass from 277 5-m² quadrats (5 × 1 m quadrats) spanning 34 reef sites in PPB surveyed during September–November 2013 (methodology from Ling et al. 2015). Overlaid squares and arrows show responses in reef state to experimental manipulation of sea urchin biomass on kelp dominated (black arrows, overgrazing) and on urchin barren (white arrows, kelp bed recovery) patch-reefs of 1 × 1 m (redrawn from Kriegisch et al. 2016) indicating catastrophic regime shift and thus hysteresis effect of overgrazing for this system (after Ling et al. 2015).

populations residing in kelp bed habitats and urchin barrens experiencing otherwise similar conditions; such that demographic differences between these alternative states could be assessed. Study sites were selected to represent the typical reef habitats of each of the four biogeographically distinct zones of PPB, northern, southeastern, southwestern, and western PPB (after Johnson et al. 2015). Given restricted availability of both kelp bed and urchin barrens habitats within close proximity (within ~100 m) within each zone of PPB, the selected sites were thus considered fixed for analyses considering effects of

site and habitat on urchin population parameters. In northern PPB, both extensive urchin barrens (37.8701° S; 144.8936° E) and patchy kelp beds (37.8693° S; 144.8936° E) occur at Williamstown (Fig. 1a). In western PPB, sea urchin barrens dominate while kelp beds were absent at Long Reef (37.8713° S; 144.8941° E, Fig. 1a). In southeastern PPB, large barrens patches (38.2142° S; 145.0316° E) co-occur among kelp beds (38.2143° S; 145.03206° E) at Mornington (Fig. 1a). In southwestern PPB, kelp beds (38.1489° S; 144.7240° E) and barrens (38.14840° S; 144.7238° E) were present at St. Leonards (Fig. 1a).

All study sites were composed of boulder reefs interspersed with flat rock slabs and ranged from 2.5 to 4.5 m in depth and experienced similar wave exposure, i.e., all sites experienced 13–18% of the maximum wave exposure experienced at PPB Heads (as derived by Hill et al. 2010). Where present, kelp beds consisted predominantly of *Ecklonia radiata* and also included the ephemeral introduced Japanese kelp *Undaria pinnitifida* in northern and western PPB. Fucoids such as *Cystophora monilifera* and *Sargassum* sp. also formed beds in shallow water (<1.5 m depth) at all sites except Long Reef where perennial macroalgae were absent. In 2012, planar percentage cover of standing kelp (*Ecklonia radiata* and/or *Undaria pinnitifida*) was recorded to the nearest 5% within 25 1-m² quadrats laid randomly within a 25 × 10 m grid (laid on the local reef where each urchin population was also sampled) and subjected to a two-way ANOVA testing the singular and interactive effects of the factors site and habitat on standing kelp cover.

Local sea urchin density for each study population was estimated at the time of tagging by collecting all individuals within defined plots on the reef (Table 1). Local trends in sea urchin abundance and kelp cover over the course of the study were also assessable from three permanent 1 × 1 m plots, spaced by 50 m, that were established adjacent to the monitored urchin populations and sampled bimonthly within kelp beds at Williamstown, Mornington, St. Leonards, and on the barrens at all sites inclusive of Long Reef. Trends in sea urchin density remained broadly stable throughout the study at Williamstown, Mornington, and Long Reef, while kelp bed cover showed evidence of decline at Williamstown (Reeves et al. 2018) and Mornington when urchin densities approached the overgrazing threshold of ~8 urchins/m² (Kriegisch et al. 2016; see Appendix S1: Fig. S1a, b). For kelp beds at St. Leonards, urchin density was observed to steadily increase toward ~6 urchins/m² during the study period while kelp remained relatively stable (Appendix S1: Fig. S1c). Kelp cover remained negligible on all urchin barrens; however, a notable seasonal pulse of *U. pinnitifida* (<10% cover) was recorded on barrens at Long Reef during October (Appendix S1: Fig. S1d). Notably, seasonal temperature variation was consistent across sites over the duration of the study, with a mean annual water temperature of 17.36°C (minimum 10°C to maximum 24°C; see Appendix S2: Fig. S1).

TABLE 1. Study populations of *Heliocidaris erythrogramma* from kelp bed and barren grounds as tagged with tetracycline in Port Phillip Bay, winter 2013.

Habitat	Site	No. tagged	Plot size	Local population density (individuals/m²)	Tagging date	Sampling date	No. sampled	Days at liberty	No. tags recovered	Recovery rate (%)
Kelp bed	Williamstown	306	6 × 10 m	5.04	24 Sep 2013	15 Sep 2014	350	356	38	10.9
Barren	Williamstown	305	3 × 10 m	10.83	24 Sep 2013	15 Sep 2014	351	356	56	16.0
Kelp bed	Mornington	302	6 × 10 m	5.06	2 Aug 2013	22 Sep 2014	352	416	47	13.4
Barren	Mornington	300	5 × 10 m	5.82	8 Aug 2013	22 Sep 2014	352	410	21	5.9
Barren	Long Reef	300	3 × 4 m	23.76	7 Aug 2013	14 Sep 2014	473	393	39	8.2
Kelp bed	St. Leonards	–	6 × 10 m	1.50	–	17 Sep 2014	–	–	–	–
Barren	St. Leonards	–	5 × 10 m	6.67	–	17 Sep 2014	–	–	–	–

Note: In total, 1,513 individual urchins were chemically tagged and 201 tagged individuals were recaptured from a total of 1,878 resampled 12 months later, equating to an overall tag-recapture rate of 10.7%.

Monitoring and tagging of sea urchin populations

Monitoring size structure for the five *H. erythrogramma* populations, i.e., two occurring within kelp beds (Williamstown and Mornington) and three on urchin barrens in Port Phillip Bay (Williamstown, Mornington, and Long Reef), occurred annually from 2012 to 2015. Test diameter was measured to the nearest millimeter using knife-edge Vernier calipers for a minimum of 300 individuals in each population (see Table 1) whereby all individuals within defined plots were sampled to ensure robust size distributions. Note that, even though plots were exhaustively searched in situ, involving turning over small rocks up to ~0.5 m diameter, small urchins in their first year of life (<20 mm test diameter [TD]) were rarely encountered due to their small size and highly cryptic habit. In September 2013, 300 individuals from each of the five populations were chemically tagged using tetracycline (after Pederson and Johnson 2008, Ling and Johnson 2009, Ling et al. 2009b). That is, for each habitat at each site, divers collected all sea urchins from permanently marked plots, of up to 6 m × 10 m, until the minimum 300 individuals were obtained (Table 1). Sea urchins were gently prized from the reef and placed in mesh catch bags that were brought to the surface and remained submerged alongside the research vessel. Each sea urchin was injected with tetracycline hydrochloride via a small-gauge hypodermic needle at a concentration of 10 g/L in seawater (after Pederson and Johnson 2008). So that all sea urchins received a standard dose of the tetracycline solution (0.006 mL/g wet mass), test diameter (TD) measurements were used to estimate wet body mass (W) using the power function ($W = 0.0005TD^{2.9211}$; $R^2 = 0.85$; S. Ling, *unpublished data*). Following injection, the chemically tagged sea urchins were promptly returned to their original experimental plot where they were allowed to grow for ~12 months (Table 1).

Recapture of tagged sea urchins and measurement of jaw growth

Experimental plots were revisited in September 2014 when ≥350 sea urchins were captured from each tagged population (Table 1). Following measurement of test diameter, the complete Aristotle's lantern was dissected and stored frozen. Once retrieved from the freezer, the Aristotle's lantern of each urchin was placed in a specimen jar that was filled with household bleach (12.5% sodium hypochlorite) to dissolve connective tissues and to expose individual jaw pieces. After 24 h of bleaching, the component pieces of the Aristotle's lantern were thoroughly rinsed. Once dry, jaws pieces were exposed to ultraviolet light in a dark room to determine the presence or absence of a fluorescent tetracycline tag. For jaws with a tetracycline tag present, the jaw was photographed under UV light (with Vernier caliper for scale) under 20× magnification using a camera mounted to a dissecting microscope (Fig. 2a).

The image was then imported to ImageJ software (open source imaging software, *available online*) and calibrated allowing accurate measurement of growth from the epiphysis junction to the tetracycline tag (Fig. 2a).[2] The urchin jaw length at the time of tagging (To) was derived by subtracting the growth increment (ΔT) from the jaw length at the time of sampling ($T + 1$). For all tagged individuals, growth at the oral tip was not observed. To relate jaw growth to overall increase in urchin size, allometric conversions between jaw length and test diameter for each population was established by measuring both parameters for $n = 200$ individuals at each site (Appendices, Table A1). An indicator of starvation, the ratio of jaw length to test diameter is known to increase in low food environments, i.e., urchins from barrens typically have smaller test diameters for a given jaw length (Ebert 1980, Ling and Johnson 2009). Thus to determine if this signal was also present for urchins within Port Phillip Bay, the ratio between jaw length and test diameter was tested for populations across sites and habitats using two-way ANOVA.

Raw jaw growth increments were converted to jaw growth per 365 d and linearized using log-transformation before subjecting the different site × habitat combinations (for data from Williamstown and Mornington sites where both habitats existed) to two-way ANCOVA
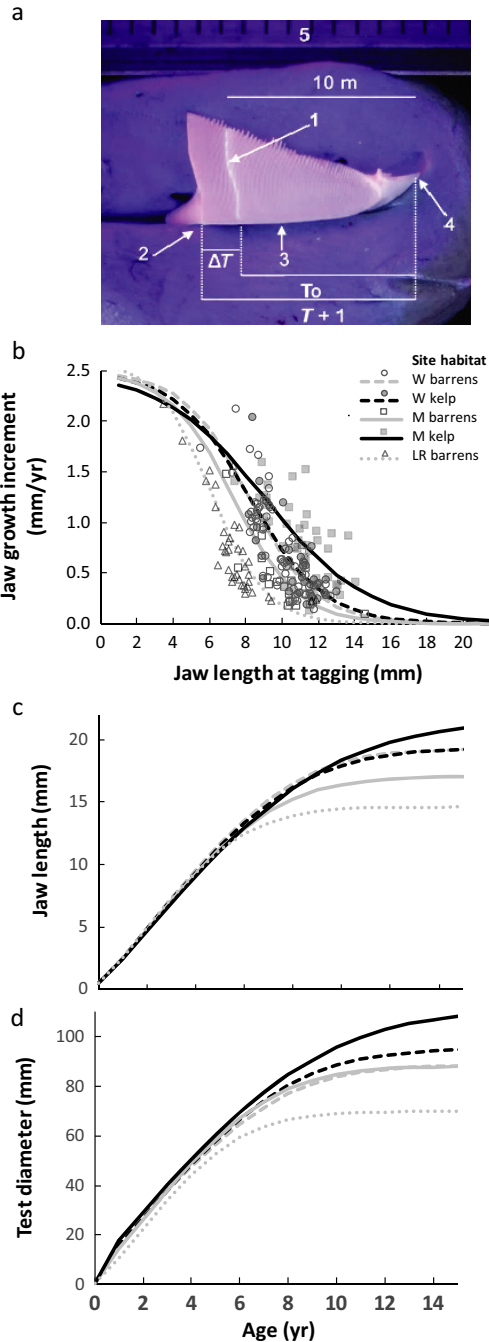
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[2] http://rsbweb.nih.gov/ij/

using initial jaw length at time of tagging as the covariate. Annual jaw growth was then compared across all populations, inclusive of the Long Reef barrens population, using one-way ANCOVA with pairwise post-hoc contrasts following Bonferroni adjustment of alpha. For ANOVA/ANCOVA, data were checked for conformity to assumptions of homoscedasticity and normality. Where appropriate, ANCOVA (with Model II covariate) was undertaken by first testing for homogeneity of slopes among sites. If homogeneity of slopes was indicated, analysis proceeded to compare intercepts.

Fitting of inverse logistic growth models

For recapture of tetracycline-tagged *H. erythrogramma*, the relationship between jaw growth increment (ΔT) and jaw size at tagging (To) was best described by an inverse logistic function (as per Ling and Johnson 2009, Ling et al. 2009b). Optimal fits for the inverse logistic functions were determined by minimizing the sum of negative log-likelihoods for each growth parameter (after Ling and Johnson 2009, Ling et al. 2009b). The inverse logistic equation is

$$\Delta L = \frac{Max\Delta L \times \Delta_t}{1 + e^{Ln(19)\frac{\left(L_t - L_{50}^m\right)}{\left(L_{95}^m - L_{50}^m\right)}}} + \varepsilon_{L_t}$$

where $Max\Delta L$ is the hypothetical asymptotic maximum jaw growth increment at some initial size of sea urchin that sets the exponential term to zero; Δ_t is the actual time increment between tagging and recovery, i.e., ~1 yr; L_t is the size when first tagged; L_{50}^m is the initial length at which the midpoint between the $Max\Delta L$ and zero growth increment is reached; and L_{95}^m denotes the initial length at which 95% of the difference between zero and maximum increment is reached; ln(19) is a scaling parameter that defines the L_{95}^m point. The error term ε_{L_t} is additive and normal, and assumed to have a mean of zero and standard deviation σ_{Lt}, which is also defined as a function of predicted length (Haddon et al. 2008).

Given that recently settled *H. erythrogramma* juveniles remain cryptic (<20 mm test diameter), the in situ diver-collected samples rarely included these animals. However, when fitting growth models to tag and recapture data, estimating jaw size at settlement is important for anchoring the size at age relationship, thus a value of 0.47 mm, as measured for *H. erythrogramma* by Pederson and Johnson (2008), was used as the jaw length at

FIG. 2. (a) Tetracycline tag (1) on an *Heliocidaris erythrogramma* jaw from Port Phillip Bay under ultraviolet light. The epiphysis junction (2), external edge (3), and oral tip (4) are also indicated. Growth increment (ΔT) was measured from the edge of the epiphysis junction to the tetracycline tag in Image J, Vernier calipers (5) were used to calibrate scale (as seen at top of image, graduations are in millimeters). Jaw length at the time of tagging (To) was calculated by subtracting the growth increment ΔT from ($T + 1$); photograph of jaw was taken using a dissecting microscope under 20× magnification. (b) Annual jaw growth increments (symbols) and optimal fits of inverse-logistic growth curves (lines) for five populations across kelp beds and barrens at Williamstown (W), Mornington (M), and Long Reef

(FIG. 2. *Continued*)

(LR). (c) Growth curves of jaw length at given age, and (d) growth curves of test diameter at given age, lines as per panel b. For optimal graphical display, only optimal model fits are shown for panels b–d, for 95% confidence intervals around each fit see Appendix S4: Figs. S1–S3.

the time of settlement. Growth curves were compared between each habitat/site combination using likelihood ratio tests, after Haddon (2001).

Relationships between growth rates, availability of kelp, and body condition

Routine collections of 30 *H. erythrogramma* from barrens and kelp bed populations (where available) at Williamstown, Mornington, and Long Reef were performed every ~2 months over 18 months (15 sampling periods in total) from October 2012 to March 2014. These collections involved mature sea urchins only within the size range 55–60 mm test diameter (maturity is reached at >40 mm test diameter; after Dix 1977). During the peak reproductive season across PPB, sampling also included kelp bed and barrens populations from St. Leonards. Using Pearson's correlation coefficients, urchin growth rate (standardized as mean growth rate of a 10-mm jaw) for each of the five populations was correlated with (1) standing kelp (as estimated above); (2) amount of drift kelp captured by individuals (Vanderklift and Wernberg 2008); (3) relative abundance of kelp within the gut contents; and (4) gonad-somatic indices as a measure of body condition estimated during the peak reproductive season (December).

All drift kelp attached to individual sea urchins was weighed and subjected to three-way ANOVA (after using a log +0.001 transformation) to sequentially test the factors site, habitat, and period. For correlation between individual growth rate and rate of drift kelp capture, drift kelp was expressed as the grams of kelp per gram of urchin to account for availability of drift kelp across the urchin population.

The percentage of gut contents identifiable as kelp was assessed by spreading the dissected gut contents, composed of thousands of individual boluses, evenly across a Petri dish and estimating the planar percentage cover by eye to the nearest 5%. Gut content data required square-root transformation to stabilize variance and was subjected to three-way ANOVA sequentially testing the factors site, habitat, and period. The non-kelp component of gut contents chiefly included coralline algae and/ or filamentous turf algae with a mix of sediment particles rolled into an individual bolus, as opposed to kelp, which was typically rolled into a monospecific bolus.

Sea urchin growth rate was regressed against gonad mass from the five populations for which growth was measured in situ (i.e., kelp bed and barrens populations at Williamstown and Mornington and barrens population from Long Reef). In addition, gonad mass obtained during the peak reproductive season was subjected to two-way ANOVA (following square-root transformation) to test the factors of site and habitat by utilizing the three sites (Williamstown, Mornington, and St. Leonards) where both kelp beds and urchin barrens coexisted.

Age dynamics and projections of monitored populations

Age structures of *H. erythrogramma* study populations at Williamstown, Mornington, and Long Reef over the four-year monitoring period were constructed from optimal fit field-calibrated models of growth. Solving for age-at-size from the growth models, age-structure dynamics of populations within kelp beds and on barrens was assessable through 2012 to 2015. Given that recently settled *H. erythrogramma* juveniles remained cryptic, few individuals within the first or second year of life were sampled in situ during either ongoing monitoring or destructive sampling for tagged individuals. Thus for the purposes of tracking recruitment pulses, recruits for each population were defined as individuals less than three years old.

To project population dynamics of each *H. erythrogramma* study population, and for the PPB population overall, age-structured Leslie-matrix population models with stochastic recruitment were constructed to infer the stability of alternative kelp beds and urchin barren states in to the future. The Leslie matrix form is

$$\begin{pmatrix} n_1(t+1) \\ n_2(t+1) \\ n_3(t+1) \\ n_4(t+1) \end{pmatrix} = \begin{pmatrix} F_1 & F_2 & F_3 & F_4 \\ P_1 & 0 & 0 & 0 \\ 0 & P_2 & 0 & 0 \\ 0 & 0 & P_3 & 0 \end{pmatrix} \times \begin{pmatrix} n_1(t) \\ n_2(t) \\ n_3(t) \\ n_4(t) \end{pmatrix}$$

where n is the number of individuals of age classes 1–4; t is time, which is 1 yr; F is fecundity, i.e., the number of recruits per adult female in each age class 1–4; and P is survival probability, i.e., the proportion of individuals in the current age class surviving to be counted in the next age class.

Age-structured survival (P) for each population and PPB overall were generated from the mean survival of age classes over four years (2012, 2013, 2014, 2015) for up to nine tractable cohorts (Appendix S6). The estimated age of each individual was rounded down to whole years, that is, a 3.8-yr-old individual was designated as a 3-yr-old given it was yet to experience its' fourth birthday, as opposed to rounding to 4 yr of age. Also, given that additional collection effort was made for purposes of ensuring sufficient tag returns in 2014 (see Table 1), survival estimates and thus projection matrices themselves, were based on the first 300 randomly collected individuals within each population within each year as sampled from within the original boundaries of the experimental plots (see Table 1). Fecundity (F) was estimated by calculating the number of recruits per adult female per age class assuming a 1:1 sex ratio. Given juvenile sea urchins are typically highly cryptic and under sampled, recruits were hereby assigned as those age classes poised to emerge into the adult population, which varied among populations given that age-at-emergence was population specific (Appendix S6). To provide more realistic starting abundances (i.e., n) within each age class for each local population, each population was scaled up to 1 ha in size, although projected trends were insensitive to this scaling.

Given evidence for limited gene-flow of *H. erythrogramma* across PPB populations owing to a lecithotrophic larval dispersal window of 7 d maximum (Johnson et al. 2015), projection models were run using both local and regional estimates of fecundity (*F*). That is, the number of recruits per adult female per age class was projected both from within each local population and from the PPB population as a whole. Notably, projections for adjacent kelp bed/barrens populations were qualitatively insensitive to choice of local kelp bed/barrens recruitment rates (only affecting the speed to exceed carrying capacity or population crash), and for modeling purposes any migration of adults between adjacent populations was assumed to be negligible relative to recruitment. Furthermore, stochasticity of recruitment was modeled by drawing randomly from a normal distribution centered on the mean fecundity for each local population or PPB as a whole. Projections were run for 10 times the maximum observed longevity with PPB and were examined relative to the inferred carrying capacity (set as the maximum density of urchins observed for PPB).

Size-specific rates of disease for kelp beds and barrens populations

Sea urchins obtained during the tag recovery process (Table 1) were assessed for lesions, which were scored as either present or absent for each individual. Lesions typically manifested as an open wound in the test of ~2 cm in diameter and appeared to be characteristic of that caused by the opportunistic pathogen *Vibrio anguillarum* described for *H. erythrogramma* in southeastern Australia (Sweet et al. 2016). However, the nature of the disease, epizootic or otherwise, was not firmly established during our study noting that the marine amoeba *Paramoeba invadens* has also been described to cause mass mortality of temperate urchins elsewhere (reviewed by Feehan and Scheibling 2014). Test diameter was recorded for each individual enabling rates of urchins with lesions within each population to be expressed per size and age-class (following conversion of size to age using population-specific growth models). Presence of lesions was analyzed using a binomial family GLM (presence of lesions "1" or not "0") with logit link function with the following terms added sequentially, i.e., site, size, and habitat and followed by two-way and three-way interactive effects. Size classes were divided into small, 40–50 mm; medium, 55–65 mm; and large, 70–80 mm test diameter categories.

Size-specific rates of predation in kelp beds and urchin barrens

Abundance of putative urchinivorous predators (chiefly wrasses, e.g., *Notolabrus tetricus* and *Neoodax balteatus*, Monocanthids, plus predatory invertebrates, e.g., *Nectocarcinus* sp., see Appendix S3: Table S1) were assessed along six belt transects (25 m long by 2 m wide)

laid within each habitat/site combination. Notably, spiny lobsters (*Jasus edwardsii*), a voracious predator of *H. erythrogramma* (Pederson and Johnson 2006), were historically present and locally abundant on reefs in Port Phillip Bay, however, not a single individual was observed in over 800 person dives during the broader study of urchins in this system from 2012 to 2015. Nevertheless, total abundance of putative urchinivorous predators (Appendix S3: Fig. S1a), plus the ratio of predators to urchin prey (Appendix S3: Fig. S1b) was observed to be higher within kelp beds than on barrens at all sites where both habitat types were present. Thus, to test if the increased presence of predators in kelp beds resulted in higher predation rates on *H. erythrogramma*, urchins of both small and large size classes were tethered on open reef surfaces within kelp beds and/or barrens at each study site. Twelve *H. erythrogramma* in each size class were tethered in situ by drilling monofilament through the test (using hypodermic needle) and crimping on swivel clips; which were then attached to 6 mm diameter anchor chain pegged in lengths of 2 m across flat boulders. Tethered urchins were deployed for 3 d, after which the status of tethered individuals was recorded as either dead or alive. Tethers with missing urchins or the remains of sea urchins attached were recorded as mortality events. All non-consumed urchins were observed to be healthy and showed tenacious attachment to the substratum as per local non-tethered individuals by the conclusion of deployment. Mortality (dead "1" or alive "0") data was analyzed using the same binomial family GLM with logit link function, and the same order of sequential terms as was used per analysis of disease above.

Density-dependent scaling of population parameters

To examine possible density-dependent population feedbacks, relationships between urchin population parameters and local population abundance were examined. Relationships were examined across the study populations and then, where appropriate, scaled across Port Phillip Bay as a whole (Fig. 1a). For the study populations, mean rates of growth, prevalence of disease, predation mortality, recruitment, and reproductive potential were regressed against local population density (i.e., no. individual urchins/m², from Table 1). While growth rates were not measured for St. Leonards kelp bed and barrens populations, all other parameters (i.e., disease, predation, recruitment, and reproductive potential) were measured for both of these populations, thus regressions for these parameters across study populations were inclusive of St. Leonards populations. Regressions of disease prevalence were based on mature individuals (i.e., 4- and 5-yr olds that had been exposed to disease over many years), while predation rates for each study population were established by pooling total mortality and calculating the proportion of all urchins, across both small and large size classes, consumed during tethering trials. In addition to per capita

reproductive potential (i.e., g gonad/individual), total population-level reproductive potential (i.e., g gonad/m^2) was also scaled against population abundance to determine potential population-level fertilization success for the free-spawning *H. erythrogramma* (after Whale and Peckham 1999, Ling et al. 2012).

For scaling population parameters against urchin density for Port Phillip Bay as a whole, *H. erythrogramma* density was established for each survey site by divers counting all individuals within a 50 × 2 m transect. Age, predation risk, per capita reproductive potential, total reproductive potential, urchin biomass, and kelp bed cover were regressed against urchin density across PPB. For age, habitat/zone-specific growth was used to predict mean age from the average size of $n = 10$ randomly selected urchins at each of 34 rocky-reef survey sites (see Fig. 1a). Predation risk was determined for all survey sites based on the per capita abundance of putative urchin predators per square meter, as per tethering experiments (see also Appendix S3: Fig. S1a,b), and as measured along the same 50 × 2 m for urchinivorous invertebrates and 50 × 10 m for urchinivorous fishes. For per capita reproductive potential, each survey site was assigned to habitat/zone-specific patterns in gonad-somatic index, which was multiplied by mean body mass predicted from the $n = 10$ test diameters following conversion of test diameter (TD) to mass (W) using the power function $W = 0.0005TD^{2.9211}$. Estimates of mean urchin body mass per site were then used to estimate urchin biomass per square meter. Kelp bed cover was estimated as the planar percentage cover of the benthos by divers who assessed cover (to nearest 5%) within 10 contiguous 5 × 1 m quadrats along the 50 m transect line at each site.

All linear regressions between population parameters and urchin density were performed in R (using ordinary least squares) on raw and/or log-transformed data to achieve best fit.

RESULTS

Sea urchin growth in kelp beds and on barrens

Analysis of covariance indicated that, for a given initial size, urchin growth was higher within kelp bed habitats than on urchin barrens, but this result was dependent on site (i.e., significant habitat by site interaction; two-way ANCOVA type III test on log transformed annual jaw growth increment data; test for homogeneity of slopes, $F\text{calc}_{3,154} = 0.28$, $P = 0.84$; effects of site, $F_{1,157} = 30.01$, $P < 0.0001$; habitat, $F_{1,157} = 0.0184$; $P = 0.89$; site × habitat, $F_{1,157} = 52.14$, $P < 0.0001$). Examining this interactive effect by site revealed urchins to grow significantly faster within kelp beds than barrens at Mornington, but urchin growth in kelp beds was not significantly different from that on barrens at Williamstown (see raw data symbols in Fig. 2b). Analysis of covariance for all five urchin populations together, i.e., inclusive of the

barrens-only population at Long Reef, revealed differences in mean annual growth increments ranked highest to lowest as follows: Mornington kelp beds > Williamstown kelp beds = Williamstown barrens > Mornington barrens > Long Reef barrens (rank order based on significant groupings at the Bonferroni-adjusted alpha of $P < 0.01$; one-way ANCOVA, type III test on log-transformed annual jaw growth increment data; test for homogeneity of slopes, $F_{4,191} = 1.38$, $P = 0.24$; effect of population, $F_{1,195} = 44.57$, $P < 0.0001$).

Optimal growth curves

Fitting of optimal inverse logistic growth curves and comparisons between populations using likelihood ratio tests revealed significantly different patterns of growth between all populations except for kelp bed and barrens populations at Williamstown, which were statistically indistinguishable (Fig. 2b; for detailed growth parameters and 95% confidence intervals, see Appendix S4: Fig. S1–S3). Estimation of age-for-given-size, revealed that urchin growth within Port Phillip Bay (PPB) asymptotes at ~7–9 yr of age (Fig. 2b). Conversion of jaw lengths to test diameters (TD), using population-specific allometric conversions (Appendix S5: Table S1), revealed clear differences in maximum sizes across the study populations, ranging from ~60 to ~100 mm TD (Fig. 2c). Test diameter was also smaller for a given jaw length for barrens urchins relative to those from kelp beds (two-way ANOVA, effect of habitat, $F_{1,800} = 70.55$; $P < 0.0001$; site, $F_{1,800} = 201.06$, $P < 0.0001$; site × habitat, $F_{1,800} = 0.02$, $P = 0.90$; see Appendix S5: Fig. S1).

Relationships between growth rates, availability of kelp, and body condition

The cover of standing kelp, mass of captured drift kelp, and percentage of kelp in the gut were significantly higher within kelp beds relative to barrens habitats (Table 2a–c). While gonad mass was typically higher for kelp bed urchins than those on barrens, the effect of habitat on gonad mass was not statistically significant, although significant variability was detected among sites (Table 2d). Temporal sampling indicated significant variability in drift kelp capture by urchins and also the proportion of gut contents as kelp through time (Table 2b, c). Growth rate of *H. erythrogramma* was positively correlated with greater availability of standing kelp (Pearson's correlation coefficient = 0.86), drift kelp (PCC = 0.83), percentage of kelp in the gut (PCC = 0.71), and body condition as indicated by gonad mass (PCC = 0.91; cf. Fig. 3a–e).

Age dynamics and projections of monitored populations through time

Predicted age-structure of urchin populations, estimated by converting size to age using the population-

TABLE 2. Analysis of variance summary tables testing for the effects of (a) site and habitat for the availability of standing kelp, (b) site, habitat, and period effects on captured drift kelp, and (c) percent cover of gut contents as kelp, plus (d) site and habitat effects on gonad mass.

Effect	df	SS	MS	F	Pr(>F)
(a) Standing kelp (% cover)					
Site	2	17,173	8,586	42.8	<0.001***
Habitat	1	14,090	14,090	70.3	<0.001***
Site × Habitat	1	128	128	0.6	0.43
Residuals	120	24,051	200		
(b) Drift kelp captured by urchins†					
Site	2	330	165	38.0	<0.001***
Habitat	1	45	45	10.4	0.001
Period	13	307	24	5.4	<0.001***
Site × Habitat	1	1	1	0.2	0.64
Site × Period	26	375	14	3.3	<0.001***
Habitat × Period	13	284	22	5.0	<0.001***
Site × Habitat × Period	13	118	9	2.1	<0.001***
Residuals	2,029	8,799	4		
(c) Gut contents as kelp‡					
Site	2	3,608	1,804	319.2	<0.001***
Habitat	1	5,325	5,325	942.2	<0.001***
Period	13	5,303	408	72.2	<0.001***
Site × Habitat	1	606	606	107.2	<0.001***
Site × Period	26	3,200	123	21.8	<0.001***
Habitat × Period	13	2,227	171	30.1	<0.001***
Site × Habitat × Period	13	1,005	77	13.7	<0.001***
Residuals	2,029	11,468	6		
(d) Gonad mass§					
Site	2	11	5	8.8	<0.001***
Habitat	1	1	1	2.3	0.13
Site × Habitat	1	0.1	0.1	0.2	0.64
Residuals	372	233	0.6		

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.
†Response variable (log(grams kelp + 0.001)).
‡Response variable (square root(% cover)).
§Response variable (square root (gonad mass)). Post-hoc pooling of habitat (given as site × habitat interaction) revealed a significant effect of habitat (df = 1,372, $F = 8.644$, $P < 0.01$).

specific growth models, revealed few *H. erythrogramma* to live beyond 7 yr of age in Port Phillip Bay (95% percentile of 6.7 yr; Fig. 4a). Age structure and apparent longevity varied depending on site (Fig. 4b–d), with younger age structures consistently found on the barrens of Long Reef, Mornington, and Williamstown relative to older age distributions within the kelp beds at Mornington and Williamstown (Fig. 4c, d). Predicting age from size for each population in each year revealed broadly stable age distributions over the 4 yr of sampling (i.e., 2012, 2013, 2014, 2015), with populations centered on modal ages of either 3-, 4-, or 5-yr olds (Fig. 4b–d). The only notable exception was at Long Reef, where in 2012 a pronounced recruitment event resulted in a modal age class of 2 yr (Fig. 4b). Across remaining populations, recruitment appeared much lower with only the Williamstown barrens population demonstrating a recruitment pulse as evidenced by a secondary mode of 2-yr olds also during 2012 (Fig. 4c). Other than Long Reef and the Williamstown barren populations in 2012, age

structure generally appeared as a unimodal distribution skewed slightly toward relatively older individuals within each population (Fig. 4; see also Appendix S6).

Leslie matrix population projections indicated all populations to have the potential for unchecked population growth beyond maximum observed densities (i.e., presumed carrying capacity of 60 individuals/m^2) in PPB in <40 yr; however, such population growth was highly dependent on simulations of local or regional recruitment rate (Fig. 5; see Appendix S6 for derivation of population parameters). Depending on the relative frequency of local to regional recruitment rates, all populations were also capable of demonstrating stability through time (Appendix S6, Fig. S1).

Size-specific rates of disease and predation for kelp bed and barrens populations

Examination of the presence of disease for *H. erythrogramma* across PPB revealed significant effects of site,
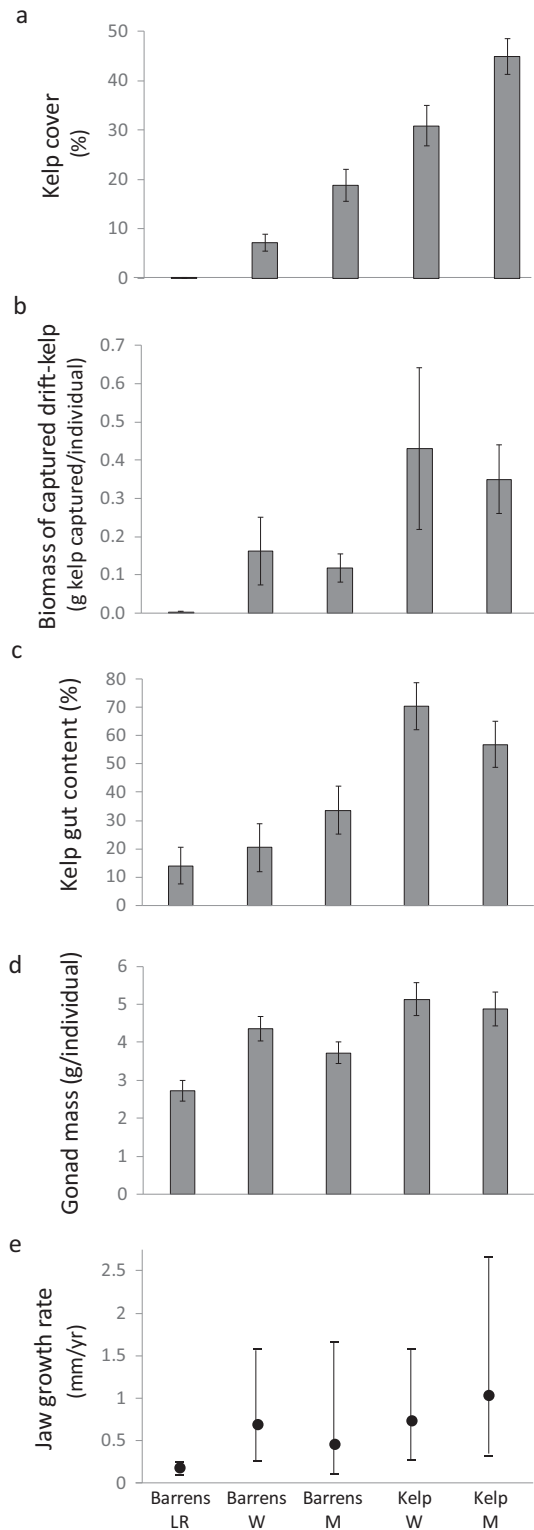
size, and habitat (Table 3a). Disease rates were highest at Williamstown and lowest at St. Leonards, with large urchins on urchin barrens demonstrating highest prevalence (Fig. 6a). The effect of size was also dependent on habitat, with the presence of lesions being most frequent for large individual urchins from barrens populations (Table 3a).

Assay of relative predation rates on urchins obtained via tethering also revealed significant effects of site, size, and habitat (Table 3b). Rates of predation were highest on small urchins within kelp beds at all sites (Fig. 6b). The effect of site was driven by higher rates of predation at the St. Leonards reef, where one-half of all large tethered urchins were also consumed in addition to the highest rates of predation on small urchins also occurring at this site (Fig. 6b).

Density-dependent scaling of population parameters

Across the study populations, mean growth rate of sea urchins was observed to exponentially decline with increasing density (Fig. 7a). Prevalence of disease among mature individuals was observed to logarithmically increase with increasing population density of study populations (Fig. 7b), while predation rate exponentially declined with increasing density (Fig. 7c). Recruitment was also density-dependent with recruitment of juveniles increasing with increasing adult density (Fig. 7e). Per capita reproductive potential exponentially decreased with increasing density, while total population-level reproductive potential, in terms of grams of gonad per square meter, exponentially increased as population density increased (Fig. 7e) and was thus positively associated with increasing local recruitment (cf. Fig. 7d, e).

Scaling population parameters across all surveyed sites in Port Phillip Bay revealed mean age of sea urchins to decline exponentially with increasing density (Fig. 8a). Predation risk for urchins also declined exponentially as population density increased (Fig. 8b). Trends in reproductive potential at the scale of PPB were similar to those indicated across the study populations, whereby per capita reproductive potential exponentially declined with increasing density but total reproductive potential exponentially increased within increasing population density (cf. Fig. 8c, 7e). Examination of the trend in biomass indicates that the probability of urchin populations exceeding the biomass threshold of overgrazing increases as population density increases (Fig. 8d). Examination of kelp bed cover across urchin population density indicates that urchin densities and

Fig. 3.   Patterns of food availability for each sea urchin population. (a) Standing kelp cover for each reef environment, (b) drift kelp capture, (c) percentage of urchin gut contents as kelp, (d) gonad mass during peak reproductive conditioning, (e) mean growth rate of a 10-mm jaw piece for each population

(Fig. 3. *Continued*)
(from growth model in Fig. 2b). Note for panel c, the non-kelp component of gut contents chiefly included coralline algae and/or filamentous algae with a mix of sediment particles. Values are mean ± SE; except panel e, which shows mean and 95%CI.
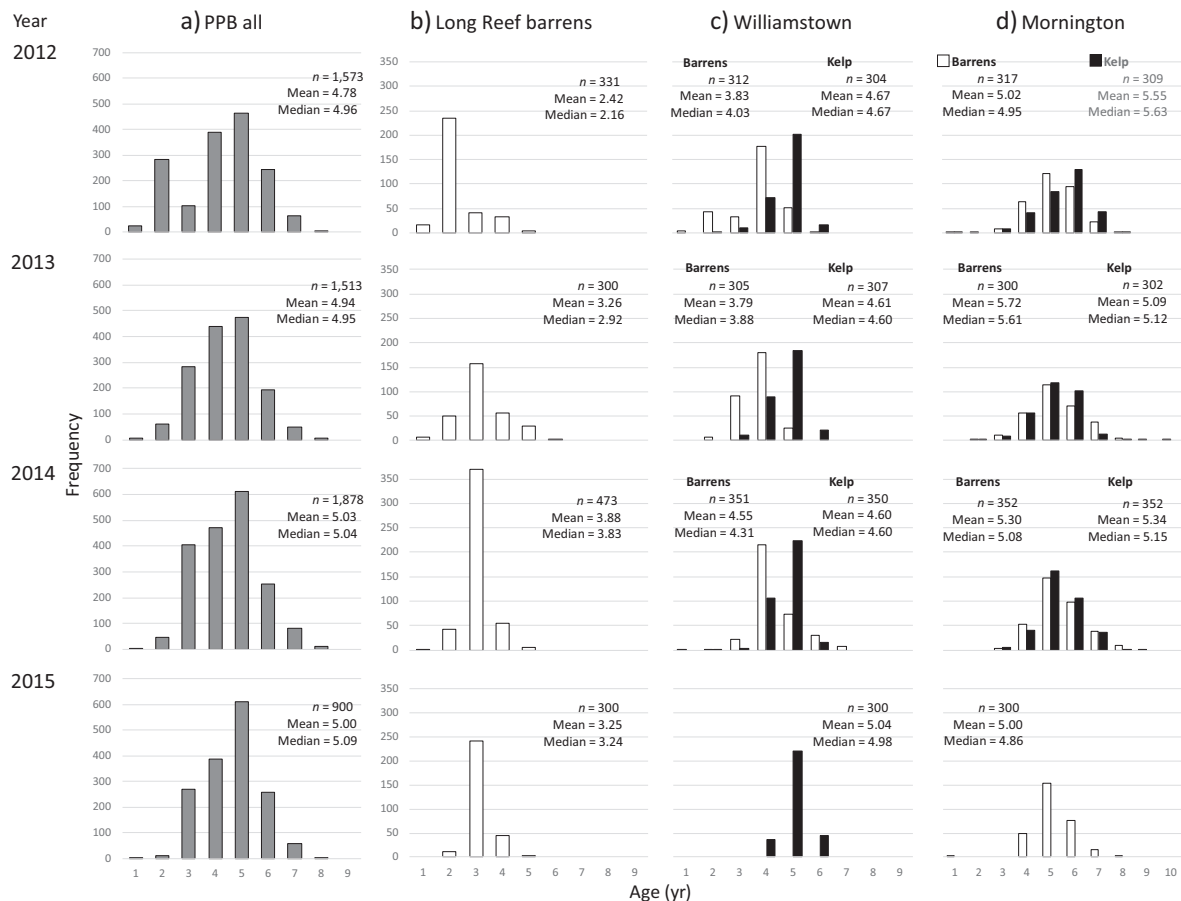
Fig. 4. Frequency histograms of sea urchin age, rounded to nearest whole year, for each population in Port Phillip Bay from 2012 to 2015. (a) All PPB populations combined; (b) Long Reef barrens; (c) Williamstown barrens (gray lines) and kelp beds (black lines); (d) Mornington barrens (open bars) and kelp beds (filled bars). Both Williamstown barrens and Mornington kelp were unable to be sampled in 2015. Overlaid on each subplot are the number of samples for which age at given size was predicted (*n*) plus the mean and median of raw age estimates for each population in each time period. Note that age values have been rounded down, i.e., a 3.8-yr-old individual remains a 3-yr-old (as opposed to being rounded up to a 4-yr-old). Refer to Appendix S6 for full data set and analysis of changes/cohort trends plus estimation of age-specific mortality for each population.

biomass can continue to increase well beyond the collapse of kelp (cf. Fig. 8d, e), but that population parameters experience inflection consistent with kelp collapse (cf. Fig. 8a–d, e).

DISCUSSION

Declines in individual sea urchin growth and body condition with decreasing kelp resources

The theory of consumer–resource cycles states that overconsumption of food resources will be followed by population collapse of the consumer. These feedback cycles are theorized for predator–prey, parasite–host, disease–host, and herbivore–plant systems in nature (Murdoch et al. 2003). Paradoxically, such a consumer–resource cycle does not occur during the process of sea urchin overgrazing of kelp beds and formation of persistent urchin barren grounds. Here, our results show several

mechanisms that enable survival of sea urchins on barrens once the food resource (kelp) has been completely consumed, including reduced growth and body condition plus a switch in diet. That is, despite variable effects across habitats and sites, examining the availability of standing and allochthonous "drift kelp" across populations revealed both individual growth rates and body condition of urchins to decline as the availability of food diminished (Fig. 3). Test diameter to jaw length ratio, used as a proxy for starvation, also declined for urchins on barrens (Meidel and Scheibling 1999, Pederson and Johnson 2008; Ling and Johnson 2009, Foster et al. 2015). Therefore, these results at the individual level align with prior research also indicating persistence of urchins on barrens owing to a flexible body plan and the ability to persist on a diet of encrusting/filamentous algae once nutritious kelp has been grazed away (Chapman 1981, Johnson and Mann 1982, 1988, Ling and Johnson 2009, Livore and Connell 2012).
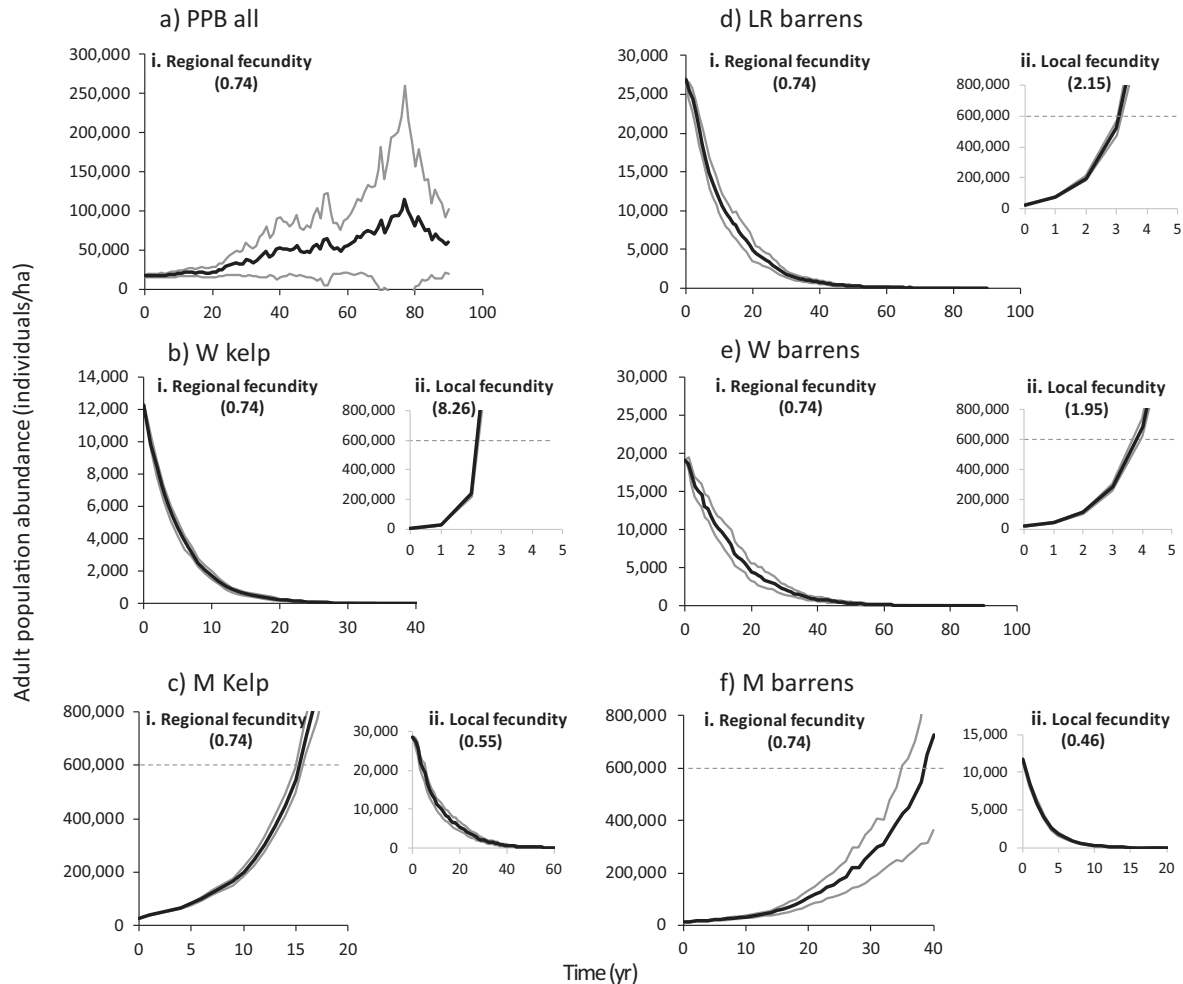
Fig. 5. Leslie matrix projections of adult *H. erythrogramma* populations (exclusive of emergent recruits and cryptic juveniles) in (a) Port Phillip Bay as a whole and (b–f) for each study population as derived from age-specific survival and (i) regional and (ii) local estimates of fecundity (see Appendix S6, Table S2). Dashed lines indicate the theoretical carrying capacity of 600,000 urchins/ha based on the maximum observed densities within PPB. Projections were run until means reached carrying capacity, crashed to 0, or for a maximum of 90 yr, i.e., 10 times maximum population longevity of ~9 yr. Values on both axes thus vary for optimal display of trends. Gray projections indicate the lower and upper 95% confidence intervals of 100 model simulations of stochastic recruitment variability by drawing randomly from a normal distribution of fecundity rates from the local/regional population (centered on mean and down to 0.001, i.e., 1 recruit per 1,000 adults).

Despite declines in the individually based parameters of growth and body condition, population-level recruitment, reproductive potential (g gonad/m²) and overall population size all increased as kelp availability declined (Fig. 2b). As such, positive density dependence was evident for total reproductive potential, recruitment, and overall biomass. The positive feedback between stock size and recruitment acts to stabilize sea urchin populations as they build in size during and also after the overgrazing collapse of kelp beds. Therefore, while theory predicts urchin population collapse once kelp food source declines, our results show that this positive feedback persists throughout the process of kelp loss even though food conditions and per capita growth declines.

Decreasing predation on barrens, but increase in disease

Consistent with reduced predator abundance in the absence of kelp habitat, predation rates on sea urchins were lower on barrens than within kelp beds. While positive density-dependent relationships were observed for total reproductive potential, recruitment, and overall biomass, a negative density-dependent relationship was evident between predation rates and urchin population size. That is, predation rates were higher within kelp beds when overall urchin population size was low and small recruit-sized urchins were most vulnerable (Fig. 6b). Thus, predation emerged as a mechanism capable of limiting population size of urchins before overgrazing occurs, as predator abundance was higher when reefs

TABLE 3. Analysis of deviance tables testing for the effect of site, size, and habitat for (a) presence of disease and (b) predation on sea urchin populations.

Effect	df	Deviance	Residual df	Residual deviance	Pr(>Chi)
(a) Disease					
Null			2504	1102.2	
Site	3	21.5	2501	1080.6	<0.001***
Size	2	10.4	2499	1070.2	<0.01**
Habitat	1	8.1	2498	1062.2	<0.01**
Site × Size	5	10.1	2493	1052.1	0.07
Site × Habitat	2	2.9	2491	1049.2	0.24
Size × Habitat	2	6.5	2489	1042.8	0.04*
Site × Size × Habitat	4	2.4	2485	1040.3	0.66
(b) Predation					
Null			167	216.5	
Site	3	13.5	164	203.0	<0.01**
Size	1	7.4	163	195.6	<0.01**
Habitat	1	5.5	162	190.1	0.02*
Site × Size	3	1.3	159	188.8	0.72
Site × Habitat	2	2.9	157	185.9	0.24
Size × Habitat	1	0.6	156	185.3	0.45
Site × Size × Habitat	2	0.4	154	184.9	0.83

Note: GLM models were binomial, link = logit, with terms added sequentially (first to last).
*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

occur in the kelp bed state (Appendix S3: Fig. S1). Importantly however, the risk of predation declined exponentially as population size increased (Fig. 8b).

In contrast to predation, the prevalence of disease was higher for populations on barrens than within kelp beds. Examining rates of disease against population size for mature individuals with a greater lifetime disease exposure (i.e., 4- and 5-yr olds), revealed disease prevalence to scale positively with increasing population size. Corroborating our findings, Constable (1989) also recorded the occurrence of sick and dying sea urchins among the high-density aggregations he recorded in Port Phillip Bay (reviewed by Keesing 2013). The observed positive density dependence suggests that, while disease appears to limit population size by disproportionately affecting older individuals, the disease-causing lesions within the urchin test appeared insufficiently virulent over the period of our study to reduce urchin population density sufficiently low enough to allow kelp bed recovery (i.e., below 4 urchins/m^2; after Kriegisch et al. 2016). However, diseased-based collapses of sea urchins are known to be stochastic in nature (e.g., Lafferty 2004). Thus, while not observed in PPB during our study or prior work (reviewed by Keesing 2013), mass disease-driven mortality may be capable of ultimately controlling urchin populations and driving regime shift back to kelp dominance within this system (e.g., Scheibling and Hennigar 1997). Importantly, as observed here, the death of older individuals on barrens appeared offset by recruitment of an abundance of younger urchins within these populations as observable from stable age distributions through 2012–2015 (Fig. 4). Indeed, despite habitat differences in population parameters, density-dependent feedbacks acted to stabilize populations on both barren grounds and within kelp beds.

Shifting demographics of overgrazing

For populations occurring within kelp beds, while urchins grew faster than on barrens, there were relatively few young individuals (Fig. 4). While we did not assess rates of urchin settlement, our observed high rates of predation mortality on small urchins within kelp beds explains why there are few young recruits within kelp beds (Fig. 6b; see also Hernández et al. 2010). However, observations of "feeding-fronts" chiefly composed of emergent adult urchins climbing and actively grazing kelp beds (S. Ling, *personal observation*) indicates that the right-skewness of *H. erythrogramma* ages within kelp beds could also be driven by net migration of more mobile larger/older urchins (Flukes et al. 2012; *see also* Lauzon-Guay and Scheibling 2007). Thus, the combined increase in predation mortality of young urchins within kelp beds (also see Rowley 1990) and potential for greater migration of older individuals to kelp beds indicates an overgrazing mode of *H. erythrogramma* contingent on adult urchins grazing from the edges of kelp beds (outside in), as opposed to significant recruitment of juveniles among kelp. As such, *H. erythrogramma* is behaviorally similar to Strongylocentrotids not only by its mode of barrens formation (Feehan et al. 2012, Filbee-Dexter and Scheibling 2017), but also in its propensity to switch from a passive/cryptic grazer of detached kelps to an active over-grazer of standing kelp beds under conditions of low drift kelp supply (Harrold and
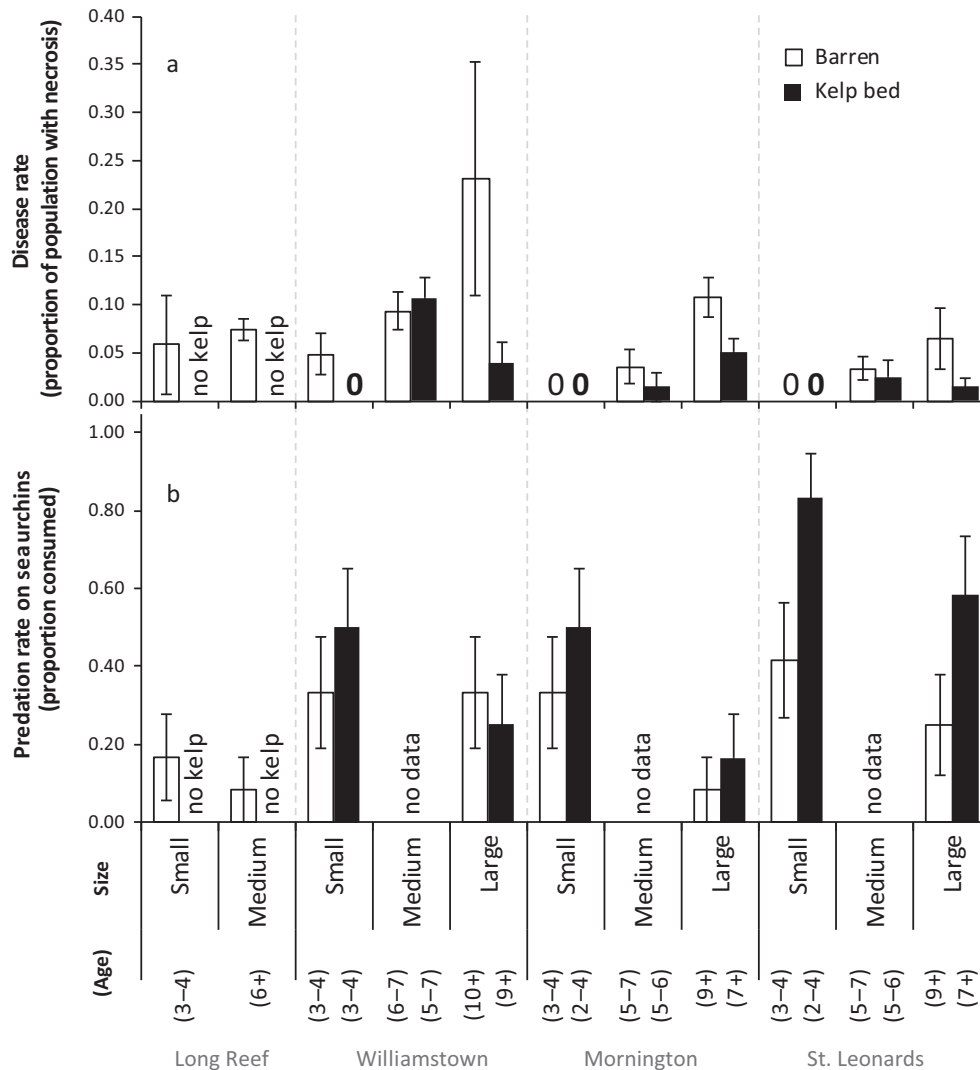
Fig. 6.   Rates of (a) disease and (b) predation for sea urchins by size class for populations within kelp beds and on barrens (mean ± SE). Size classes consisted of small, 30–40 mm; medium, 50–60 mm; and large, 70–80 mm test diameter. Note that for panel a, 0 indicates a complete absence of disease. The mean age range of respective small, medium, and large size classes, as estimated from the population-specific growth model, are shown in parentheses.

Reed 1985, Ling et al. 2010, Kriegisch 2016). Notably, grazing by *H. erythrogramma* therefore contrasts with the primary overgrazing mode of the sympatric Australian sea urchin *Centrostephanus rodgersii*, which typically forms urchin barrens from the inside out by recruiting within kelp beds and creating incipient barrens patches, which coalesce into large-scale barrens features (Flukes et al. 2012).

Persistent urchin populations despite declining kelp

Our results within the Port Phillip Bay system revealed persistence of urchin populations within alternative kelp bed and barrens states owing to density-dependent population feedbacks. In terms of the barren grounds

themselves, urchin barrens in western Port Phillip Bay have persisted over a period of at least 7 yr from 2009 (S. Ling, *personal observation*; and were also locally reported in 1980s; Constable 1989), which is notably greater than a complete population turnover based on longevity of urchins at ~6 yr in this location (Fig. 4). Thus, the barrens state in this system is apparently "stable" according to the definition of Connell and Sousa (1983) whereby the population or community must be followed and remain persistent for a minimal period of at least one complete turnover of the population. In contrast, kelp beds appear unstable, as two of the three kelp beds were grazed down by resident urchin populations during our study (Appendix S1: Fig. S1). That is, overgrazing occurred despite urchin populations
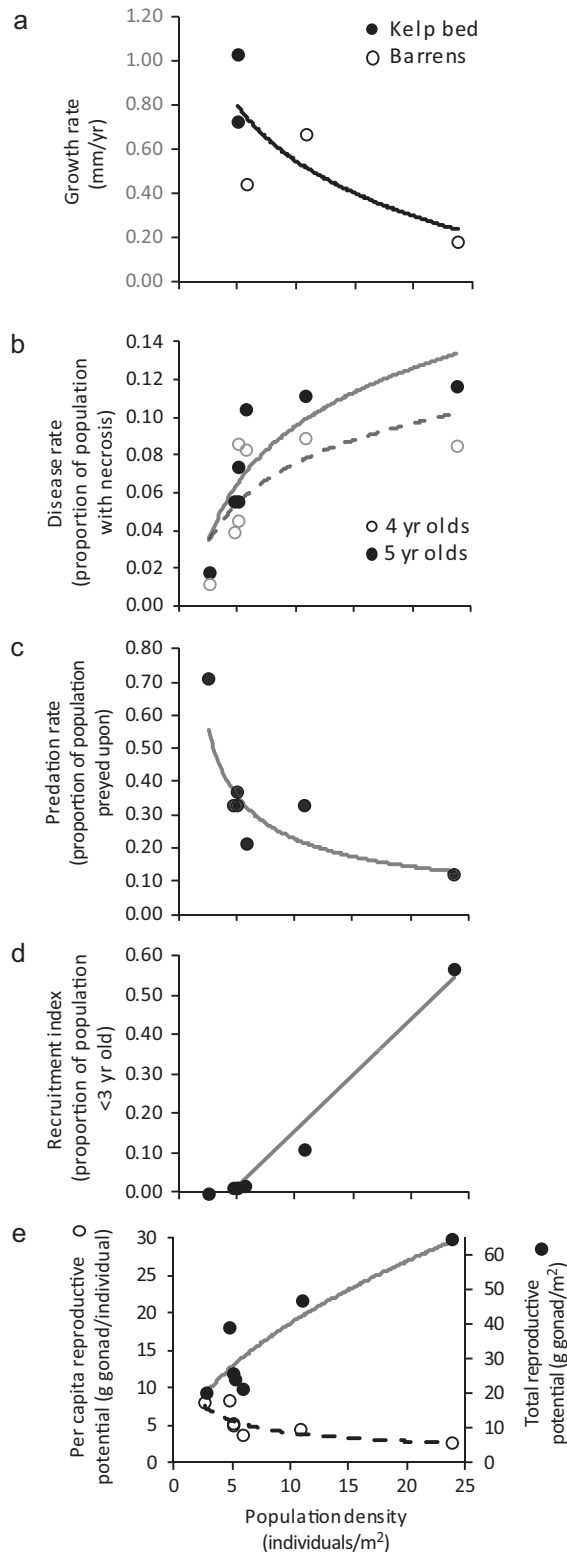
showing stable age structures and broad consistency in abundance. Providing urchin densities remain high within kelp beds and that drift kelp supply remains low, behavioral switch to destructive grazing in exceedance of the tipping-point of kelp bed collapse is to be expected (Harrold and Reed 1985), followed by an ensuing shift in urchin demographics toward the stable barrens regime (Fig. 4).

Potential for unchecked "density-independent" population growth

Projecting the dynamics of *H. erythrogramma* study populations, and for the PPB population overall, age-structured Leslie matrix population projections indicated that all populations had the potential for unchecked population growth beyond maximum observed densities in PPB (i.e., presumed carrying capacity ~60 individuals/m^2) in <40 yr. However, projections of rapid population growth were highly dependent on whether local or regional recruitment rate was simulated (Fig. 5). Likewise, projection of populations crashing to extinction was also contingent on whether local or regional recruitment rates were simulated (Fig. 5). Qualitative similarity in projections between kelp beds vs. barrens populations within locations (Fig. 5b–e, c–f), suggests that potential migration of larger/older adults from barrens toward kelp beds, which was not explicitly accounted for in the modeling, would unlikely affect the overall qualitative nature of local projections over multi-generational time-scales. Moreover, all populations were able to achieve broadly stable trends through time depending on the relative frequency of local to regional recruitment rates (Appendix S6, Fig. S1). For urchin populations in the north and west of PPB (i.e., Williamstown kelp bed, Williamstown barrens, and Long Reef barrens populations), high local recruitment rates were on average only required once in every ~14–18 yr. For these populations, if local recruitment rates occurred more frequently than once every ~1.5 decades, then

(FIG. 7. *Continued*)

populations; $y = -0.361\ln(x) + 1.377$, $R^2 = 0.70$; $F_{1,3} = 10.35$, $P < 0.05$. (b) Disease prevalence among 4-yr-old urchins vs. population density across all $n = 7$ populations (inclusive of St. Leonards kelp and barrens populations); $y = 0.0305\ln(x) + 0.0054$, $R^2 = 0.50$; $F_{1,5} = 5.009$, $P = 0.08$; disease prevalence among 5-yr-old urchins vs. population density, $n = 7$; $y = 0.0441\text{Ln}(x) - 0.0064$, $R^2 = 0.68$; $F_{1,5} = 13.94$, $P = 0.01$. (c) Overall predation rates vs. population density, $n = 7$; $y = 1.04(\text{density})^{-0.66}$, $R^2 = 0.74$; $F_{1,5} = 14.28$, $P < 0.05$. (d) Recruitment index vs. population density, $n = 7$; $y = 0.028x - 0.13$, $R^2 = 0.97$; $F_{1,5} = 152.1$, $P < 0.0001$. (e) Per capita reproductive potential vs. population density (open circles), $n = 7$; $y = 11.88x^{0.53}$, $R^2 = 0.70$; $F_{1,5} = 11.49$, $P < 0.05$; and total population-level reproductive potential vs. population density (solid circles), $n = 7$; $y = 11.88x^{-0.47}$, $R^2 = 0.75$; $F_{1,5} = 14.63$, $P < 0.05$.
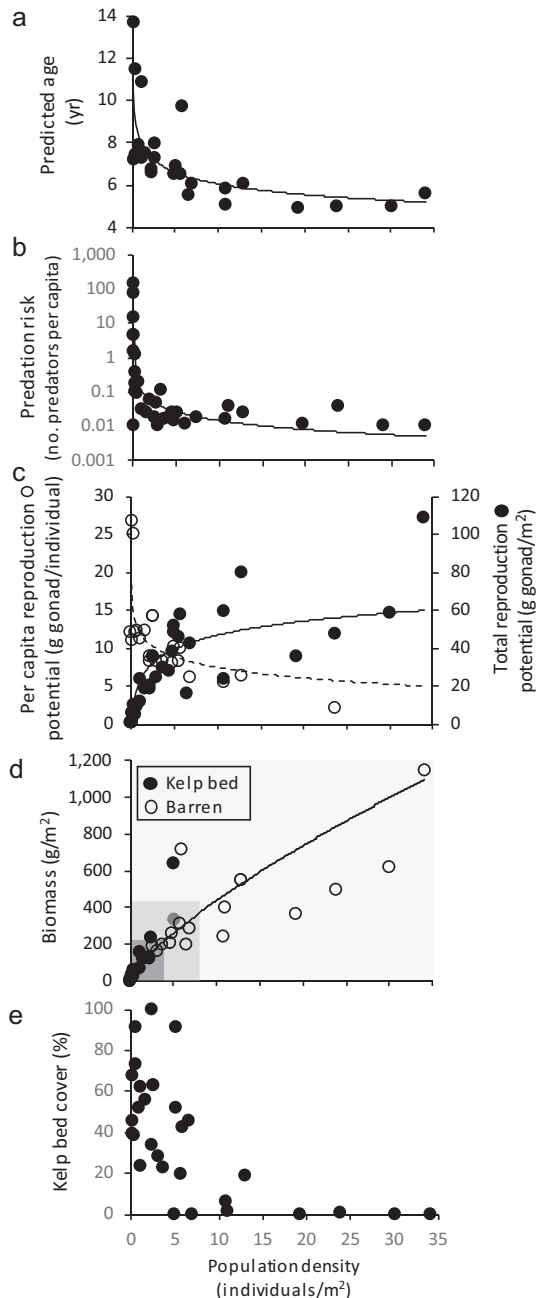
FIG. 7. Density-dependent scaling of sea urchin population parameters across study populations. (a) Growth rate vs. population density across Williamstown (kelp and barrens), Mornington (kelp and barrens), and Long Reef (barrens)

populations increased exponentially beyond the notional carrying capacity within a few generations.

In contrast, for southern PPB where local recruitment rates were low, both Mornington kelp bed and Mornington barrens populations only avoided local extinction, and demonstrated stable trends, if relatively higher regional recruitment rates occurred on average during three out of every 10 years and three out of every four years, respectively. For southern populations, regional recruitment rates every year resulted in unchecked population growth beyond the carrying capacity within 15 or 40 yr for the kelp bed and barrens populations respectively (Fig. 5). Importantly, while projection simulations highlight the importance of recruitment rates for driving population dynamics, hereby our measurement of post-settlement processes in the field reveal that strong density dependence will act to keep exponential population growth in check. Likewise, negative density dependence, for example elevated per capita risk of predation and Allee effects on reproductive success, appears to make it difficult for urchin populations to grow when population size is small and the reef ecosystem exists in the kelp-dominated state.

Collectively our results indicate that catastrophic urchin overgrazing and the maintenance of resultant barrens is underpinned by positive density-dependent feedbacks. That is, urchin populations build in size within kelp beds then further increase once barren grounds have formed, at which point, they appear to oscillate around the carrying capacity. The increase in abundance and biomass on barrens occurs despite declines in individual performance as hereby measured by growth, body condition, and reproductive potential. Importantly, population release of urchins within kelp beds appears to manifest as a switch from negative feedback of predatory control (Fig. 7c) to positive feedback, whereby increasing densities of urchins fuels ongoing population increase throughout the process of overgrazing, acting to increase recruitment and ongoing maintenance of barren grounds (Fig. 8d). Given the strong feedbacks involved, understanding the destabilizing mechanisms triggering urchin population release within kelp beds (e.g., environmental change and/or loss of predators; reviewed by Ling et al. 2015), or alternatively the destabilizing mechanisms occurring within barrens populations (e.g., stochastic population-wide disease events, after Lafferty 2004, Feehan and Scheibling 2014) is important for anticipating critical shifts in urchin populations and entire reefscapes.

FIG. 8. Density-dependent upscaling of sea urchin population parameters across $n = 34$ sites within Port Phillip Bay, September–November 2013. (a) Mean predicted age for given test diameter (based on zone-specific growth rates, see Fig. S9) vs. population density; $y = 8.05(\text{density})^{-0.124}$, $R^2 = 0.55$; $F_{1,29} = 17.53$, $P < 0.001$. (b) Predation risk (no. predators per capita) vs. population density, $y = -0.72\ln(\text{density}) - 2.3458$, $R^2 = 0.70$; $F_{1,28} = 66.46$, $P < 0.0001$. (c) Per capita reproductive potential vs. population density; $y = 10.57(\text{density})^{0.688}$, $R^2 = 0.62$; $F_{1,29} = 47.68$, $P < 0.001$; and total reproductive potential vs. population density; $y = 10.55(\text{density})^{-0.313}$, $R^2 = 0.58$; $F_{1,29} = 39.24$, $P < 0.001$. (d) Biomass vs. population density; $y = 78.32(\text{density})^{0.749}$, $R^2 = 0.91$; $F_1 = 278.4$, $P < 0.0001$; large and small shaded boxes represent respective overgrazing and kelp recovery tipping points in biomass and

(FIG. 8. *Continued*)

density (after Kriegisch et al. 2016). (e) Kelp bed cover vs. population density; given inherent known nonlinearity of overgrazing, fitting of data in panel e was not attempted (Ling et al. 2015); arrows represent urchin population densities of overgrazing (filled arrow) and kelp recovery (open arrow), as per panel d.

Implications for population control

Our findings indicate that attempts to achieve control of urchin populations must be able to recognize density-dependent effects that appear to help drive the evident hysteresis effect of overgrazing, which acts to make recovery of kelp on urchin barren grounds very difficult (Ling and Johnson 2009, 2015). Here, our research indicates that the most effective way of achieving urchin population control is to increase mortality of large urchins in kelp beds via either direct culling/harvesting of urchins (Tracey et al. 2015, Sanderson et al. 2016) and/or rebuilding predator guilds capable of consuming large urchins (Ling and Johnson 2009, Johnson et al. 2013). This approach is likely most effective because of the observed negative feedback between predation rate and population size, with the highest rates of predation occurring for small urchins at low population density within kelp beds. Thus, removing large urchins from kelp beds would effectively achieve control of urchins throughout all size/age-classes of the population.

Conversely, culling of large urchins on barrens would appear to stimulate faster growth of an abundance of smaller/younger individuals that recruit on barrens at a high rate (Andrew and Byrne 2001). That is, removal of larger adults from barrens would simulate the putative effect of disease, whereby disease was more prevalent for older/larger individuals, yet appeared to have little controlling influence on the population dynamics of urchins on barrens. Thus, to affect urchin population control on barrens, all size classes would need to be targeted as occurs during a disease epidemic (reviewed by Feehan and Scheibling 2014) or locally intensive culling (Tracey et al. 2015, Sanderson et al. 2016). However, given the observed density dependence of recruitment, culling beyond highly localized scales (e.g., tens to hundreds of square meters) to achieve sustained urchin population control, would require removal of sufficient urchins to drive down population abundance and ultimately local recruitment rates. Indeed, such an Allee effect has been attributed to the lack of recovery of *Diadema antillarum* to pre-epidemic population abundances in the Caribbean (Levitan et al. 2014, Rodríguez-Barreras et al. 2018). That is, such broad-scale declines in abundance and recruitment appear important for recovery of kelp bed systems beyond localized scales.

Conclusion

Regime shifts vary in their nature, from linear to abrupt and from reversible to varying degrees of irreversibility depending on the strength of hysteresis (reviewed by Scheffer et al. 2001). However, linking observed regime shifts to critical transition theory is not an easy task (Conversi et al. 2015). For real ecosystems, validating regime shift characteristics such as the existence of tipping-points and stabilizing or destabilizing feedbacks defining hysteresis is only practically achievable through field experimentation. Here our study, involving extensive collection of field data and population modeling, has revealed that shifts in sea urchin population dynamics underpin the stability of urchin barrens as an alternative stable state of collapsed kelp beds. This indicates that management of desired ecosystem states must consider potential state-dependent population feedbacks, whereby management efforts are likely to be far more achievable prior to the establishment of new regimes whereby reinforcing population feedbacks can create hysteresis. Finally, while much attention is justifiably concentrated on detection of early warning signals of imminent ecological collapse, which typically focuses on temporal variability in landscape features or derived community metrics, here we have shown that understanding the population dynamics of single but pivotal species can be important for understanding pending ecological change and resultant hysteresis once change has occurred.

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Supporting Information