



# Habitat fragmentation causes collapse of kelp recruitment

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**ABSTRACT:** Kelp forests in many regions are experiencing disturbance from anthropogenic sources such as ocean warming, pollution, and overgrazing. Unlike natural disturbances such as storms, anthropogenic disturbances often manifest as press perturbations that cause persistent alterations to the environment. One consequence is that some kelp forests are becoming increasingly sparse and fragmented. We manipulated patch size of the kelp *Ecklonia radiata* over 24 mo to simulate persistent habitat fragmentation and assessed how this influenced the demography of macro- and microscopic juvenile kelp within the patches. At the beginning of the experiment, patch formation resulted in short-term increases in *E. radiata* recruitment in patches <1 m<sup>2</sup>. However, recruitment collapsed in those same patches over the extended period, with no recruits observed after 15 mo. Experimental transplants of microscopic and macroscopic juvenile sporophytes into the patches failed to identify the life stage impacted by the reductions in patch size, indicating that the effects may be subtle and require extended periods to manifest, and/or that another life stage is responsible. Abiotic measurements within the patches indicated that kelp were less able to engineer the sub-canopy environment in smaller patches. In particular, reduced shading of the sub-canopy in smaller patches was associated with proliferation of sediments and turf algae, which potentially contributed to the collapse of recruitment. We demonstrate the consequences of short- and longer-term degradation of *E. radiata* habitats and conclude that habitat fragmentation can lead to severe disruptions to kelp demography.

**KEY WORDS:** *Ecklonia radiata* · Macroalgae · Patch · Canopy · Ecosystem engineer · Abiotic · Press perturbation

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## 1. INTRODUCTION

Kelp (Order Laminariales) dominate shallow coastal environments in temperate and subpolar latitudes around the world (Steneck & Johnson 2014, Krumhansl et al. 2016, Wernberg et al. 2019a). These ecosystem engineers (Jones et al. 2010) create spatially complex habitats with sub-canopy environments that support diverse and productive ecosystems (Teagle et al. 2017, Wernberg et al. 2019b). Most natural disturbances within kelp forests can be described as pulse perturbations that cause rapid alterations to species

and the habitat (Bender et al. 1984, Reed et al. 2011). For example, storms may remove or thin the kelp canopy (Kitting 1937, Dayton & Tegner 1984), and change sub-canopy conditions (e.g. light, sedimentation) and the understory community (Dayton et al. 1984, Kennelly 1987a). Increasingly, however, kelp habitats around the world are experiencing disturbances from anthropogenic sources, such as ocean warming and overgrazing (e.g. Johnson et al. 2011, Krumhansl et al. 2016, Wernberg et al. 2019a). Many of these anthropogenic disturbances manifest as press perturbations with persistent alterations to the envi-

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ronment and the kelp canopy. Kelp habitats in many places around the world are suffering degradation and becoming increasingly sparse and fragmented (Ling et al. 2015, Krumhansl et al. 2016, Filbee-Dexter & Wernberg 2018, Wernberg et al. 2019a).

Marine heatwaves and ocean warming have caused significant losses of kelp in multiple locations globally (Johnson et al. 2011, Wernberg et al. 2016, Smale et al. 2019). Despite wholesale mortality in some areas, variation in thermal tolerance can result in patchy resistance and recovery, especially at the margins of warming events. Increasing water temperatures are also linked to overgrazing of kelp by range-extending herbivores such as subtropical fishes (Vergés et al. 2016) and the urchin *Centrostephanus rodgersii* (Johnson et al. 2011, Ling & Keane 2018). In these cases, kelp habitats are persistently disturbed and fragmented into decreasingly small patches prior to extirpation (Flukes et al. 2012, Vergés et al. 2016, Ling & Keane 2018).

Habitat fragmentation and reductions in patch size will likely result in increased edge effects (by increasing the ratio of patch edge to patch area) and changes to the abiotic conditions within these areas (Dayton et al. 1984, Murcia 1995, Layton et al. 2019a). These effects may be of particular importance if they interrupt internal drivers that support demographic processes, such as intraspecific facilitation via an 'environment-engineer feedback' (Cuddington et al. 2009, Jones et al. 2010, Layton et al. 2019a). Indeed, breakdown of this feedback may explain the slow recovery of some kelp species often observed after large-scale losses (Dayton et al. 1992, Connell et al. 2008; also see Angelini & Silliman 2012).

To examine whether persistent reductions in patch size affect the demography of the kelp *Ecklonia radiata*, we created 10 different-sized patches of kelp, ranging from 0.1–2025 m<sup>2</sup>, and maintained these for 24 mo to simulate persistent local-scale habitat fragmentation. Within the experimental patches, we assessed: (1) changes in density of juvenile and adult *E. radiata*, (2) survivorship and recruitment of microscopic and macroscopic juvenile kelp, and (3) whether changes to the sub-canopy abiotic environment (e.g. irradiance, sedimentation, scour, and water flow) caused by reductions in patch size were associated with shifts in kelp demography. We hypothesized a positive relationship between patch size and recruitment of *E. radiata*, especially at smaller patch sizes, where a greater patch edge to patch area ratio creates proportionately larger areas where the environment-engineer feedback and sub-canopy

environment may be compromised. Further, while we hypothesized that reductions in patch size will increase irradiance within the sub-canopy, the effects on sedimentation, scour, and water flow within the sub-canopy are less understood and predictable, despite these abiotic factors having the potential to shape sub-canopy communities (Kennelly 1987a, Wood 1987, Flukes et al. 2014) and kelp demographics (Kirkman 1981, Schiel & Foster 2006, Watanabe et al. 2016).

## 2. MATERIALS AND METHODS

### 2.1. Study species and site

*Ecklonia radiata* is a stipitate kelp (sensu Dayton et al. 1984) that rarely grows taller than 1.5 m. This species is the most widespread and abundant habitat-forming kelp across Australasia and provides the foundation of the Great Southern Reef, Australia's continental-scale temperate reef system that supports high levels of biodiversity, endemism, and economic value (Bennett et al. 2016, Wernberg et al. 2019b).

The field site, located within Fortescue Bay in south-east Tasmania, Australia (43.1374° S, 147.9682° E; Fig. 1), is semi-exposed, subject to irregular ocean swells, and features extensive rocky reef dominated by *E. radiata*. In February 2014, we established 10 approximately square patches of kelp of 0.1, 0.3, 0.9, 2.7, 9, 25, 73, 225, 676, and ~2025 m<sup>2</sup> at a depth of 14 m within a largely continuous stand of *E. radiata* (mean  $\pm$  SE: 14.5  $\pm$  2.5 kelp m<sup>-2</sup>, n = 30) and across an area of similar reef profile, wave exposure, turbidity, and tidal current. This range of patch sizes allowed detection of potential critical thresholds at small patch sizes and steady progression up to the larger 'intact' kelp habitats (>500 m<sup>2</sup>). Moreover, *E. radiata* forests often contain patches of this size, especially following habitat degradation (e.g. urchin overgrazing). Patches were separated from each other by at least 5 m and created by clearing all canopy-forming algae (i.e. any species with adults >300 mm in height) from a 2 m wide 'buffer' around each patch: this distance is larger than even the longest *E. radiata*, and so ensured that patches were physically isolated from the surrounding stand of kelp. Buffer areas were monitored every 6 wk, and any new canopy-forming algae were removed. The largest patch did not have a buffer, as it was a naturally isolated (by sand) patch reef. *Centrostephanus rodgersii* urchins were removed

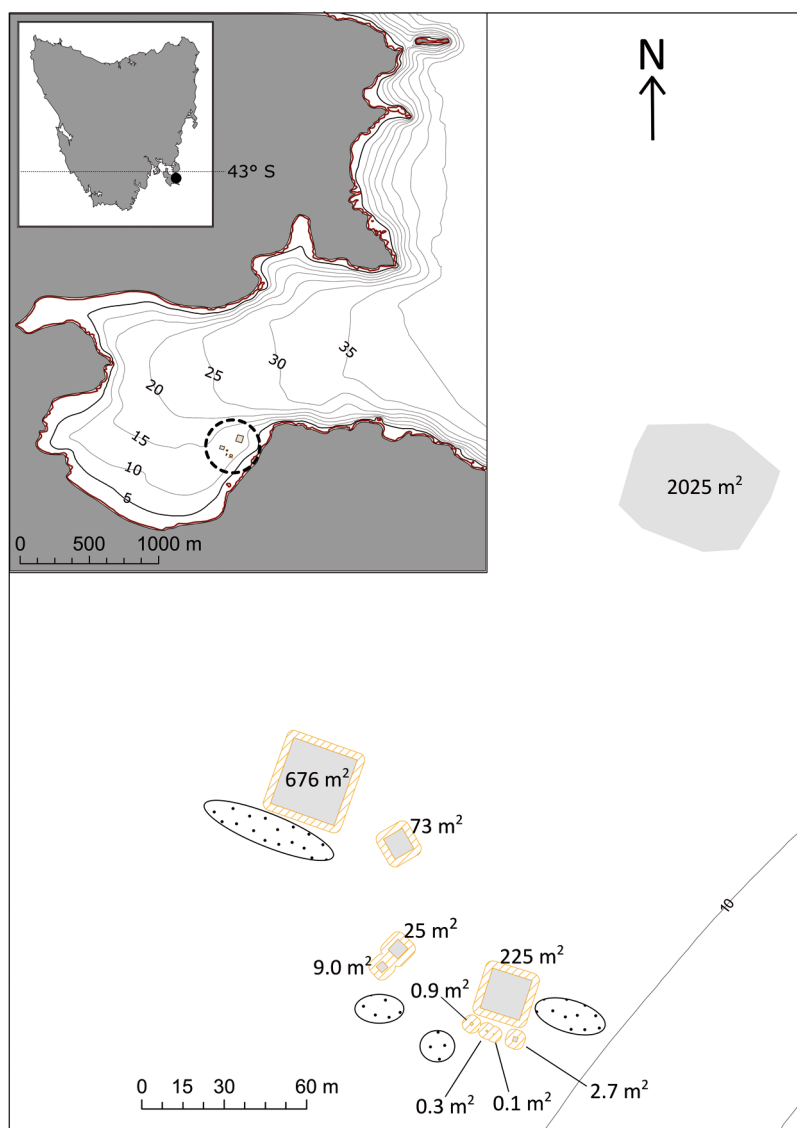


Fig. 1. Experimental patches at the study site within Fortescue Bay, Tasmania (insets). Red line indicates coastline (inset). Patches (light grey) were situated within a largely continuous stand of *Ecklonia radiata* kelp (not illustrated) and were physically isolated by 2 m wide 'buffers' (approximate dimensions depicted as hatched areas) that were cleared of any canopy-forming macroalgae. Patches were separated from each other by at least 5 m. The largest patch (2025 m<sup>2</sup>, irregular shape) was naturally occurring and surrounded by sand. The black-dotted areas represent approximate locations of sea urchin (*Centrostephanus rodgersii*) barrens

from the patches and buffer areas at the beginning of the experiment (~570 individuals), as destructive overgrazing by this range-extending species (see Johnson et al. 2011, Flukes et al. 2012) could influence the experimental treatments (i.e. decrease patch size) and inhibit our assessment of the primary aims.

## 2.2. Kelp demographics

### 2.2.1. Juvenile and adult sporophyte densities

Kelp density assessments were conducted at the start of the experiment (February 2014), and then seasonally (every  $12.5 \pm 1$  wk, mean  $\pm$  SE) in autumn 2014 (April), winter 2014 (July), spring 2014 (October), summer 2015 (February), autumn 2015 (May), winter 2015 (July), spring 2015 (October), and summer 2016 (January). *E. radiata* sporophytes were classed as either juveniles (stage 1) or adult (stages 2 and 3, sensu Kirkman 1981), which provided estimates of recruitment (stage 1) and the proportion of juveniles that survived to mature (stages 2 and 3) in each patch. In the 5 smallest patches ( $\leq 9$  m<sup>2</sup>), all visible ( $>5$  mm) sporophytes were censused, whereas the 5 largest patches were subsampled, and all visible sporophytes were counted within 5 randomly positioned 1 m<sup>2</sup> quadrats. Sporophyte density was then scaled to 1 m<sup>2</sup>. This scaling exaggerated estimates of sporophyte abundance in patches  $<1$  m<sup>2</sup>, although it did not affect the overall interpretation of results.

### 2.2.2. Growth and survivorship of macroscopic juveniles

To determine the growth rates and survivorship of macroscopic juvenile kelp in each patch, stage 1 juvenile sporophytes (50–170 mm in length) were collected from the surrounding stand of *E. radiata* and transplanted into each patch. Each juvenile was measured to the nearest 2 mm and hole-punched at the proximal end of the lamina above the meristem to determine growth. Ten juvenile sporophytes were then threaded through the twine of rope at 100 mm intervals, and 1 rope was secured in the centre of each experimental patch. After  $42 \pm 1$  d, the growth of each transplanted sporophyte was measured to the nearest 2 mm *in situ*, and the sporophyte was hole-punched again in the original proximal position. If a

sporophyte was missing, the position was noted, and the individual was recorded as not surviving. After  $90 \pm 5$  d, the ropes were collected, and growth and survivorship were determined again. Preliminary analyses revealed that growth rates of the sporophytes ( $\text{mm wk}^{-1}$ ) after 90 d were linear and independent of initial sporophyte length (Table S1 in the Supplement at [www.int-res.com/articles/suppl/m648p111\\_supp.pdf](http://www.int-res.com/articles/suppl/m648p111_supp.pdf)). Juveniles were transplanted in autumn (March), winter (June), and spring (September) in 2015 and in summer in 2016 (January), although juveniles transplanted during summer 2016 were only installed for 42 d due to termination of the experiment and destructive sampling of the patches.

### 2.2.3. Post-recruitment survivorship of microscopic sporophytes

Lab-cultured microscopic sporophytes were outplanted to examine the survivorship of this life stage in each patch. Blank microscope slides deployed at the same times measured background rates of natural recruitment of *E. radiata* propagules and acted as controls. Outplanting occurred in spring 2014 and spring 2015. The reproductive tissue for spore-release was collected from stage 3 *E. radiata* from the surrounding stand of kelp, and culturing following the methods of Mabin et al. (2013) and Tatsumi & Wright (2016). Briefly, zoospores were settled onto fully-frosted microscope slides submerged in UV-sterilized and filtered ( $0.2 \mu\text{m}$  pore-size) seawater, and then cultivated for 42 d. Following this period, 10 randomly selected slides were assessed to determine mean sporophyte abundance prior to outplanting ( $\sim 8050 \pm 400$  [mean  $\pm$  SE] sporophytes slide $^{-1}$ ). Four randomly selected slides with cultured sporophytes, and 4 control slides (which had been curing in filtered seawater during the culturing process) were then attached in random order to a plastic rack. The racks were transported to the experimental site submerged in seawater, and 3 racks (i.e. 12 slides with sporophytes and 12 control slides) were installed in the approximate centre of each patch. After  $49 \pm 3$  d the racks were collected and transported back to the lab for quantification of sporophytes.

### 2.3. Abiotic environment

Measurement of sub-canopy irradiance, water flow, sediment deposition, and sediment accumulation were conducted following the methods of Layton

et al. (2019a). Briefly, cylindrical sediment traps positioned above and below the kelp canopy in the centre of each patch measured ambient and sub-canopy rates of sediment deposition, respectively (dry weight  $\text{g d}^{-1} \text{m}^{-2}$ ). Measurement occurred during autumn (March), winter (June), spring (September) in 2015 and summer 2016 (January) over a period of  $44 \pm 1$  d. The depth of accumulated sediments covering the substratum was measured to the nearest 1 mm using a small ruler at 2–8 random locations within each patch (depending on patch size; Table 1) during autumn (March), winter (June), and spring (September) in 2015 and summer 2016 (January). Ambient and sub-canopy water flow was assessed using the dissolution of plaster clod cards (% mass loss) positioned above and below the kelp canopy, respectively. Clod cards were installed for 72 h in autumn (March), winter (June), and spring (September) in 2015 and summer 2016 (February). A LI-COR LI-193 spherical sensor ( $330^\circ$ ) was used to measure photosynthetically active radiation (hereafter called irradiance) beneath and above the kelp canopy in the centre of each patch. These measurements occurred over 60 s in each position and took place in autumn (March), winter (June), and spring (September) in 2015, and summer (January) 2016 (although data obtained from this final period were unusable due to equipment malfunction).

Scour, i.e. the physical abrasion caused by kelp lamina, was quantified using glazed ceramic tiles ( $200 \times 200$  mm) coated with black paint. The paint was easily removed when kelp laminae brushed the tile, and so the percentage of paint removed provided a relative measure of scour across patch sizes. The percentage paint loss over  $\sim 72$  h for each tile was determined from photographs using ImageJ

Table 1. Details of the experimental *Ecklonia radiata* patches in Fortescue Bay, Tasmania. See Fig. 1 for a map of the study site

Patch	Patch size ( $\text{m}^2$ )	$\text{Log}_3(\text{patch size})$ [ $\log_3(\text{m}^2)$ ]	Sediment accumulation replicates (n)
1	0.1	−2.10	2
2	0.3	−1.10	2
3	0.9	−0.10	4
4	2.7	0.90	8
5	9	2.00	8
6	25	2.93	8
7	73	3.91	8
8	225	4.93	8
9	676	5.93	8
10	2025	6.93	8

software (v. 1.48), and mean scour was quantified for each patch. Scour was measured during autumn 2015 (March) and summer 2016 (January). Sampling was also attempted during winter and spring but was abandoned due to inclement weather.

## 2.4. Data analysis and statistics

Abiotic data were time-averaged across seasons to simplify analyses and temporal autocorrelation, where replicates represent the number of seasons when measurements were taken (i.e. sediment deposition  $n = 4$ , sediment accumulation  $n = 4$ , water flow  $n = 4$ , irradiance  $n = 3$ , and scour  $n = 2$ ).

Data were primarily analysed using linear regression of the response variable against patch size. Test assumptions were assessed using diagnostic plots of model residuals, and data were transformed when necessary based on values of  $\lambda$  from Box-Cox plots. In one instance, data could not be appropriately transformed due to the influence of an outlier. For completeness, we present the full data along with the test after excluding the outlier. Patch size was  $\log_3$  transformed prior to testing, reflecting that the span of patch sizes followed an approximately  $\log_3$  scale (see Table 1 for transformed patch sizes). Principal component analysis (PCA) was used for multivariate exploration of the relationship between patch size and abiotic factors. PCAs were based on correlation matrices and used mean measurements per patch to achieve a balanced design. For clarity, PCA figures display patch numbers instead of patch size (numbers increase from 1 to 10 from smallest to largest; Table 1).

Data on the density of juvenile kelp were often strongly nonlinear, but analyses using generalized linear models and generalized additive models were rejected due to uncaptured curvilinearity and overfitting, respectively. Subsequently, some of these data were analysed using nonlinear regression. Nonlinear regression uses an iterative procedure to estimate model parameters based on a user-specified function, which we specified as a negative-power function based on graphical exploration of the data. P-values and confidence intervals cannot be robustly calculated for nonlinear regression (Bates & Watts 1988, Quinn & Keough 2002), so we primarily utilised nonlinear regression as a graphical tool. This approach was used sparingly and only when important curvilinearity was not captured by linear regression. A pseudo- $r^2$  was calculated for nonlinear regression models from the linearised form of a log-log model (of which a negative-power function is the nonlinear form). Analyses

were conducted using the 'MASS', 'lattice' (both for diagnostics and regression testing), 'nlstools' (for non-linear regression), and 'ggfortify' (for PCA) packages in R (version 3.2.5, R Core Team 2018), with  $\alpha = 0.05$ . Figures are presented with untransformed response variables for clarity and were produced using the 'ggplot2' package in R, and 'Inkscape'.

## 3. RESULTS

### 3.1. Density of juvenile sporophytes

Initial mean density of juvenile *Ecklonia radiata* was  $1.7 \pm 0.28 \text{ m}^{-2}$  (mean  $\pm$  SE) and did not differ across patches (Table 2). In autumn 2014, approximately 8 wk after the creation of the patches, there was a dramatic increase in the density of juveniles in the 4 smallest patches ( $<3 \text{ m}^2$ , Fig. 2). Nonlinear regression identified a strong negative power relationship between density of juveniles and patch size (Fig. 3A). The density of juvenile sporophytes in most patches continued to increase in winter 2014, and for many patches, including the 4 smallest, the densities observed in this season were the highest during the study (Fig. 2). The highest density recorded ( $\sim 170$  juveniles  $\text{m}^{-2}$ ) was in the smallest patch, although this was exaggerated somewhat due to scaling of density per  $\text{m}^2$ . During this season, the relationship between density of juveniles and patch size was again strongly and negatively nonlinear (Fig. 3B). In spring 2014, the density of juveniles in most patches

Table 2. Regressions of density of juvenile *Ecklonia radiata* and patch size over 8 seasons. The response variable and associated transformations are noted in the first column. Season notation (A–H) matches Figs. 2 & 3. Significant relationships for linear regression tests denoted in **bold**

Data analysed	$F$ (df)	p
Initial $(Y + 0.01)^{0.75}$	1.946 (1, 8)	0.201
(A) Autumn 2014 <sup>a</sup>		
(B) Winter 2014 <sup>a</sup>		
(C) Spring 2014 $(Y)^{-0.55}$	32.62 (1, 8)	<b>&lt;0.001</b>
(D) Summer 2015 <sup>a</sup>		
(E) Autumn 2015 <sup>a</sup>		
(F) Winter 2015 $(Y + 0.01)^{0.3}$	12.59 (1, 8)	<b>0.008</b>
(G) Spring 2015 $(Y + 0.01)^{0.1}$	5.601 (1, 8)	<b>0.045</b>
(H) Summer 2016 <sup>b</sup> $(Y + 0.01)^{0.25}$	21.89 (1, 7)	<b>0.002</b>

<sup>a</sup>Nonlinear relationship that was unable to be tested for significance (see Section 2.4 for details); <sup>b</sup>Model where an outlier barred testing; in this case, the presented results are with the outlier excluded



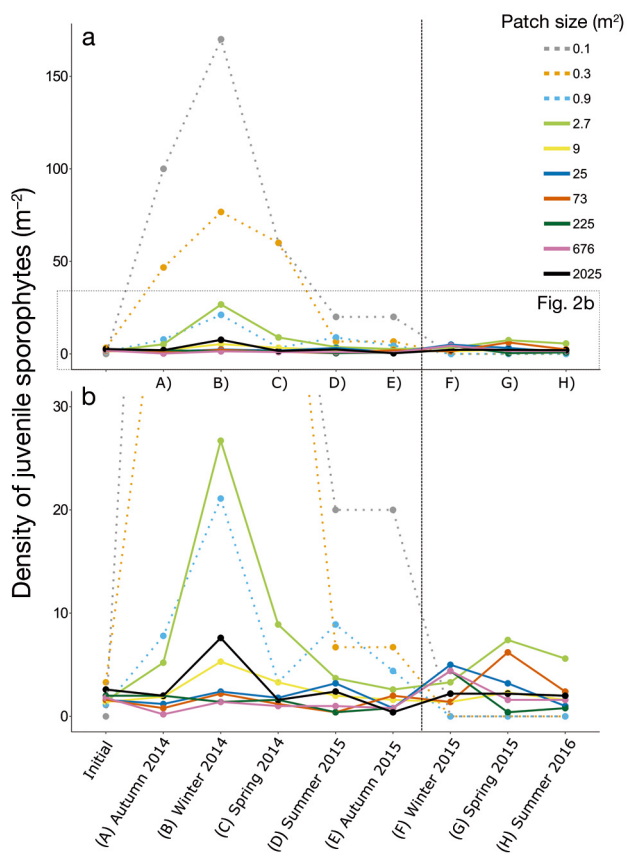


Fig. 2. Density of juvenile *Ecklonia radiata* in 8 seasons for 10 different patch sizes. Season notation (A–H) matches Table 2: (a) full scale, (b) magnified version with the y-axis scale adjusted for clarity. The 3 smallest patches (those  $<1\text{ m}^2$ ) are shown as dotted lines and the remaining patches as solid lines. The vertical dashed line indicates the time after which juvenile kelp were no longer present in the 3 smallest patches

declined almost as steeply as it had risen, but the overall pattern was still of decreasing density of juveniles with increasing patch size. This relationship was linear and significant during spring 2014 (Fig. 3C, Table 2), and strongly nonlinear (and still negative) during summer 2015 and autumn 2015 (Fig. 3D,E). This period, approximately 8 mo after the patches were created, was the beginning of a general decline in the density of juveniles in the smaller patches, from which the 3 smallest patches never recovered (Figs. 2 & 3).

Approximately 16 mo after the beginning of the experiment and between the autumn and winter 2015 samples, the density of juveniles in the 3 smallest patches declined to 0 (Fig. 2). For the remaining 8 mo of the experiment, no juvenile sporophytes were detected in these patches, despite this time period including the season of peak recruitment. Over the short pe-

riod between the autumn and winter 2015 samples, the relationship between the density of juveniles and patch size also changed dramatically, shifting from strongly negative in autumn to significantly positive in winter, so that densities of juvenile *E. radiata* now increased significantly with patch size (Fig. 3E,F, Table 2). Unlike in the smallest patches, in patches  $>2.7\text{ m}^2$  there was a small increase in the density of juveniles over the same period (Fig. 2).

The remaining seasons saw relatively minor changes in the density of juveniles, although some patches experienced slight increases in juveniles in spring 2015 (Fig. 2). Similarly, the relationship between the density of juveniles and patch size remained significantly positive (Fig. 3, Table 2). The final sampling period in summer 2016 saw slight decreases in the density of juveniles in most patches from the previous seasons (Fig. 2), although there was still a relatively high density of juveniles in the  $2.7\text{ m}^2$  patch (i.e. the outlier in Fig. 3H). Excluding the outlier, the relationship with patch size was significant and positive as in the previous 2 seasons (Fig. 3H, Table 2).

### 3.2. Density of adult sporophytes

The initial density of adults at the start of the experiment was mostly similar among patches, although somewhat elevated in the 2 smallest patches due to scaling density per  $\text{m}^2$  (Fig. 4). In most patches throughout the experiment, the density of adult sporophytes was relatively stable, the exceptions being the  $0.1$ ,  $0.3$ , and  $2.7\text{ m}^2$  patches (again, fluctuations are accentuated by scaling). Seasonal peaks in the density of adults were less clear than for juveniles, but in the smallest patches, the maximum density of adult kelp tended to occur in summer and autumn 2015 (Fig. 4). Over the final 8 mo of the study (i.e. the period after recruitment had declined to 0), the densities of adult sporophytes in the 3 smallest patches slowly declined but were still equal to or higher than the other patches.

### 3.3. Transplanted macroscopic juveniles

There was no effect of patch size on the survivorship of transplanted macroscopic *E. radiata* juveniles at either the 42 or 90 d period within seasons or when pooled annually (Table S2). However, the growth rates of juveniles transplanted during autumn and spring 2015 did increase with patch size, but only over the initial 42 d period (Table S2). During winter

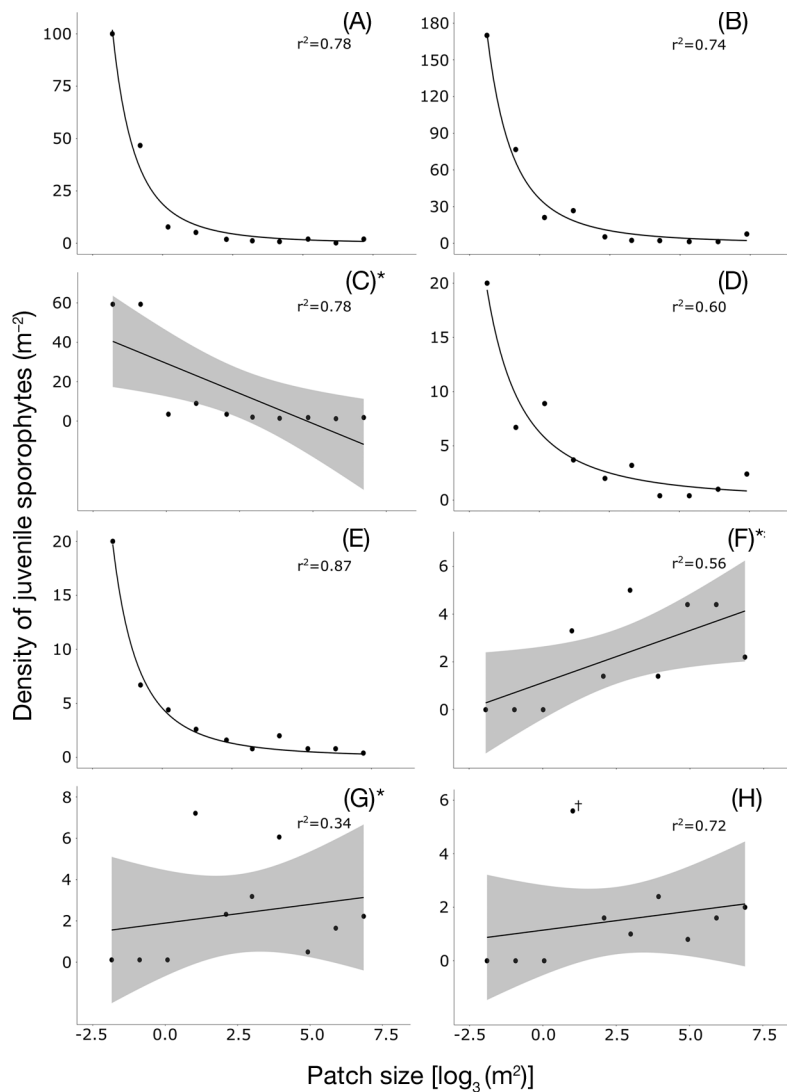


Fig. 3. Nonlinear and linear regression of the relationship between density of juvenile *Ecklonia radiata* and patch size over 8 seasons. Season notation (A–H) matches Table 2 and Fig. 2. Significant non-zero slopes ( $p < 0.05$ ) for linear regression tests are denoted with an asterisk. Nonlinear regressions cannot be tested for significance. The cross in panel (H) denotes the outlier that, when removed, resulted in a significant relationship (see Table 2)

2015 or summer 2015, growth rates were not influenced by patch size.

### 3.4. Recruitment and survivorship of microscopic sporophytes

During spring 2014, natural recruitment onto the blank ‘control’ slides was extremely low, only 3 microscopic sporophytes were observed across all the patches, and so these data were not analysed. During spring 2015, natural recruitment of microscopic sporo-

phytes occurred across all but 2 patches with a total of 55 recruits, although this was not influenced by patch size ( $F_{1,8} = 0.046$ ,  $p = 0.836$ ). As such, we did not adjust estimates of the survivorship of outplanted microscopic sporophytes for natural recruitment (although the test results did not differ if the adjustment was made).

During spring 2014, the number of surviving outplanted microscopic sporophytes decreased significantly with patch size ( $F_{1,8} = 6.992$ ,  $p = 0.030$ ) (Fig. 5). In contrast, survivorship of the microscopic sporophytes outplanted in spring 2015 was not influenced by patch size ( $F_{1,8} = 0.555$ ,  $p = 0.478$ ) (Fig. 5), although survivorship in spring 2015 overall was far greater relative to spring 2014 (totals of 930 vs. 472 across all slides).

### 3.5. Abiotic measurements

There was no effect of patch size on dissolution rates of above-canopy clod cards (i.e. ambient water flow) (Table S3). Similarly, we detected no effect of patch size on the relative dissolution rates of sub-canopy clod cards ( $F_{1,38} = 2.559$ ,  $p = 0.118$ ) (Fig. 6B). However, rates of scour did increase significantly with patch size ( $F_{1,18} = 7.820$ ,  $p = 0.012$ ), and scour in patches  $< 3 \text{ m}^2$  was typically very low (Fig. 6C).

Mean  $\pm$  SE above-canopy irradiance was  $162 \pm 7 \mu\text{mol photon m}^{-2} \text{ s}^{-1}$ , but this varied widely across seasons ( $100\text{--}235 \mu\text{mol photon m}^{-2} \text{ s}^{-1}$ ), and maximum values were up to  $396 \mu\text{mol}$

$\text{photon m}^{-2} \text{ s}^{-1}$ . Above-canopy irradiance increased significantly with patch size during autumn and winter (but not spring) (Table S3), which we interpret as a spurious pattern arising from chance timing of sampling; in autumn, irradiance correlated with the time of the day that measurements were made, while in winter it related to changing cloud cover. This did not influence interpretation of the results, however, since the response of sub-canopy irradiance showed the opposite trend, with sub-canopy irradiance decreasing significantly with patch size ( $F_{1,118} = 58.5$ ,  $p < 0.001$ ) (Fig. 6D).

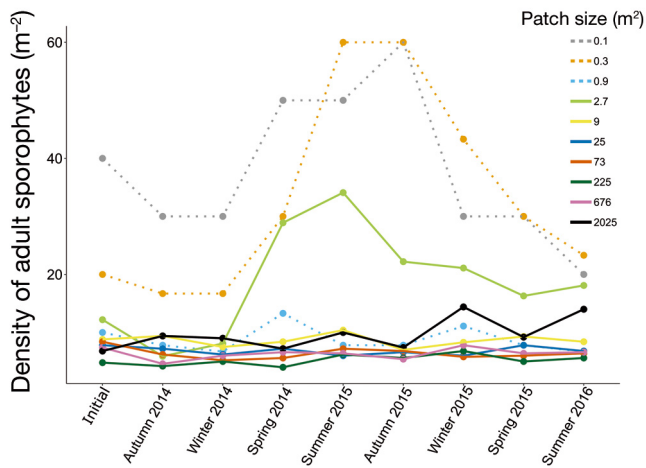


Fig. 4. Density of adult *Ecklonia radiata* in 8 seasons for 10 different patch sizes. The 3 smallest patches (those <1 m<sup>2</sup>) that experienced an eventual collapse in recruitment (see Fig. 2) are shown as dotted lines and the remaining patches as solid lines

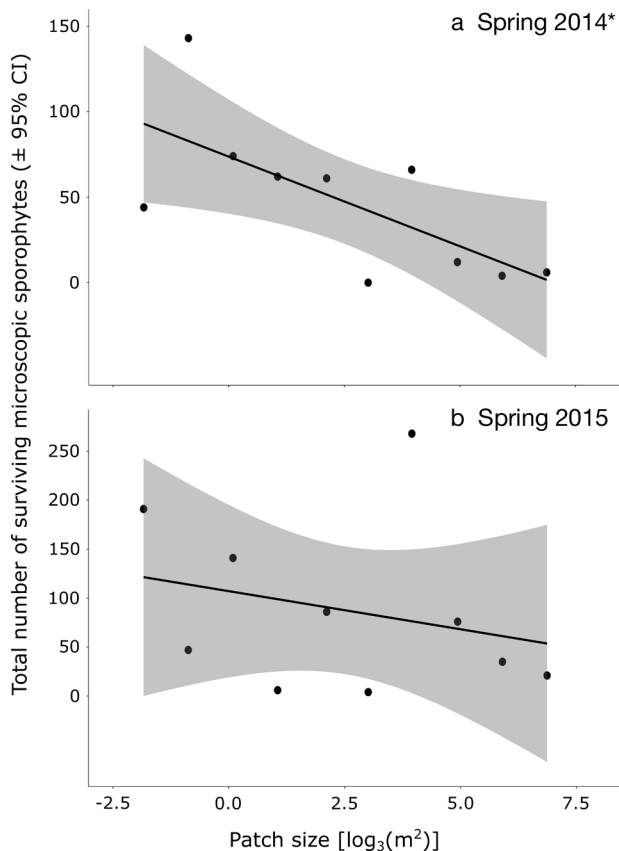


Fig. 5. Linear regression of the relationship between total number of surviving *Ecklonia radiata* microscopic sporophytes ~49 d after outplanting in (a) spring 2014 and (b) spring 2015. Seasons with significant relationships ( $p < 0.05$ ) are denoted with an asterisk

The mean  $\pm$  SE rate of above-canopy sediment deposition was  $54 \pm 7$  g DW d<sup>-1</sup> m<sup>-2</sup>, but we detected no influence of patch size on above-canopy (Table S3) or sub-canopy rates of sediment deposition ( $F_{1,38} = 0.291$ ,  $p = 0.593$ ) (Fig. 6E). The sediments collected in the traps were mostly fine sands (250–62  $\mu$ m), with some silt and coarser sands. Notably, we rarely observed any sediments freely accumulated on the substratum. Instead, sediment particles accumulated within algal turfs consisting mostly of filamentous green and red algae, to form a turf-sediment matrix. Overall, we detected no influence of patch size on the accumulation of sediments within the sub-canopy ( $F_{1,18} = 2.313$ ,  $p = 0.137$ ). However, during the seasons that coincided with and followed the collapse in recruitment (i.e. winter and spring 2015, and summer 2016), we observed that the turf-sediment matrix was deeper in smaller patches and that sediment accumulation decreased significantly with patch size ( $F_{1,28} = 9.825$ ,  $p = 0.004$ )

PCA of the multivariate abiotic data captured ~83% of dataset variability along components 1 and 2. The 3 smallest patches were separately clustered along component 1 and were characterised by high levels of sub-canopy irradiance, sediment accumulation, and water flow (Fig. 6A). The remaining patches were scattered along component 2.

## 4. DISCUSSION

We observed that a persistent press disturbance, i.e. the reduction in the size of *Ecklonia radiata* patches, ultimately resulted in the collapse of recruitment of juvenile kelp in patches <1 m<sup>2</sup>. However, this disturbance initially resulted in a short-term increase in recruitment in those same patches. Experimental transplants of microscopic and macroscopic juvenile sporophytes did not identify the life stage impacted by the persistent reductions in patch size. However, abiotic measurements suggest patches that experienced recruitment collapse had lower rates of scour and higher sub-canopy irradiance and sediment accumulation relative to larger patches. The results demonstrate the protracted effects of disturbance and the consequences of short- and long-term degradation of *E. radiata* habitats.

### 4.1. Responses to disturbance

The swiftness of the increase in recruitment observed in the 4 smallest patches immediately follow-



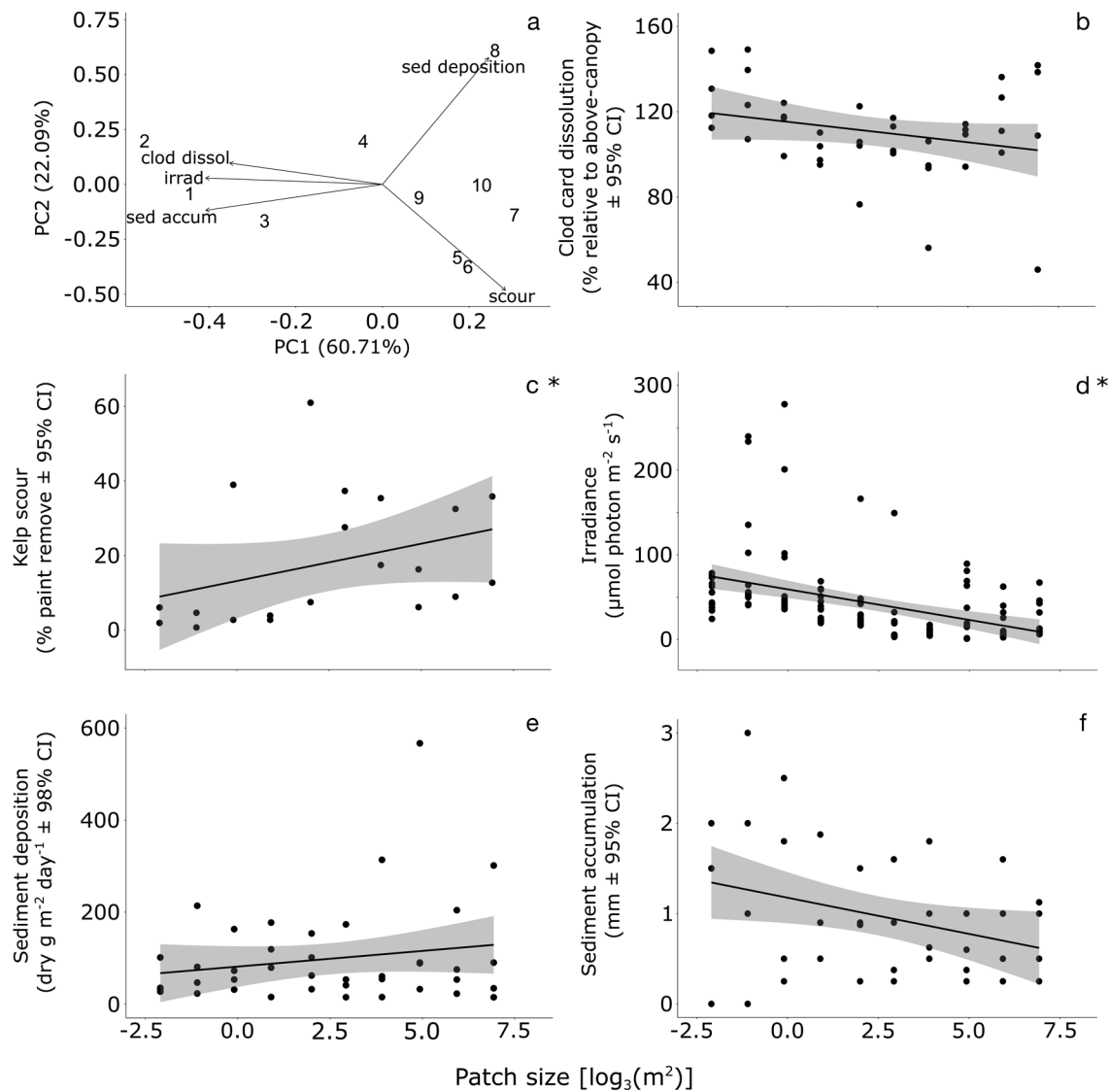


Fig. 6. PCA and effects of *Ecklonia radiata* patch size on sub-canopy abiotic factors: (a) PCA of sub-canopy abiotic factors, with patches labelled 1–10 from smallest to largest (see Table 1); (b) water flow; (c) kelp scour; (d) irradiance; (e) sediment deposition; (f) depth of accumulated sediments on the reef substratum. Abiotic factors with significant relationships ( $p < 0.05$ ) are denoted with an asterisk

ing patch creation means it was unlikely the result of chance settlement of new kelp propagules. Moreover, patch creation occurred in summer, the period of lowest reproductive output for *E. radiata* (Mabin et al. 2013). Instead, this recruitment pulse likely originated from the growth of pre-existing, but non-visible, sporophytes already within the sub-canopy. This phenomenon, often described as a 'seed bank' (Kinlan et al. 2003, Schiel & Foster 2006), occurs in many large brown macroalgae, including *E. radiata* (Kirkman 1981, Kennelly 1987a, Flukes et al. 2014), and is likely a life-history trait that aids rapid replen-

ishment of the canopy following a pulse disturbance (Kirkman 1981, Kinlan et al. 2003).

The mechanism that drives the suspension and resumption of development is still unknown, but low and high light levels, respectively, are likely to be important drivers (Kirkman 1981, Kinlan et al. 2003). Indeed, sub-canopy irradiance was significantly higher within the smaller patches (Fig. 6D) and may explain why the recruitment pulse was observed only in the 4 smallest patches.

Following the initial pulse in recruitment, the density of juveniles continued to rise for one more season

across most patches. While this may have occurred due to delayed effects of the disturbance, it more likely reflected recruitment of juvenile kelp following the peak reproductive period in autumn (Mabin et al. 2013); a similar peak was observed in the second year of the study in those patches  $>1\text{ m}^2$  that did not suffer recruitment collapse (Fig. 2). The lag between peak reproduction in autumn and the observed peak in recruitment was  $\sim 12.5\text{ wk}$ , which provides an estimate of the timeframe between sporulation and recruitment as a visible sporophyte ( $\sim 5\text{ mm}$ ). The decline that followed presumably indicated the end of the seasonal peak in reproduction, but also the loss of sporophytes from the juvenile cohort due to mortality and/or maturation into stage 2 sporophytes (i.e. the adult cohort).

#### 4.2. Examination of the different life-stages

Although typically not of equal magnitude, peaks in adult density lagged those of juvenile density by approximately 2 seasons or 25 wk. This suggests the timeframe of development from stage 1 to stage 2 *E. radiata* at our site. The density of juvenile kelp in the smaller patches partly translated to increased densities of adult kelp, although clearly not every juvenile sporophyte survived to enter the adult cohort (cf. peak densities Figs. 2 & 4). One exception to this was the fourth smallest patch ( $2.7\text{ m}^2$ ), which had a maximum density of adult kelp higher than the maximum density of juvenile kelp. Kelp density in this patch was censused, so this could have only occurred from juveniles developing from non-visible to stage 2 sporophytes over the  $\sim 12.5\text{ wk}$  period between samples, which is possible at times of rapid growth (see Kirkman 1981). This patch also had a greater proportion of stage 2 sporophytes in the adult cohort relative to other large patches (pers. obs.). Nevertheless, the overall lack of a relationship between peak density of juveniles and adults in each patch suggests considerable mortality of juvenile sporophytes.

Although we observed mortality in the transplanted macroscopic juveniles, there was no influence of patch size on their survivorship. However, these sporophytes were installed for  $\sim 90\text{ d}$ , which is approximately half of the 25 wk we estimate that it typically takes stage 1 sporophytes to develop to stage 2 at the field site. Therefore, it is possible that a longer installation period was required to detect differences across the treatments. The negative effects of abiotic stressors may also be subtler on deeper reefs such as those studied here and require longer timeframes to

induce responses (Novaczek 1984, Wood 1987, Dayton et al. 1992). Indeed, work conducted on shallower reefs (6.5 m) in Tasmania demonstrated significant positive effects of patch size on the survival of macroscopic juvenile *E. radiata* deployed for the same duration (Layton et al. 2019a).

It is unclear whether herbivory affected the survivorship of the transplanted juveniles, and while mesograzers such as the small gastropod *Phasianotrochus* spp. were present (but never in high abundances), we did not observe any signs of grazing. Moreover, *Olisthops cyanomelas*, the primary fish species to consume *E. radiata* in southern Australia, rarely occurs in southeastern Tasmania and was not observed during our work. While the range-expanding *Centrostephanus rodgersii* were removed from the patches at the beginning of the experiment, their presence otherwise would have overwhelmingly increased destructive overgrazing of all macroalgae within the sub-canopy, including the adult and juvenile *E. radiata*. However, areas of *E. radiata* and other canopy-forming macroalgae kelp in shallower and/or more wave-exposed locations appear more resilient to overgrazing by *C. rodgersii* urchins, potentially due to increased dislodgement of urchins due to wave action and kelp scour (Ling et al. 2015, Ling & Keane 2018). Ultimately, the absence of *C. rodgersii* seems likely to have led to an underestimation of the importance of patch size for *E. radiata*, since higher levels of kelp recruitment over a larger area would be required for patch stability, had urchins been present.

In some seasons, the growth rate of the transplanted macroscopic juvenile sporophytes increased significantly with patch size over the initial 42 d period following transplanting. While this effect was not consistent across seasons nor detectable at the 90 d stage, it suggests that stage 1 sporophytes in smaller patches may require longer to develop and become reproductively viable (Novaczek 1984). The slowed growth of juveniles in small patches also suggests that the decline in density of juvenile kelp in these patches was not due to their accelerated development into the adult cohort.

It follows then that the persistent decline and eventual absence of juvenile kelp we observed in the smaller patches is more likely due to impairment or cessation of recruitment, where removal of kelp from the juvenile cohort was not replenished sufficiently by recruitment of new sporophytes. However, we initially detected that post-settlement survivorship of the outplanted microscopic sporophytes was higher in smaller patches (Fig. 5), potentially due to lower

amounts of abrasion from kelp scour, and/or higher levels of sub-canopy irradiance, which can facilitate growth (Tatsumi & Wright 2016). The following year, in spring 2015, patch size had no influence on the post-settlement survivorship of the microscopic sporophytes, nor on natural recruitment of these microscopic juveniles. Thus, while patch size had inconsistent effects on microscopic sporophytes, there was an indication that small patches became less suitable for microscopic sporophytes over time (Fig. 6F). This may reflect development of the turf–sediment matrix over time in the smaller patches, presumably itself the result of higher sub-canopy light levels in these patches (Fig. 6; Layton et al. 2019a).

#### 4.3. Spore supply, the sub-canopy environment, and habitat resilience

Irrespective of the life stage involved, patches  $<1\text{ m}^2$  did eventually exhibit a complete absence of *E. radiata* recruits. Moreover, this occurred at the time of the expected seasonal peak in recruitment, which was observed in patches  $>1\text{ m}^2$ , suggesting a collapse of this demographic process.

This cessation of recruitment is especially striking considering that the experimental patches were embedded within a large stand of *E. radiata*, and so would not likely have been subject to the reduced propagule supply and poor connectivity that would be expected in a fully fragmented kelp forests (Dayton et al. 1984, Reed 1990, Bennett & Wernberg 2014). Given the proximity of the surrounding stand of *E. radiata*, each experimental patch likely had a similar level of propagule supply, so we surmise that supply-side dynamics were not responsible for the collapse in recruitment. Accepting this, then the only difference between patches where recruitment collapsed and where it did not, was the abiotic environment in which propagules settled and recruited.

The accumulation of sediments in the sub-canopy of smaller patches, typically trapped within the filamentous turf algae, may be of particularly importance. It is well recognised that sediments and turf algae inhibit the recruitment of *E. radiata* and other kelp, potentially via smothering and substratum instability (Kennelly 1987b, Valentine & Johnson 2005, Watanabe et al. 2016) and/or changes in benthic chemistry (Layton et al. 2019b). Despite detecting no overall effect of patch size on sediment accumulation, the data examined from the periods coinciding with and following the collapse in recruitment indicates that levels of sediment accumulation

were significantly higher in the smaller patches. Thus, the sub-canopy environment clearly changed over time in these patches, potentially contributing to impaired recruitment of new juvenile kelp.

Increased sub-canopy irradiance and decreased kelp scour in the smaller patches (Fig. 6) are 2 likely mechanisms that promoted increased cover of turf algae and thus increased entrainment of sediments (Kennelly 1989, Irving & Connell 2006, Layton et al. 2019a). Notably, turf algae tend to be less productive and prevalent on deeper reefs compared to shallow reefs (Copertino et al. 2005), likely due to decreased irradiance, which explains why turf algae were slow to establish in our patches. This may also explain why we detected no effects of patch size on natural recruitment of microscopic juveniles, because the blank microscope slides were not deployed for sufficient time to develop a cover of turf algae and sediments. A more rapid and negative response to reductions in patch size was observed in outplanted microscopic *E. radiata* at shallower depths in Tasmania (Layton et al. 2019a).

What is apparent from our results is the nonlinear response to patch size, suggesting the existence of possible thresholds. The nonlinear relationship between patch size and the density of newly recruited kelp was very strong immediately following patch creation and became weaker and more linear as time progressed. Of particular interest is that the fourth smallest patch ( $2.7\text{ m}^2$ ) responded to the initial disturbance following patch creation but did not experience the same eventual collapse in recruitment. This may represent a critical patch size where ecosystem engineering by *E. radiata* was sufficient to maintain the sub-canopy environment and ensure patch resilience despite the ongoing perturbation (Layton et al. 2019a). The eventual failure in kelp recruitment in the smaller patches seems to represent the consequences of patch sizes below this threshold. This appears to be linked to increasing sediment accumulation, and perhaps other abiotic stressors (see Fig. 6A), which is consistent with observed phase-shifts of structurally complex, productive, and biodiverse kelp forests to less complex, less biodiverse, and less productive turf-dominated ecosystems (Connell et al. 2008, Filbee-Dexter & Wernberg 2018, Layton et al. 2019a, Wernberg et al. 2019a).

Our results suggest that habitat fragmentation has the potential to influence the long-term resilience and stability of *E. radiata* habitats by disrupting recruitment. Impaired recruitment also means that smaller kelp patches may be less likely to recover

even after the perturbation has ceased (see Angelini & Silliman 2012). In this instance where reductions to kelp patch size have disrupted the juvenile cohort, the surviving adult cohort may be unable to promptly or sufficiently replenish the population (Wernberg et al. 2010). This may lead to post-disturbance populations that consist only of adult kelp which could perish after 1 generation. While such demographic disruptions may be difficult to detect (Caley et al. 1996), they might represent opportune circumstances for human intervention and ecological restoration (Johnson et al. 2017, Layton et al. 2020).

#### 4.4. Conclusion

We have demonstrated that fragmentation of kelp forest and persistent reductions in patch size, like those caused by many anthropogenic stressors, can lead to the collapse of effective recruitment in patches of *E. radiata* smaller than 1 m<sup>2</sup>. Notably, collapse still occurred without the propagule supply being compromised due to reproductive isolation of small patches of kelp from conspecifics. Our results suggest that the impaired ability of *E. radiata* to engineer abiotic change within small patches with proportionally larger edge effects leads to the degradation of the sub-canopy environment over time. In our case, this resulted in the proliferation of turf algae and entrained sediments in small patches, which we suspect ultimately disrupted the settlement and recruitment of juvenile kelp. This occurred despite an initial response to kelp removal and patch creation as a marked increase in recruitment in patches smaller than 3 m<sup>2</sup>. This dual-response—a potential short-term resilience mechanism to pulse disturbances, but an eventual cessation of recruitment—highlights the importance of long-term observations in the field. We suspect that the depth of the experimental patches (~14 m) may have contributed to the protracted response we observed, chiefly because of the relatively low irradiance and slower formation of the turf-sediment matrix than occurs at shallower depths. We conclude that habitat fragmentation can cause considerable disruptions to the demography of *E. radiata* in smaller kelp patches, which has clear consequences for the resilience and recovery of kelp forests in the face of increasing anthropogenic threats.

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