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Implications of Climate-Induced Localised Extinction of Bull Kelp (*Durvillaea amatheiae*) for Holdfast Macrofauna

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Abstract: Globally, work is being undertaken to preserve biodiversity and prevent further species extinctions. Yet, without adequate data about the presence of species within ecosystems, hidden extinctions can occur without our knowledge. Given that poleward range retractions are projected for bull kelp (*Durvillaea amatheiae*) in southeastern Australia, there is the potential for hidden extinctions to occur in associated macrofaunal species. However, this risk cannot be assessed due to the limited data on the invertebrate macrofauna associated with *D. amatheiae*. We documented macrofauna within *D. amatheiae* holdfasts, with the objective of establishing a first analysis of the holdfast fauna for this kelp and identifying, where possible, any host-specific taxa. Holdfasts were collected at six locations, spanning most of the range of *D. amatheiae* on the southeastern Australian mainland. Macrofauna were removed from holdfasts and identified to the lowest possible taxonomic level. Modelling was applied to determine factors correlated with patterns of assemblages among locations. Holdfast assemblages were found to vary significantly among locations and exhibited a latitudinal gradient in assemblage structure. The northernmost location (Aragunnu), which has the highest risk of *D. amatheiae* range retractions, was found to have distinct species assemblages and generally higher diversity and abundance than locations further south. However, no host-specific taxa were identified in samples, indicating that there is a low risk of multiple hidden species extinctions occurring in holdfast macrofauna, due to future range retractions of *D. amatheiae*. Rather, most of the macrofauna taxa in *D. amatheiae* holdfasts were found to also occur in association with the sympatric golden kelp *Ecklonia radiata*, which is not expected to undergo range retractions at the latitudes where losses of *D. amatheiae* are projected. Overall, there is an urgent need to develop strategies to combat projected future range retractions of *D. amatheiae* to reduce impacts on the species that rely on *D. amatheiae* for habitat.

Keywords: invertebrate; marine; climate change; range shift; New South Wales



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1. Introduction

The world is facing an unprecedented extinction crisis [1] with consequent, increased efforts to protect biodiversity and prevent further species extinctions. However, due to a lack of data regarding species distributions and habitat requirements, particularly for invertebrates [2,3], species extinctions may be occurring without our knowledge. One of the major drivers of species extinctions is loss of habitat, caused by anthropogenic impacts, such as land clearing and climate change [4,5]. Climate change is causing habitat loss by driving the poleward range retraction of many habitat-forming foundation species, both on land [6] and in coastal waters [7,8]. In coastal waters, range shifting by foundation macroalgal species, such as kelps, can have major consequences for other species that are dependent on these habitats for food and shelter [9,10]. Concerningly, under some

future climate scenarios, modelling predicts local extinctions of some kelp species in southeastern Australia by 2100 [11], which may in turn lead to hidden extinctions among the species that are dependent on these macroalgae. Given the Australian Government's recent commitment to work towards preventing further species extinctions in Australia [12], there is a need to improve our understanding about the potential for loss of species that are dependent on kelp habitats when poleward range contractions of kelp occur.

Of particular concern is the impact that range contractions by bull kelp (*Durvillaea amatheiae*, [13]) will have on dependent species in southeastern Australia. *Durvillaea amatheiae* is endemic to southeastern Australia, including eastern and western, but not northern, Tasmania [13]. It is an intertidal species inhabiting wave-exposed rocky reefs and is currently found along the mainland Australian coast from Aragunnu (36.59° S, 150.04° E) in New South Wales (NSW) to Wilson's Promontory (39.06° S, 146.46° E) in Victoria [13,14]. This species is projected to become extinct on mainland Australia by 2100, under Representative Concentration Pathway 6.0 [11]. Kelps from the genus *Durvillaea* are important foundation species, providing habitat for low-intertidal and subtidal marine communities [15–17]. Therefore, any range contractions for *D. amatheiae* will generate negative impacts for dependent species and may precipitate hidden extinctions. Closely related *Durvillaea* spp. in New Zealand have already experienced local extinctions during marine heatwaves in 2017/2018 [15], leading to long-term community shifts [18], indicating that fears for the future of *D. amatheiae* and its dependent species in Australia are not unfounded.

However, little is known about the faunal assemblages associated with *D. amatheiae*, so the risk of hidden extinctions under range contractions cannot presently be assessed. Previous research has demonstrated that other habitat-forming macroalgal species (e.g., *Ecklonia radiata*, *Durvillaea antarctica*) can shelter diverse faunal assemblages, particularly within their holdfasts [17,19,20]. Additionally, holdfast macrofauna can vary significantly among locations [17] and different kelp species can shelter unique assemblages [21–23]. Consequently, given the range contractions projected for *D. amatheiae* and the current limited data available on the holdfast macrofauna associated with this species, more data are needed to determine whether *D. amatheiae* holdfast macrofaunal assemblages are unique and, thus, at risk of localised extinction.

To address this knowledge gap, surveys of holdfast fauna were conducted at locations across most of the mainland geographic range of *D. amatheiae* in southeastern Australia. The main objectives of the study were to conduct a first analysis of the holdfast fauna for this kelp, to compare *D. amatheiae* holdfast macrofaunal assemblages against previous macrofaunal data obtained from holdfasts of the co-occurring kelp *E. radiata*, and to determine whether *D. amatheiae* holdfasts contain host-specific taxa at risk of local extinction when *D. amatheiae* range retractions occur. We also examined whether holdfast macrofaunal assemblages varied among locations, to ascertain whether northern populations, which are threatened by imminent poleward range retractions, are distinct and, thus, in greater need of increased protection. Finally, we examined whether macrofaunal assemblages were influenced by the physical size of the holdfasts from which samples were collected, to determine whether larger *D. amatheiae* holdfasts contain more diverse assemblages and, thus, are deserving of increased levels of protection.

2. Materials and Methods

2.1. Study Area

Durvillaea amatheiae holdfasts were collected in January 2022 from six locations (Table 1) spread over ~230 km of the coastlines of New South Wales and Victoria, with locations spanning most of the current range of the species on mainland Australia (Figure 1). The study area was selected to include locations spread from the current northern distributional limit of *D. amatheiae* (Aragunnu, NSW, Australia) to Cape Conran in Victoria, as this region is where incipient range retractions are expected to occur over coming decades [11]. Sampling excluded sites in Bass Strait and Tasmania, as *D. amatheiae* is expected to persist in these areas in the short to medium term [11].

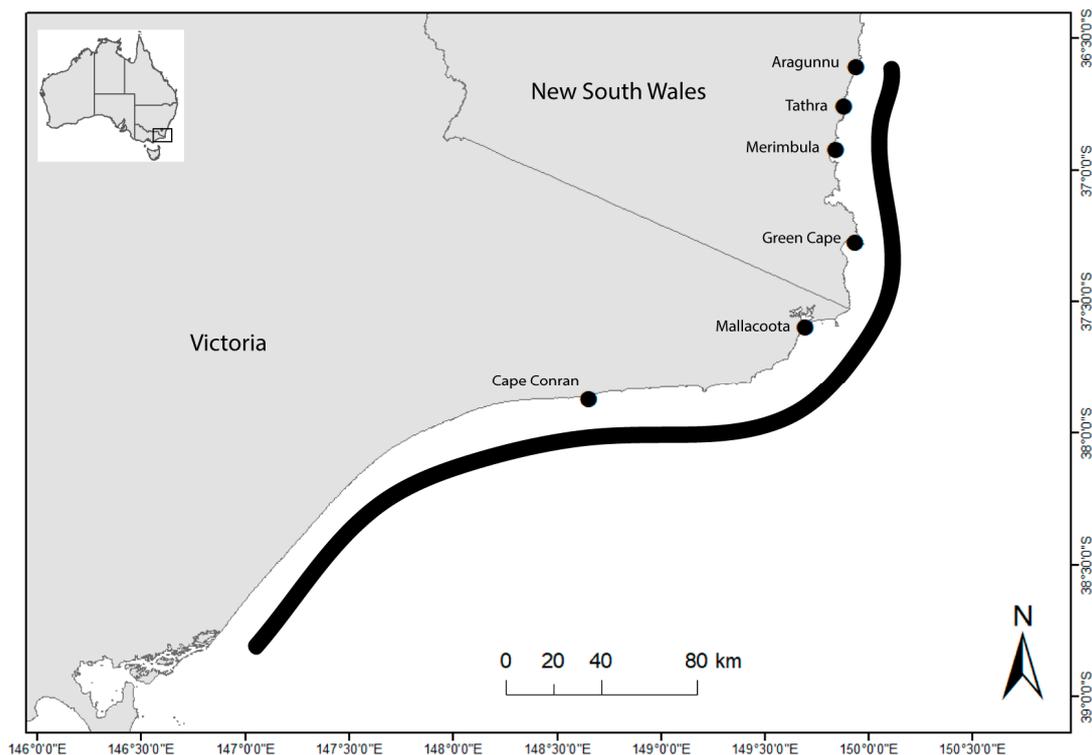


Figure 1. Study area in southeastern Australia, *Durvillaea amatheiae* sampling locations (black dots), and *D. amatheiae* current distribution on mainland Australia, excluding Tasmania (solid line).

Table 1. Survey locations and number of *Durvillaea amatheiae* holdfast samples collected.

Location	Latitude (° S)	Longitude (° E)	Samples	Mean Annual Sea Surface Temperature (°C)
Aragunnu	36.5910	150.0435	10	18.38
Tathra	36.7379	149.9846	10	18.12
Merimbula	36.9005	149.9371	7	17.94
Green Cape	37.2552	150.0133	10	17.51
Mallacoota	37.5719	149.7648	10	16.98
Cape Conran	37.8125	148.7268	10	15.83

2.2. Holdfast Sampling

At each location, holdfast samples were collected haphazardly across a section of the lower intertidal zone spanning ~100 m, with 7–10 holdfasts collected at each location (Table 1). All sampling locations were on wave-exposed intertidal rock platforms, with locations spanning a latitudinal gradient in sea surface temperatures of ~2.5 °C (Table 1). Only seven samples were collected at Merimbula due to difficulties associated with safely accessing the rock platform at this site. Holdfast samples were collected at low tide by cutting the kelp stipe immediately above the holdfast, levering the holdfast off the substrate, and placing the holdfast into a calico bag, ensuring that the entire holdfast was collected, along with any material and organisms trapped under the holdfast, as recommended by Smith and Simpson [24]. Holdfast removal was conducted using a broad-bladed scraper, which was held under the holdfast during transfer to the sampling bag to prevent, as much as possible, any loss of fauna or sediment during sampling. Any sediment or fauna remaining on the rock after holdfast removal was added to the sampling bag. Holdfast samples were preserved by immediately immersing the entire bag into 7% buffered formalin.

2.3. Holdfast Geometry

The holdfast diameter, thickness, volume, stipe diameter, and sediment content were recorded to allow examination of whether these factors influenced macrofaunal assemblages [20,25]. Holdfast volume was measured by submerging the holdfast in water and measuring the volume of water displaced. Sediment content was measured by washing holdfast samples over a 1 mm sieve and measuring the dry weight of the sediment material that passed through the sieve.

2.4. Macrofaunal Sampling

Prior to sampling, holdfasts were thoroughly rinsed to remove formalin, and holdfasts were then dissected under a fume hood, by cutting each holdfast into sections of approximately 10 mm width. Each section was carefully examined by eye to locate macrofauna and further dissected if necessary to remove all macrofauna. Macrofauna samples from each holdfast were then stored in individual glass vials, containing 70% ethanol. Macrofauna samples were subsequently examined to count and identify species to the lowest taxonomic level possible [24]. Many specimens were very small, or juveniles, making identification to species level difficult. Individuals from *Mytilidae* spp. were likely to be a combination of juveniles of a few species. Similarly, *Hyale* sp. were likely a combination of a few species, with the condition of many specimens making it difficult to identify obvious diagnostic features. *Nematoda* spp. and *Nemertea* spp. were pooled into two groups, one for each of these taxa. A type collection for the samples collected, preserved in 70% alcohol, was retained for future reference.

2.5. Comparison with *Ecklonia Radiata* Holdfast Fauna

Data on *E. radiata* holdfast fauna from southern NSW were obtained from surveys conducted between 1989–1991 [26]. These data were compared against the fauna identified in *D. amatheiae* holdfasts in the current study, thereby enabling determination of the overlap in assemblages between *D. amatheiae* and *E. radiata*, and the potential for loss of host-specific taxa.

2.6. Statistical Analysis

All statistical analyses were conducted using PRIMER v7 software [27,28]. Prior to analyses, samples with only a single animal in the whole sample (i.e., one sample at Aragunna and three at Cape Conran) were removed, as these were found to be extreme outliers. For comparisons among assemblages, similarity matrices for species counts were constructed using the Bray–Curtis similarity measure, with data square-root transformed to reduce the influence of abundant species. Permutational multivariate analysis-of-variance (PERMANOVA) analyses were used to test for significant differences in assemblages among locations. Pairwise tests were applied to identify location pairs with significant differences in assemblages, with similarity percentage (SIMPER) analyses used to identify the species making the largest contributions to the significant differences among locations. Similarities of average assemblages among locations were visualised using a metric multidimensional scaling (mMDS) plot, which showed the relative similarity of average assemblages and 95% confidence intervals for average locations obtained using bootstrap averaging [28].

Tests for significant correlations between species richness/abundance and holdfast diameter were conducted using Pearson's product-moment correlations in R [29]. PERMANOVA analyses were used to test for significant differences in species richness and total faunal abundance among locations, with data standardised by holdfast diameter to compensate for the effect of variations in holdfast sizes among locations.

Distance-based linear modelling (DistLM) [27] was used to examine relationships among assemblages and environmental and physical explanatory variables. DistLM model selection was conducted using the "BEST" procedure, to examine potential alternate models, with the Akaike information criteria (AIC) used to select the most parsimonious model, as recommended by Burnham et al. [30]. Six explanatory variables were selected for testing

in models: sample latitude, holdfast diameter, holdfast thickness, holdfast volume, stipe diameter, and sediment weight.

Correlations among all explanatory variables were examined, prior to modelling, to determine whether excessive autocorrelation existed (i.e., $|r| > 0.7$), as recommended by Dormann et al. [31]. This analysis identified that holdfast diameter, holdfast thickness, holdfast volume, and stipe diameter were all highly correlated with each other. Consequently, only the best performing of these variables for explaining assemblage variation (i.e., holdfast diameter) was retained in modelling to represent this group of variables. This left three of the original six explanatory variables for model development: latitude, holdfast diameter, and sediment weight.

3. Results

3.1. Holdfast Geometry and Habitat Description

Holdfasts of *D. amatheiae* consisted of dorso-ventrally flattened, approximately conical discs, with smooth upper surfaces (Figure 2a). The average diameters of collected holdfasts ranged from 37.5 to 130.0 mm, which is typical of *D. amatheiae* holdfasts, which are generally <10 cm in width [13], although larger holdfasts were observed in the field, particularly in Victoria (personal observation). Stipe diameters ranged from 7.22 to 29.50 mm, with each holdfast generally supporting a single stipe, although two of the holdfasts collected had three stipes. The undersides of holdfasts were found to closely follow the contours of the rocks to which they were attached, growing over organisms that were already attached to the substrate (Figure 2b). This growth pattern provided limited space for establishment of macrofauna, with most fauna found living in the spaces formed by overgrowth of previously established organisms (mostly turfing algae, barnacles, and mussels). There was little evidence that fauna were creating additional living space by burrowing into holdfasts, although single individuals of a burrowing eophliantid amphipod were found in three holdfasts from Eden and Cape Conran.

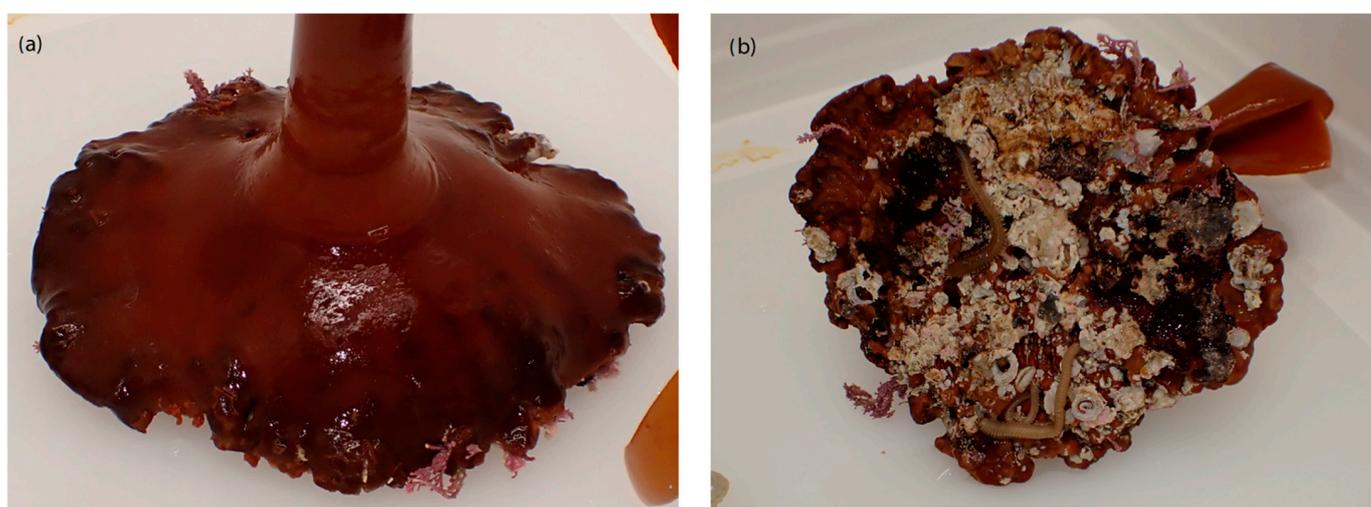


Figure 2. Typical *Durvillaea amatheiae* holdfast (ex situ) showing (a) top surface and (b) underside and overgrown organisms.

3.2. Macrofaunal Assemblages

The *D. amatheiae* holdfasts examined ($n = 57$) contained 1040 macrofauna from 51 discrete taxa in nine phyla (Table A1). The most diverse phyla were Annelida (24) and Crustacea (14), while the most numerous species were the bivalves *Lasaea australis* (413) and *Mytilidae* spp. (96). Both of the bivalves, as well as barnacles, were present as live individuals and also, in some cases more frequently, as dead animals (not counted) overgrown by the holdfast matrix.

As far as could be determined, based on a comparison of the species found in *D. amatheiae* holdfasts with those found in previous research in *E. radiata* holdfasts (personal communication 2023 to SDAS), all taxa identified in *D. amatheiae* holdfasts also occur in *E. radiata* holdfasts within the region [26]. This overlap in holdfast fauna indicates that *D. amatheiae* holdfasts shelter few, if any, host-specific taxa.

PERMANOVA analyses identified significant differences in *D. amatheiae* holdfast assemblages among locations ($p < 0.001$, Figure 3, Table A3), with pairwise testing identifying that assemblages at all locations were significantly different from each other ($p < 0.022$ all tests, Table A4). Holdfasts at Aragunnu sheltered the greatest diversity of macrofaunal species (33) and the greatest diversity of Annelida (14) and Mollusca (9), whereas Green Cape had the greatest diversity of Crustacea (10, Table 2). It should be noted that a lower numbers of species may have been recorded at Merimbula, as fewer samples were collected at this location. SIMPER analyses identified that differences in macrofaunal assemblages among locations were primarily driven by differences in abundances of the two dominant species, *L. australis* and *Mytilidae* spp., with these two species contributing over 23% to the total difference among locations (Table 3).

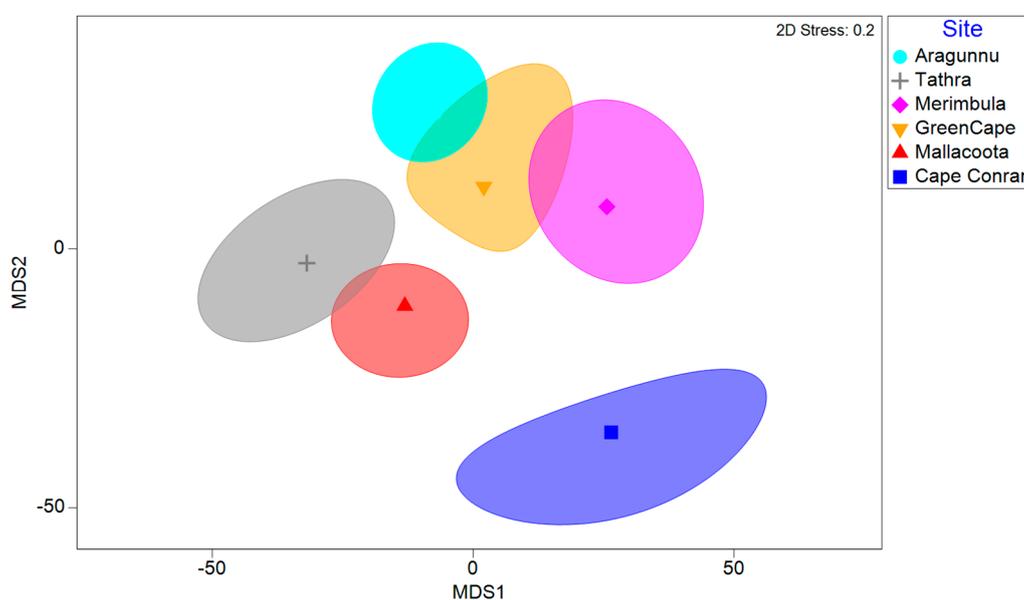


Figure 3. Metric multidimensional scaling plot showing relative similarity of average *Durvillaea amatheiae* macrofaunal holdfast assemblages at sampling locations in southeastern Australia. Ellipses indicate 95% confidence limit on location of average assemblages.

Table 2. Total number of macrofauna species in *Durvillaea amatheiae* holdfasts by phylum at sampling locations in southeastern Australia across all holdfasts sampled (N).

Phylum	Aragunnu (10)	Tathra (10)	Merimbula (7)	Green Cape (10)	Mallacoota (10)	Cape Conran (10)	Total (57)
Annelida	14	9	11	13	11	6	24
Cnidaria	0	1	0	1	0	0	1
Crustacea	9	3	7	10	3	1	14
Foraminifera	0	0	1	0	0	0	1
Insecta	1	0	0	0	0	0	1
Mollusca	7	3	3	4	3	2	7
Nematoda	1	1	1	1	1	1	1
Nemertea	1	1	1	1	1	1	1
Platyhelminthes	0	0	0	1	0	0	1
Total	33	18	24	31	19	11	51

Table 3. Contributions of individual species to dissimilarity among average *Durvillaea amatheiae* macrofaunal holdfast assemblages at sampling locations in southeastern Australia.

Species	Contribution to Differences among Assemblages %	Cumulative Contribution %
<i>Lasaea australis</i>	15.9%	15.9%
<i>Mytilidae</i> spp.	7.8%	23.7%
<i>Syllis gracilis</i>	7.4%	31.1%
<i>Ceratonereis</i>	6.8%	37.9%
<i>Lumbrinereis</i> sp. 2	4.9%	42.7%
<i>Nemertea</i> spp.	3.9%	46.6%
<i>Nereididae</i> sp. 2	3.3%	49.9%
<i>Nematoda</i> spp.	2.9%	52.8%

3.3. Macrofaunal Species Richness and Abundance

PERMANOVA analysis found significant differences in species richness ($p < 0.001$) and in abundance ($p < 0.001$) among locations, taking differences in holdfast diameters among locations into consideration. Pairwise testing showed that, on average, Aragunnu, Green Cape, and Merimbula had significantly more diverse assemblages than Mallacoota, Tathra, and Cape Conran (Figure 4a). Similarly, Aragunnu, Green Cape, and Merimbula had a significantly higher abundance of macrofauna than Tathra, while Cape Conran had significantly fewer macrofauna than all the other sites (Figure 4b).

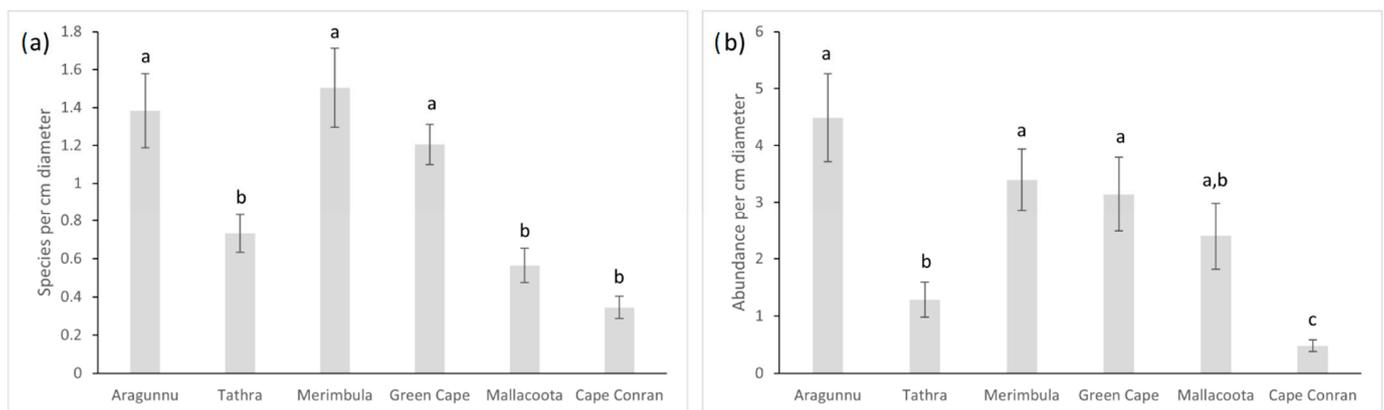


Figure 4. (a) Average number of macrofaunal species in *Durvillaea amatheiae* holdfasts at sampling locations in southeastern Australia standardised by holdfast diameter and (b) average abundance of macrofauna per holdfast standardised by holdfast diameter. Bars indicate standard error; different letters indicate significant differences among locations.

3.4. Factors Associated with Variations in Macrofaunal Assemblage Structures

Modelling identified a strong association between latitude and macrofaunal assemblage structure ($p < 0.001$), a weak association among assemblages and holdfast diameter ($p = 0.031$), and no significant association among assemblage structure and sediment weight ($p = 0.055$). The overall best model developed explained 11% of the variations in assemblage structure and contained two explanatory variables, latitude and holdfast diameter (Table 4). Examining the effects of diameter showed that both species richness ($p = 0.006$) and fauna abundance ($p = 0.0004$) increased significantly with increasing holdfast diameter (Figure 5).

Table 4. Distance-based linear models trialled, explanatory variables for models, and model performance in explaining variations in macrofaunal assemblages in *Durvillaea amatheiae* holdfasts.

Model	Explanatory Variables	AIC	R ²	RSS
1	Latitude, holdfast diameter	413.18	0.110	115,030
2	Latitude	413.73	0.066	120,690
3	Latitude, sediment content	414.05	0.095	116,940
4	Latitude, diameter, sediment	414.53	0.121	113,630
5	Holdfast diameter	415.36	0.037	124,470
6	Sediment content	415.51	0.034	124,820
7	Diameter, sediment	416.21	0.057	121,800

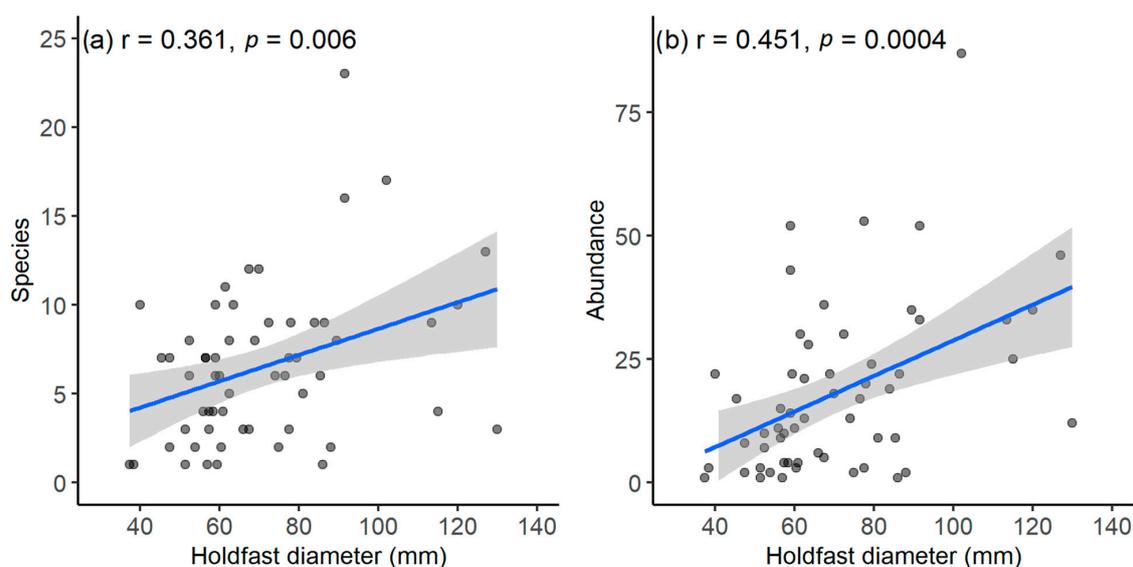


Figure 5. Pearson's correlations between *Durvillaea amatheiae* holdfast diameter and (a) number of macrofaunal species in holdfast and (b) abundance of macrofauna in holdfast. Blue line indicates Pearson's correlation best-fit to data and shaded area indicates standard error on best-fit.

4. Discussion

Data from the current study provide valuable new insights into the macrofaunal species that dwell within *D. amatheiae* holdfasts, with significant differences in holdfast assemblages detected among locations. However, contrary to our expectations, we find that there is a low probability that projected range retractions by *D. amatheiae* (as per Martínez et al. [11]) will lead to multiple localised extinctions in *D. amatheiae* holdfast macrofauna. This is due to the *D. amatheiae* holdfast taxa identified having a substantial overlap with the macrofauna of co-occurring *E. radiata* holdfasts [24]. Consequently, *D. amatheiae* holdfast macrofauna will largely remain extant within *E. radiata* holdfasts when range retractions of *D. amatheiae* occur, given the expected continued presence of *E. radiata* at the latitudes where *D. amatheiae* range retractions are anticipated [11,32]. Additionally, individual macrofaunal species from *D. amatheiae* holdfasts are likely to be able to persist within other habitats, with previous research showing that *E. radiata* holdfast macrofauna commonly occur in other habitats, such as within soft sediments, sponges, and seagrass beds [25]. Some of the more abundant species (bivalves, barnacles, and tubicolous polychaetes—Serpulidae and Spirorbidae) were found both alive and dead, the latter usually embedded in the base of the holdfast. Most of these taxa are sedentary, suggesting that they also occur on the rocky substratum and were overgrown by spreading holdfasts [20]. It is therefore likely that many macrofaunal species associated with *D. amatheiae* holdfasts are also present in other habitats and will be able to persist within these habitats when *D. amatheiae* range retractions occur. However, further research is required to confirm the presence of *D. amatheiae* macrofauna within other habitats in the region. Further research is also needed to more comprehen-

sively assess the risk of local extinctions among *D. amatheiae* holdfast macrofauna, given the possibility that undetected, rare species may occur in holdfasts. Furthermore, local extinctions may result from the broader impacts of climate change, with climate change driving species extinctions globally, by changing environmental conditions [4]. Examination of the environmental tolerances of holdfast macrofaunal species is warranted, to determine whether they are at risk from changing environmental conditions, especially given that increasing ocean temperatures are expected to drive local extinction of many marine species in southeastern Australia [11].

4.1. Comparison of *D. amatheiae* and Co-Occurring *E. radiata* Holdfast Macrofauna

This study revealed that while *D. amatheiae* holdfast macrofaunal assemblages showed differences among sampling locations, the overall faunal complement is highly depauperate in comparison to that present in the holdfasts of co-occurring *E. radiata*. Data collected in an investigation of *E. radiata* holdfasts in Jervis Bay (~175 km to the north of Aragunnu) indicated average faunal densities of 0.99–6.29 individuals.mL⁻¹ of holdfast habitat [25], which is more than double the values recorded in this study (average = 0.6 individuals.mL⁻¹, range of 0.01 to 3.06, Table A2). Similarly, species richness in *E. radiata* is much higher, with Smith [26] recording 32,283 individual animals from 292 discrete taxa (mostly identified to species level) from 59 holdfasts in Jervis Bay, and Anderson et al. [33] recording 351 species of macrofauna from 80 *E. radiata* holdfasts in New Zealand, whereas only 1040 individuals from 51 taxa were found in the 57 holdfasts examined in the current study. There is little doubt that the primary reason for this disparity is the morphology of *D. amatheiae* holdfasts, which are flat and discoid and provide little primary space for occupation by macrofauna relative to the highly complex structure of intertwined haptera in *E. radiata* [20]. At Macquarie Island, subantarctic, the discoid holdfasts of *D. antarctica* also support a much lower density of fauna by volume in comparison to *E. radiata*, with an average of 1.0 individuals.mL⁻¹ habitat [24].

4.2. Comparison of *D. amatheiae* Holdfast Macrofauna to Other Kelp Species

Compared to other kelp species, the macrofaunal species richness in *D. amatheiae* holdfasts in the current study (51 taxa in 57 holdfasts) was greater than that identified in *Macrocystis pyrifera* (42 taxa in 62 holdfasts) in Chile [34], but lower than that in *D. antarctica* (96 taxa in 60 holdfasts) at Macquarie Island [17]. It should be noted, however, that the size of the holdfasts examined for *D. amatheiae* (i.e., generally <10 cm) was much lower than the size reported for *D. antarctica* (up to 60 cm [24]), which potentially contributed to the differences in holdfast macrofaunal richness recorded in these two studies. Comparisons among studies from different kelp species are often confounded by differences in holdfast size, geometry, and complexity among the species, and by differences in the number and the size of holdfasts examined. Additionally, the resolution of taxonomic identification often varies among studies of holdfast macrofauna, further confounding meaningful comparisons among these studies [21].

4.3. Variations in *D. amatheiae* Holdfast Macrofauna among Locations

Macrofaunal assemblages and species richness and abundance of *D. amatheiae* macrofauna all varied significantly among the locations examined in southeastern Australia. Variations in holdfast macrofauna among locations is common for kelp species, with differences among locations also detected for *D. antarctica* at Macquarie Island [17] and *E. radiata* in New Zealand [33]. Often, differences among locations are attributed to site-level factors, such as wave exposure [17,35]; however, for *D. amatheiae*, we found that assemblage variation at a broad spatial scale exhibited a significant latitudinal gradient. The presence of latitudinal differences among *D. amatheiae* holdfast assemblages has important implications for the management of these species as range retractions at the northern edge of *D. amatheiae*'s distribution (i.e., at Aragunnu) will lead to loss of the distinct and diverse

macrofaunal assemblages that occur at this location. However, it should be noted that the macrofauna themselves are likely to persist within other habitats.

4.4. Influence of *D. amatheiae* Holdfast Size on Macrofaunal Assemblages

Overall, holdfast size was found to have a significant effect on holdfast macrofauna, with both species richness and abundance of macrofauna increasing with increased size. This was unsurprising, as it is widely acknowledged that species richness and abundance of fauna increase with increased living space, with these same increases observed in holdfast macrofauna for *E. radiata* [20,33] and *Lessonia trabeculata* [21]. It should be noted that holdfast size will generally increase with age, and it is difficult to disentangle whether larger holdfasts have greater species richness and abundance because they are larger, providing more habitat, or because they are older, which gives more time for colonization. Further research is needed to examine relationships between holdfast age and macrofaunal assemblages; however, this would need a reliable method for aging *D. amatheiae*. Aging could potentially be achieved by counting growth rings in *D. amatheiae* stipes, as has been applied for aging of *E. radiata* [36]. Interestingly, we found limited evidence that macrofauna were creating additional living space by burrowing into holdfasts, although single individuals of a burrowing eophliantid amphipod were found in three holdfasts from Eden and Cape Conran. This contrasts with observations for closely related *D. antarctica*, where extensive tunnels are created in holdfasts by macrofauna, particularly by the isopod *Limnoria stephenseni* [24]. The lack of holdfast burrows, which is consistent with the species description for *D. amatheiae* [13], limits space under and within holdfasts and restricts macrofaunal diversity and abundance when compared to kelp species with larger and more complex cavities within their holdfasts. Examination of *D. amatheiae* holdfast geometry identified that the physical dimensions of *D. amatheiae* holdfasts (i.e., holdfast diameter, thickness, volume, stipe diameter) were all closely correlated among holdfasts. Consequently, these dimensions could all be used to represent holdfast size in modelling, although we found that holdfast diameter had the strongest association with variations in macrofaunal assemblages.

5. Conclusions

Here, we provide the first quantitative insights into the macrofaunal assemblages within *D. amatheiae* holdfasts. It can be concluded that a wide range of detrimental impacts will be associated with the loss of *D. amatheiae* in southeastern Australia, particularly if range retractions occur at Aragunnu, where *D. amatheiae* holdfasts shelter distinct and relatively diverse macrofaunal assemblages. However, it is difficult to determine whether *D. amatheiae* range retractions will lead to local extinctions for individual species of *D. amatheiae* holdfast macrofauna, as many of these species are likely to co-occur in other habitats which are less at risk from climate change. Consequently, there is an urgent need to determine which species are solely dependent on *D. amatheiae* and to develop strategies to reduce impacts on those species which rely on *D. amatheiae* for habitat. Furthermore, over the longer term, the projected incipient local extinction of *D. amatheiae* itself in southeastern Australia [11], and the loss of associated fauna, will have unquantified consequences for local marine ecosystems, with more research needed to investigate likely flow-on effects. In New Zealand, where marine heatwaves led to local extinctions of several *Durvillaea* spp. [15], losses of *Durvillaea* spp. have led to a phase shift, from ecosystems dominated by *Durvillaea* spp. to ecosystems dominated by other algal species, with an associated long-term shift in the composition of local marine communities [18]. In Australia, regional loss of *D. amatheiae* will likely have similar impacts, with *D. amatheiae* acting as a foundation species in many marine food chains [16]. Additionally, loss of *D. amatheiae* will reduce ecosystem capacity for carbon capture and storage, with *Durvillaea* spp. making a substantial contribution to carbon sequestration in Australia [37]. Finally, *D. amatheiae* is culturally important, being historically used by indigenous communities for food and to make objects such as footwear and water carriers [38], with its loss likely to have as-yet unquantified cultural impacts.

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Appendix A

Table A1. Macrofauna species and abundance in *Durvillaea amatheiae* holdfasts.

Phylum	Class	Family	Species	Count	
Annelida	Polychaeta	Chrysopetalidae	<i>Chrysopetalidae</i> sp.	2	
	Polychaeta	Cirratulidae	<i>Cirriformia capensis</i>	11	
	Polychaeta	Cirratulidae	<i>Cirriformia filigera</i>	4	
	Polychaeta	Dorvilleidae	<i>Dorvilleidae</i> sp.	1	
	Polychaeta	Eunicidae	<i>Marphysa</i> sp. 1	12	
	Polychaeta	Eunicidae	<i>Marphysa</i> sp. 2	8	
	Polychaeta	Lumbrineridae	<i>Lumbrineris</i> sp. 1	1	
	Polychaeta	Lumbrineridae	<i>Lumbrineris</i> sp. 2	44	
	Polychaeta	Nereidae	<i>Ceratonereis</i>	70	
	Polychaeta	Nereidae	<i>Nereididae</i> sp. 2	21	
	Polychaeta	Nereidae	<i>Nereididae</i> sp. 3	2	
	Polychaeta	Nereidae	<i>Nereididae</i> sp. 4	1	
	Polychaeta	Phyllodocidae	<i>Eulalia</i> sp.	1	
	Polychaeta	Phyllodocidae	<i>Phyllodocidae</i> sp.	3	
	Polychaeta	Sabelliidae	<i>Idanthyrus pennatus</i>	2	
	Polychaeta	Scalibregmatidae	<i>Hyboscolex</i> sp.	9	
	Polychaeta	Serpulidae	<i>Galeolaria caespitosa</i>	7	
	Polychaeta	Sphaerodorididae	<i>Sphaerodorum</i> sp.	1	
	Polychaeta	Spionidae	<i>Spionidae</i> sp.	9	
	Polychaeta	Syllidae	<i>Sf. Syllinae</i>	3	
	Polychaeta	Syllidae	<i>Syllis gracilis</i>	80	
	Polychaeta	Syllidae	<i>Syllis</i> sp.	18	
	Polychaeta	Syllidae	<i>Syllis variegata</i>	2	
	Sipuncula	Sipuncula	<i>Sipuncula</i>	4	
	Cnidaria	Actiniaria	Actiniidae	<i>Actiniidae</i> sp.	2
	Crustacea	Amphipoda	Amphilochidae	<i>Amphilochidae</i> sp. 1	2
		Amphipoda	Amphilochidae	<i>Amphilochidae</i> sp. 2	2
Amphipoda		Aoridae	<i>Aora hebes</i>	20	
Amphipoda		Eophliantidae	<i>Eophliantidae</i> sp.	3	
Amphipoda		Hyalidae	<i>Hyale</i> sp.	25	
Amphipoda		Ischyroceridae	<i>Ischyroceros</i> sp.	25	
Amphipoda		Leucothoidae	<i>Leucothoe</i> sp.	2	
Amphipoda		Maeridae	<i>Maera mastersi</i>	1	
Cirripedia		Cirripedia	<i>Balanus amphitrite</i>	7	
Isopoda		Anthuridae	<i>Anthuridae</i> sp.	1	
Isopoda		Janiridae	<i>Janiridae</i> sp.	5	
Isopoda		Sphaeromatidae	<i>Sphaeromatidae</i>	22	
Tanaid		Tanaididae	<i>Tanaididae</i> sp.	19	
Tanaidacea		Apseudidae	<i>Apseudidae</i> sp.	1	

Table A1. Cont.

Phylum	Class	Family	Species	Count
Foraminifera	Foraminifera	Foraminifera	<i>Foraminifera</i> sp.	1
Insecta	Insect	Diptera	<i>Diptera</i> sp.	2
Mollusca	Bivalvia	Hiatellidae	<i>Hiatella australis</i>	15
	Bivalvia	Lasaeidae	<i>Lasaea australis</i>	413
	Bivalvia	Mytilidae	<i>Mytilidae</i> spp.	96
	Chitonida	Acanthochitonidae	<i>Acanthochitona</i> sp.	1
	Chitonida	Chitonidae	<i>Chitonidae</i> sp.	1
	Gastropod	Fissurellidae	<i>Emarginula</i> sp.	1
	Gastropoda	Patellidae	<i>Scutellastra peronii</i>	3
	Nematoda	Nematoda	<i>Nematoda</i> spp.	25
	Nemertea	Nemertean	<i>Nemertea</i> spp.	28
	Platyhelminthes	Platyhelminthes	Platyhelminthes	<i>Platyhelminth</i> sp.

Appendix B

Table A2. *Durvillaea amatheiae* holdfast location, dimensions, species count, fauna abundance, and fauna abundance per unit volume.

Location	Sample	Diameter (mm)	Height (mm)	Volume (mL)	Species	Abundance	Abundance Per mL
Aragunnu	A1	59.0	15	20	6	14	0.70
Aragunnu	A2	91.5	25	90	16	33	0.37
Aragunnu	A3	59.0	20	22	7	43	1.95
Aragunnu	A4	67.5	15	32	12	36	1.13
Aragunnu	A5	37.5	10	3	1	1	0.33
Aragunnu	A6	59.0	15	17	10	52	3.06
Aragunnu	A7	63.5	22	23	10	28	1.22
Aragunnu	A8	89.5	22	49	8	35	0.71
Aragunnu	A9	91.5	22	68	23	52	0.76
Aragunnu	A10	69.0	20	22	8	22	1.00
Cape Conran	CC1	57.0	12	12	1	1	0.08
Cape Conran	CC2	88.0	20	48	2	2	0.04
Cape Conran	CC3	57.5	15	15	3	4	0.27
Cape Conran	CC4	47.5	11	10	2	2	0.20
Cape Conran	CC5	38.5	10	10	1	3	0.30
Cape Conran	CC6	51.5	14	10	1	1	0.10
Cape Conran	CC7	86.0	22	70	1	1	0.01
Cape Conran	CC8	85.5	17	42	6	9	0.21
Cape Conran	CC9	67.5	10	15	3	5	0.33
Cape Conran	CC10	77.5	25	45	3	3	0.07
Green Cape	GC1	102.0	32	80	17	87	1.09
Green Cape	GC2	127.0	35	160	13	46	0.29
Green Cape	GC3	56.5	23	20	7	9	0.45
Green Cape	GC4	86.5	23	79	9	22	0.28
Green Cape	GC5	70.0	16	21	12	18	0.86
Green Cape	GC6	74.0	22	32	6	13	0.41
Green Cape	GC7	72.5	23	35	9	30	0.86
Green Cape	GC8	113.5	32	108	9	33	0.31
Green Cape	GC9	60.0	20	21	6	11	0.52
Green Cape	GC10	52.5	20	15	8	10	0.67
Mallacoota	MA1	130.0	25	135	3	12	0.09
Mallacoota	MA2	115.0	28	120	4	25	0.21
Mallacoota	MA3	120.0	25	98	10	35	0.36
Mallacoota	MA4	77.5	15	58	7	53	0.91

Table A2. Cont.

Location	Sample	Diameter (mm)	Height (mm)	Volume (mL)	Species	Abundance	Abundance Per mL
Mallacoota	MA5	62.5	15	21	5	13	0.62
Mallacoota	MA6	75.0	23	39	2	2	0.05
Mallacoota	MA7	81.0	15	32	5	9	0.28
Mallacoota	MA8	59.5	12	16	1	22	1.38
Mallacoota	MA9	76.5	15	25	6	17	0.68
Mallacoota	MA10	57.5	15	13	4	10	0.77
Merimbula	M1	61.5	17	30	11	30	1.00
Merimbula	M2	62.5	16	19	8	21	1.11
Merimbula	M3	56.5	18	18	7	15	0.83
Merimbula	M4	40.0	16	10	10	22	2.20
Merimbula	M5	56.0	16	20	4	11	0.55
Merimbula	M6	45.5	12	11	7	17	1.55
Merimbula	M7	47.5	14	9	7	8	0.89
Tathra	T1	66.0	20	29	3	6	0.21
Tathra	T2	60.5	20	20	2	3	0.15
Tathra	T3	78.0	22	29	9	20	0.69
Tathra	T4	79.5	22	36	7	24	0.67
Tathra	T5	58.5	18	20	4	4	0.20
Tathra	T6	54.0	20	20	2	2	0.10
Tathra	T7	51.5	12	10	3	3	0.30
Tathra	T8	84.0	25	50	9	19	0.38
Tathra	T9	52.5	15	20	6	7	0.35
Tathra	T10	61.0	17	19	4	4	0.21

Appendix C

Table A3. Results of PERMANOVA test for differences in *Durvillaea amatheiae* holdfast macrofaunal assemblages among locations.

Variable	df	SS	MS	Pseudo-F	P (Perm)	Unique Perms
Location	5	38131	7626.1	3.9326	0.001	998

Table A4. Results of PERMANOVA tests for differences in *Durvillaea amatheiae* holdfast macrofaunal assemblages among pairs of locations.

Location Pair	t	P (Perm)	Unique Perms
Mallacoota, GreenCape	1.6992	0.002	995
Mallacoota, CapeConran	2.3745	0.001	978
Mallacoota, Merimbula	1.9139	0.001	973
Mallacoota, Aragunnu	1.9161	0.008	993
Mallacoota, Tathra	1.6125	0.022	996
GreenCape, CapeConran	2.2959	0.001	973
GreenCape, Merimbula	1.3795	0.019	975
GreenCape, Aragunnu	1.4188	0.019	991
GreenCape, Tathra	1.7763	0.005	992
CapeConran, Merimbula	1.7273	0.008	740
CapeConran, Aragunnu	2.6244	0.001	955
CapeConran, Tathra	2.5017	0.002	975
Merimbula, Aragunnu	1.6583	0.004	951
Merimbula, Tathra	2.081	0.001	973
Aragunnu, Tathra	2.2181	0.002	991

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