

Forgotten underwater forests: The key role of fucoids on Australian temperate reefs

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Abstract

Kelp forests dominated by species of Laminariales are globally recognized as key habitats on subtidal temperate rocky reefs. Forests characterized by fucal seaweed, in contrast, receive relatively less attention despite being abundant, ubiquitous, and ecologically important. Here, we review information on subtidal fucal taxa of Australia's Great Southern Reef, with a focus on the three most abundant and widely distributed genera (*Phyllospora*, *Scytothalia*, and *Sargassum*) to reveal the functionally unique role of fucoids in temperate reef ecology. Fucal species span the entire temperate coastline of Australia (~71,000 km²) and play an important role in supporting subtidal temperate biodiversity and economic values on rocky reefs as well as in adjacent habitats. Climatic and anthropogenic stressors have precipitated significant range retractions and declines in many fucoids, with critical implications for associated assemblages. Such losses are persistent and unlikely to be reversed naturally due to the life history of these species and colonization of competitors and grazers following loss. Active restoration is proving successful in bringing back some fucoid species (*Phyllospora comosa*) lost from urban shores and will complement other passive and active forms of conservation. Fucal forests play a unique role on subtidal temperate reefs globally, especially in Australia, but are comparatively understudied. Addressing this knowledge gap will be critical for understanding, predicting, and mitigating extant and future loss of these underwater forests and the valuable ecosystem services they support.

KEYWORDS

climate change, decline, *Ecklonia radiata*, ecology, kelp, seaweed

1 | INTRODUCTION

Underwater macroalgal forests are globally recognized as key components of temperate rocky reefs where they play a disproportionately important role in supporting immense economic and ecologic value (Bennett et al., 2016; Steneck & Johnson, 2013; Steneck et al., 2002). Canopy-forming macroalgae are considered "foundation species" sensu (Dayton, 1972) that modify environmental conditions and underpin biodiversity both locally (Coleman, Vytopil, Goodsell, Gillanders, & Connell, 2007; Graham, 2004; Irving, Connell, & Gillanders, 2004;

Wernberg, Kendrick, & Phillips, 2003; Wernberg, Kendrick, & Toohy, 2005) and in adjacent habitats (Bishop, Coleman, & Kelaher, 2010; Krumhansl & Scheibling, 2012; Vanderklift & Wernberg, 2008). Although these underwater forests often comprise taxonomically diverse canopies of macroalgae from many orders, scientific attention predominately centers on species of Laminariales or true kelps (e.g., *Macrocystis*, *Ecklonia*, *Laminaria*, see however [Fraser, 2012; Bolton, 2016] for a discussion of the definition of "kelp"). This is despite macroalgal species in other orders, especially the Fucales, dominating many underwater forests globally (Steneck & Johnson, 2013;

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Thibault, Pinedo, Torras, & Ballesteros, 2005; Verges et al., 2014; Vogt & Schramm, 1991; Wernberg, Thomsen, Staehr, & Pedersen, 2004; Wernberg, Kendrick, et al., 2003; Wikström & Kautsky, 2007). Although the similar structural arrangement of laminarian and fucalean forests are often justification for their grouping in temperate reef ecology (Steneck & Johnson, 2013), inherent differences in the biology and morphology of these orders are likely to result in specific biotic associations and responses to environmental change (Hirst, 2006; Phillips, Kendrick, & Lavery, 1997; Wernberg & Connell, 2008; Wernberg, de Bettignies, Bijo, & Finnegan, 2016; Wernberg, Russell, et al., 2011). Hence, addressing the knowledge gap surrounding the specific role of fucoids on subtidal temperate reefs will be critical for understanding how these unique forests and their associated biodiversity will respond to increasing anthropogenic stressors and in informing management and conservation initiatives.

The temperate rocky reefs of the southern hemisphere are unique in that they are home to the greatest diversity of fucoid genera globally supporting 73% more species than reefs in the northern hemisphere (Steneck & Johnson, 2013). Indeed, fucoids are 6 times more speciose than laminariales in the southern hemisphere (Guiry, 2012; Steneck & Johnson, 2013). The microtidal nature of many temperate coasts in Australia means that these fucoids are predominately subtidal, a similar situation to rocky reefs of the Baltic and Mediterranean Seas. In particular, the underwater macroalgal forests that dominate more than 71,000 km² of the temperate Australian coastline (the Great Southern Reef or GSR (Bennett et al., 2016) have the highest fucoid diversity and endemism globally. These forests comprise a diverse flora of 63 species of Fucales (e.g., *Phyllospora comosa*, *Scytothalia dorycarpa*, *Cystophora* spp., *Cystosiera* spp., *Acrocarpia* spp., *Durvillaea potatorum*, and *Sargassum* spp.) with only four native species of Laminariales (e.g., *Ecklonia radiata*, *Macrocystis pyrifera*, *M. angustifolia*, and *Lessonia corrugata*) occurring as either mixed or monospecific forests (Goodsell, Fowler-Walker, Gillanders, & Connell, 2004; Turner & Cheshire, 2003; Wernberg & Connell, 2008; Wernberg, Thomsen, Tuya, & Kendrick, 2011; Wernberg, Kendrick, et al., 2003). Indeed, mixed laminariales/fucoid forests have been estimated to account for up to 64% of subtidal macroalgal forests in southern and Western Australia (Goodsell et al., 2004; Wernberg, Thomsen, et al., 2011). In particular, extensive monospecific fucoid forests comprised of *Phyllospora comosa*, *Scytothalia dorycarpa* (hereafter referred to as *Phyllospora* and *Scytothalia*, respectively) and species of *Sargassum* occur along most of the ~8,000 km temperate coast of Australia, but have only recently been the focus of research efforts spurred by climatic- and anthropogenic-induced declines (Coleman, Kelaher, Steinberg, & Millar, 2008; Phillips & Blackshaw, 2011; Smale & Wernberg, 2013; Wernberg, Bennett, et al., 2016).

To assess the knowledge base of subtidal fucoids relative to laminariales, we did a literature search (see Appendix S1 for detailed protocol) to qualitatively identify scientific publications on the most abundant subtidal habitat-forming species in Australian waters. We searched for the terms *Phyllospora comosa*, *Scytothalia dorycarpa*, *Durvillaea potatorum*, *Acrocarpia* spp., *Cystophora* spp., *Cystoseira trindis*, *Sargassum* spp., *Macrocystis* spp., *L. corrugata*, or *E. radiata* in the

title, keywords, or abstract of papers and found between 1 and 25 relevant publications for each fucoid species versus 321 relevant papers on the 3 laminarian taxa, highlighting the critical lack of specific ecological studies on fucoids relative to co-occurring laminariales. Moreover, this literature search revealed that, relative to laminariales, these fucoids have only been the focus of recent research attention with 80% of all publications on *Scytothalia* and all ecological studies on *Phyllospora* from the last decade. Given the relative lack of studies to conduct a rigorous quantitative review of the importance of subtidal fucoids, here we review knowledge on Australia's extensive subtidal fucoid forests to qualitatively demonstrate their unique role in reef ecology, and identify research gaps that should be addressed to better understand these key habitats and inform conservation and rehabilitation efforts. We specifically focus on the better studied taxa, *Phyllospora*; 25 papers, *Sargassum* spp.; 22 papers, and *Scytothalia*; 8 papers because these are the most dominant habitat-forming fucoids on the temperate subtidal reefs across Australia and all 3 taxa have undergone recent declines (Coleman, Kelaher, et al., 2008; Phillips & Blackshaw, 2011; Smale & Wernberg, 2013; Wernberg, Bennett, et al., 2016).

2 | BIOLOGY OF AUSTRALIA'S SUBTIDAL FUCOID FORESTS

2.1 | Distribution and abundance

Phyllospora comosa (C. Agardh) and *S. dorycarpa* (Greville) are closely related, monotypic species in the family Seirococcaceae (Huisman, 2000; Womersley, 1987). It is hypothesized that these Tethyan taxa speciated following historically stable, temperate conditions and a lack of mass extinction events along the southern coastline of Australia (Phillips, 2001). They largely occupy allopatric distributions from approximately ~31°S on the east (Coleman, Kelaher, et al., 2008) and west (Smale & Wernberg, 2013) coastlines of Australia, respectively, with only a narrow overlap between Robe (~37°S, South Australia) and Point Lonsdale (~38°S, Victoria; Figure 1). Both species are perennial and common on exposed rocky reefs with *Phyllospora* dominating in shallow (~0–3 m) areas in NSW and deeper (0–10 m) in Tasmania and Victoria (Edgar, 1984; James, Reid, Bone, Levings, & Malcolm, 2013). *Scytothalia* has a wider depth distribution occurring between 3 and 50 m depth (Shepherd & Womersley, 1971; Smale et al., 2010). Both species are canopy forming with *Phyllospora* growing to about 3 m height and *Scytothalia* typically about 1–2 m in height (Huisman, 2000).

In contrast, *Sargassum* is the most speciose genus of fucoids and comprises both temperate and tropical species. There are approximately 19 species of temperate *Sargassum*, many of which span the entire temperate coastline of Australia (e.g., *S. linearifolium*; Figure 1) and a broad depth range. *Sargassum* spp. are characterized by highly variable morphology making species identification difficult and much ecological research on *Sargassum* focuses on the genus level. Unlike *Phyllospora* and *Scytothalia*, *Sargassum* generally forms a mixed sub-surface canopy with plants growing to between 10 cm and 2 m in

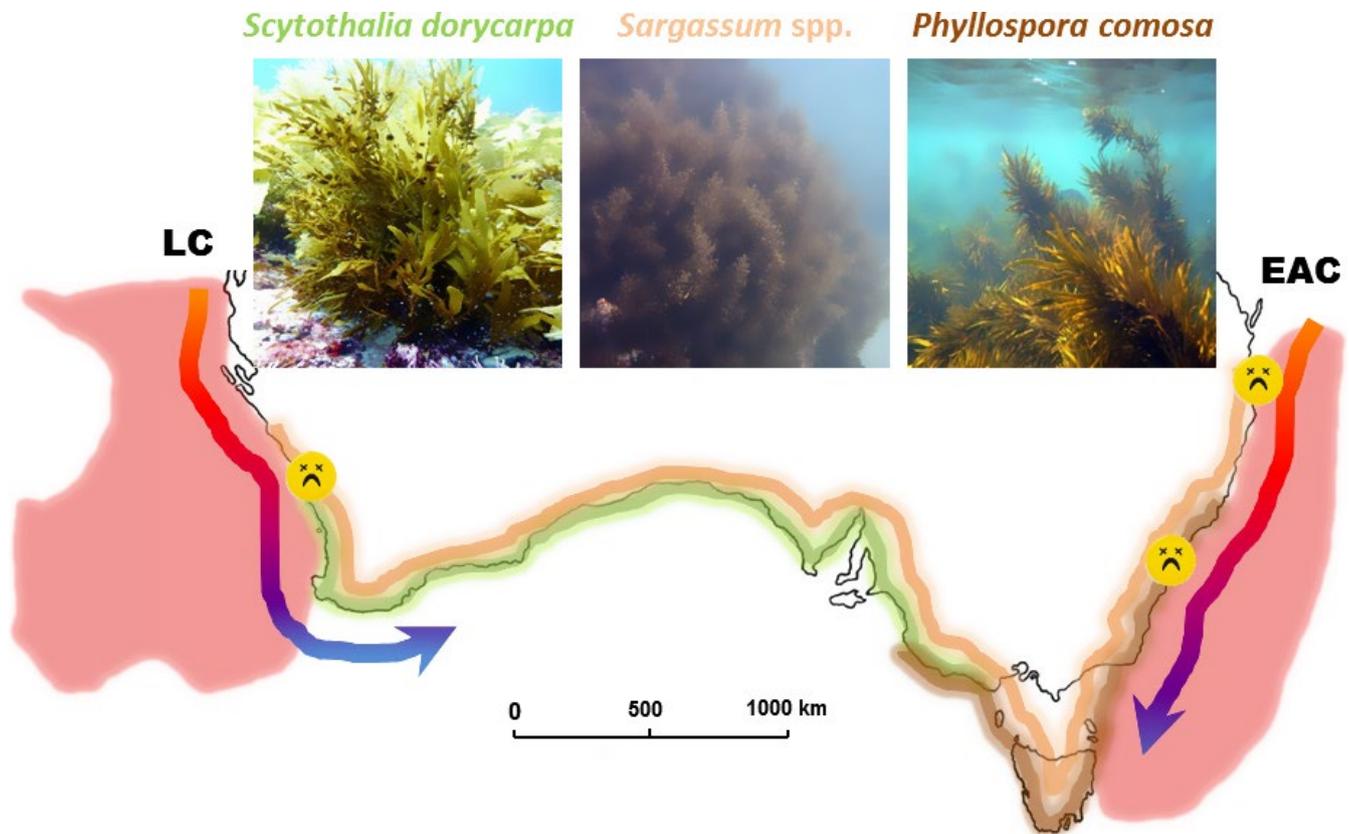


FIGURE 1 *Phyllospora comosa* (brown), *Scytothalia dorycarpa* (green), and a representative temperate *Sargassum* (*S. linearifolium*; orange) are distributed around the temperate coastline of Australia. These species are dominant or co-dominant habitat formers with the kelp *Ecklonia radiata* in the east and west, respectively. Major boundary currents shown on the east (East Australian Current; EAC) and west (Leeuwin Current; LC) coasts as well as regions of documented local extirpation (dead smiley). The ocean areas highlighted in red are global warming hotspots, where recent temperature increases have been in the top 10% globally (after Hobday and Pecl [2014])

length (Womersley, 1987). Similarly, in contrast to most other fucoids, *Sargassum* spp. are pseudo-perennial, implying they periodically shed their foliose canopy, only leaving behind the holdfast and short, basal fronds, which may account for highly variable estimates of percentage cover between seasons and over large spatial scales (Bennett & Wernberg, 2014; Thomsen, Wernberg, Staehr, & Pedersen, 2006; Thomson, Babcock, Vanderklift, Symonds, & Gunson, 2012).

The subtidal temperate reefs of Australia are unique in that fucoid forests often form extensive monospecific forests or are co-dominant in mixed forests with Laminariales (Steneck & Johnson, 2013). *Phyllospora* and *Scytothalia* both occur as monospecific and mixed algal forests, but the distribution of these forest types varies spatially. *Phyllospora* commonly occurs as monospecific forests in shallow, exposed areas (e.g., in NSW) or as mixed forests with *Ecklonia radiata* at its deeper edges (e.g., in Tasmania). Densities of *Phyllospora* are approximately 14 individuals per m² in shallow monospecific forests (Peters, 2015) and 2.5 individuals per m² in deeper mixed forests (Valentine & Johnson, 2004). *Scytothalia* also occurs as either mixed or monospecific forests in its central and southern range (Baker & Edyvane, 2003; Turner & Cheshire, 2003), but occurs as predominately mixed forests at higher latitudes in Western Australia where it is gradually replaced by warmer water Fucales such as *Sargassum* (Wernberg, Thomsen, et al., 2011). Percent cover of *Scytothalia* varies between 2% and

39% throughout its distribution (Bennett & Wernberg, 2014; Smale & Wernberg, 2013) and tends to increase with latitude (Smale et al., 2010; Wernberg, Thomsen, et al., 2011) and wave exposure (Turner & Cheshire, 2003; Wernberg & Connell, 2008). Relative to *Ecklonia*, *Scytothalia* also dominates on high relief reefs and on granite compared to limestone (Harman, Harvey, & Kendrick, 2003). Regardless, whether occurring as mixed or monospecific forests, fucoids and laminariales are integrally linked on the subtidal temperate reefs of Australia, but scientific knowledge is biased toward the latter.

Sargassum tends to form mixed stands with other fucoids and laminariales and often up to nine species of *Sargassum* co-occur within the same stand (Goldberg, 2007). Accordingly, percentage cover of *Sargassum* in Western Australia varies between 0% and 20%, with the remaining reef cover predominately being composed of *Scytothalia* (0%–40%) and *Ecklonia* (40%–86%; Bennett & Wernberg, 2014). The relative cover of *Sargassum* spp. changes on small spatial scales but has been shown to have the greatest cover at mid-latitudes (~30.5°) and be correlated with temperature (Wernberg, Thomsen, et al., 2011).

2.2 | Morphology and life history

Phyllospora and *Scytothalia* are morphologically similar with flattened thalli (Figure 1, (Womersley, 1987)) and a holdfast with densely

packed haptera. *Phyllospora* has a flattened main axis which bears many closely set lateral branches and has vesicles and a short stipe. In contrast, *Scytothalia* has flattened alternate axes. Reproductive structures (conceptacles) are produced on the entire surface of lateral branches in *Phyllospora*, whereas *Scytothalia* produces special receptacles arising from the lateral branches (Figure 2). *Sargassum* spp. have varied morphology, but are generally foliose and bushy with reproductive upper parts of the thallus morphologically distinct from the lower perennial portions of the plant which have wider basal fronds (Figure 1). *Phyllospora* and *Sargassum* both have gas-filled vesicles which assist it to be positioned above the substratum when attached and float on the surface of the water when detached following storms (Figure 2). Indeed, the presence of gas-filled vesicles facilitates long distance dispersal relative to species that lack such structures (Coleman, Chambers, et al., 2011). The morphology of all three of these fucoid taxa contrasts starkly with all co-occurring species of laminariales which, in comparison, have structurally simple thalli.

There is little published knowledge on spatial variation in morphology in each fucoid taxa, but the data that do exist demonstrate great spatial variation and suggest that local environmental conditions may dictate morphology as is known for other macroalgae (Wernberg, Coleman, Fairhead, Miller, & Thomsen, 2003). For example, stipe

length in *Phyllospora* is significantly shorter at lower latitudes in NSW with some low latitude locations (Port Stephens) characterized by plants with significantly more main axes and fewer vesicles (Coleman, unpubl. data). In contrast, others have found *Phyllospora* to be longer at its northern limits (~31°S, Port Macquarie) and stipe length to be greater in southern NSW (Peters, 2015). All other morphologic characteristics of *Phyllospora* exhibit much small-scale variation along its entire geographic distribution suggesting that morphology may be highly plastic. There are no large-scale morphologic studies within species of *Sargassum* likely because similarities in morphology among species make single-species identification challenging. It is thought, however, that local environmental conditions underpin highly plastic morphologies within species. Examining the extent of covariation in individual morphological characteristics among multiple species along environmental gradients may help elucidate what drives this plasticity (Coleman & Muhlin, 2008).

Phyllospora, *Scytothalia*, and *Sargassum* spp. have typical fucoid life history strategies producing eggs and sperm which are externally fertilized (Figure 2). *Phyllospora* is dioecious with male individuals releasing motile sperm from elongated conceptacles that fertilize stalked eggs that are released and attached to the female plant (Womersley, 1987). *Phyllospora* sex ratios are approximately 50:50 along much of the coast of NSW (Coleman, unpubl. data). Similarly, *Sargassum* can be monoecious or dioecious and many species retain fertilized eggs on the parent plant and zygotes develop for ~24 hr before release (May & Clayton, 1991; Shepherd & Edgar, 2013). In contrast, *Scytothalia* is monoecious with mostly unisexual conceptacles. Reproductive structures appear to be present on both *Phyllospora* and *Scytothalia* throughout the year (Andrews, Bennett, & Wernberg, 2014; Burrige & Hallam, 1993), but *Scytothalia* reproduction may peak in the austral winter (May to September; Andrews et al., 2014). The timing of *Sargassum* reproduction varies greatly among species (Shepherd & Edgar, 2013). There exists little information on what cues reproduction in these taxa but it is likely that, as with other fucoids, release of gametes is cued to environmental conditions including periods of calm water (Andrews et al., 2014; Figure 2), high, slack, or neap tides or lunar cycles (May & Clayton, 1991; Muhlin, Coleman, Rees, & Brawley, 2011; Pearson & Serrão, 2006). For all taxa, gamete release can easily be induced in the laboratory by subjecting individuals to a series of osmotic and hydrostatic shocks making them ideal species of studies of early life history processes.

Despite many fucoid taxa having easily manipulated life histories, there are only a handful of studies that examine factors affecting the early life history stages of *Phyllospora*, *Scytothalia*, and *Sargassum*. Laboratory studies have shown that fertilization, germling survival, and recruitment are all negatively impacted by high temperature in *Scytothalia* (Andrews et al., 2014). Moreover, the ease of inducing reproduction and growing juvenile *Phyllospora* has made this species a model system for marine toxicology studies (Burrige & Bidwell, 2002). Relative to other species, the juvenile stages (zygotes, germlings) of *Phyllospora* are particularly sensitive to a range of contaminants, including sewage effluent, oil dispersants, formaldehyde, and tributyltin with sensitivity decreasing with age (Burrige, Lavery, & Lam, 1995;

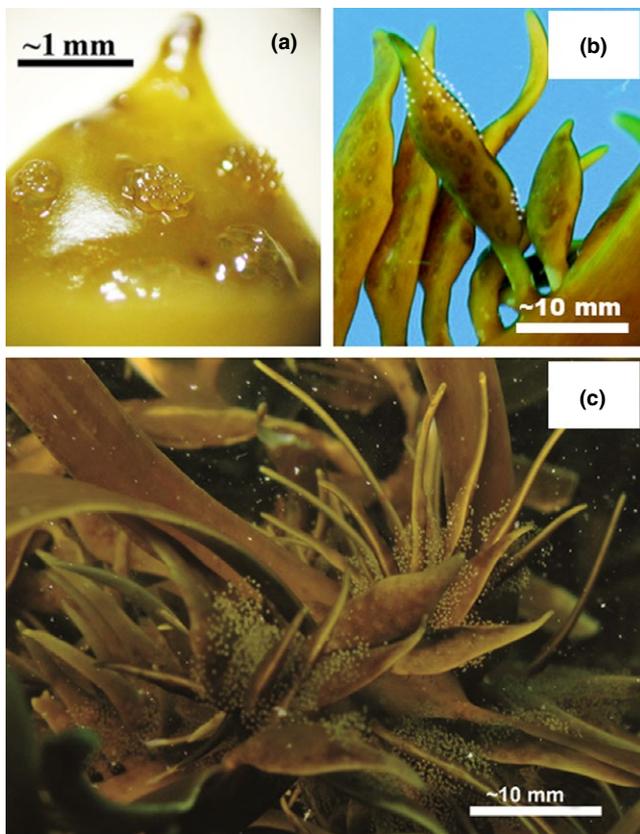


FIGURE 2 Photographs showing key aspects of *Scytothalia* morphology and life history. (a) Egg release from conceptacles. (b) Specialized receptacles (bearing multiple conceptacles) are produced on the main axis. (c) Gametes are retained in a cloud of mucous during synchronous gamete release in the field. Photos: Stefan Andrews

Burridge, Portelli, & Ashton, 1996; Burridge & Shir, 1995). Studies on other fucoids suggest that warming temperatures may impact early life history via alteration of zygote attachment time (Coleman & Brawley, 2005a) and reproductive timing (Coleman & Brawley, 2005b). Thus, further studies on the early life history stages of both *Phyllospora*, *Scytothalia*, and *Sargassum* will be crucial for understanding the mechanisms behind recent climate-mediated population declines and failure to naturally re-establish.

Dispersal of *Phyllospora* and *Sargassum* zygotes appears to occur predominately over short distances as indicated by declining recruitment within distance from adult canopies (Campbell, Marzinelli, Vergés, Coleman, & Steinberg, 2014; Kendrick & Walker, 1991, 1995). Furthermore, genetic studies confirm these observations and reveal that inbreeding in *Phyllospora* is common and gene flow may break down on scales <80 km (Coleman, Dolman, Kelaher, & Steinberg, 2008; Coleman & Kelaher, 2009). Dispersal of *Phyllospora* is also influenced by coastal topography and/or hydrodynamics with populations inhabiting enclosed bays showing significantly greater genetic structuring (Coleman, Chambers, et al., 2011). Over evolutionary scales, low genetic diversity of *Phyllospora* in southeastern Australia suggests that colonization may be recent and rapid dispersal facilitated by the presence of gas-filled vesicles (Durrant, Barrett, Edgar, Coleman, & Burridge, 2015). Indeed, gas-filled vesicles facilitate dispersal of *Phyllospora* over at least ~600 km and drift material has been found on Lord Howe Island despite the plants not growing there (Millar & Kraft, 1993). Furthermore, *Phyllospora* is often found washed up on Sydney's beaches and has dispersed in ocean currents from extant sites to the north or south (10s km; (Coleman, Kelaher, et al., 2008)). Certainly, the East Australian Current is likely to facilitate dispersal of this species (Coleman, Roughan, et al., 2011). Dispersal of fertile drift material, however, does not guarantee gene flow. Viable male and female plants need to be present in sufficient density for fertilization to occur and subsequent recruitment is likely mediated by pre-emptive competition (Coleman, Kelaher, et al., 2008) and extant environmental conditions (Smale & Wernberg, 2013). There are no genetic studies on *Scytothalia*, but the lack of vesicles to facilitate long-range dispersal as well as ecological experiments indicating a high level of ecotypic differentiation in physiology among populations (Bennett, Wernberg, Joy, De Bettignies, & Campbell, 2015), suggesting dispersal and gene flow are relatively limited, and may be less than *Phyllospora*. Certainly, the presence of gas-filled vesicles to aid dispersal and maintain gene flow among populations may be particularly advantageous in a future of increasing population fragmentation (Coleman, Kelaher, et al., 2008) and changing oceanic vectors of dispersal (Cetina-Heredia, Roughan, van Sebille, & Coleman, 2014; Cetina-Heredia, Roughan, van Sebille, Feng, & Coleman, 2015; Coleman et al., 2017). The lack of such structures combined with the predominately poleward flow of boundary currents may also explain the failure of *Scytothalia* to re-establish following climate-mediated loss at its range limits in Western Australia (Wernberg, Bennett, et al., 2016).

Recruitment processes are well studied in *Sargassum* relative to other fucoids. At mid-latitudes (~32°), the presence of an adult canopy has little influence on recruit survival until recruits are 6 months of

age, after which, canopy negatively impacts recruit survival (Kendrick, 1994). Interestingly, this pattern may be reversed at lower (warmer) latitudes where *Sargassum* recruits may rely heavily on the presence of adult canopy for survival, something that also applies to *Scytothalia* recruits (Bennett & Wernberg, 2014). Unlike most other fucoids, *Sargassum* has the ability to regenerate from remnant holdfasts that remain following loss of the thallus, which tends to decrease spatial and temporal variability in adult density (Kendrick & Walker, 1994).

2.3 | Physiology and growth

In contrast to co-occurring laminariales (e.g., *E. radiata*), research on the physiology of *Phyllospora*, *Scytothalia*, and *Sargassum* spp. is scant but will be critical to understanding the mechanisms behind recent declines in all three taxa. *Phyllospora* photosynthetic efficiency, growth, and survival appear to be negatively correlated with higher summer temperatures (22°C; Flukes, Wright, & Johnson, 2015) and in NSW, plants have higher $\delta^{13}\text{C}$, photosynthetic capacity (rETR_{max}), and concentrations of chl c and fucoxanthin compared to Tasmania. However, as with morphology (Peters, 2015), these traits appear to be highly plastic and rapidly converge under similar environmental conditions (Flukes et al., 2015). Supporting this finding, Weigner (2016) found no latitudinal pattern in *Phyllospora* tissue chemistry along a 5 degree latitudinal gradient in NSW. In contrast to *Phyllospora*, *Scytothalia* and *Sargassum* have lower pigment (Chl a, Chl c) concentrations at lower latitudes, and these tissue changes appear to be part of systematic physiologic changes of increasing respiration and decreasing net photosynthesis at lower latitudes, corresponding to higher water temperatures (Wernberg, de Bettignies, et al., 2016). *Scytothalia* from Perth (~32°S) has its physiologic optimum (highest net primary production) around 24°C (Smale & Wernberg, 2013; Wernberg, de Bettignies, et al., 2016), which is lower than co-dominant canopy-forming species including *Ecklonia* and *Sargassum* (Wernberg, de Bettignies, et al., 2016). In addition, *Scytothalia* has a narrower temperature range for optimum performance than these species, being almost half that of *Sargassum* (Wernberg, de Bettignies, et al., 2016). These short-term physiologic optima are, however, higher than observed for other biological processes. Specifically, recruitment and recruit development (Andrews et al., 2014) and linear growth (Xiao et al., 2015) have been found to decrease and eventually cease at about ~20°C. Importantly, reciprocal transplant experiments have clearly documented that these temperature thresholds vary between populations at different latitudes (Bennett et al., 2015).

3 | KEY FOUNDATION SPECIES IN SHALLOW SUBTIDAL AREAS

Subtidal fucoid forests play a key role on Australia's temperate rocky reefs as foundation species that support biodiversity (Figure 3). Indeed, despite the grouping of fucoids with Laminariales due to their structural similarity as canopy formers (Steneck & Johnson, 2013), we show here that fucoid species play unique functional roles in

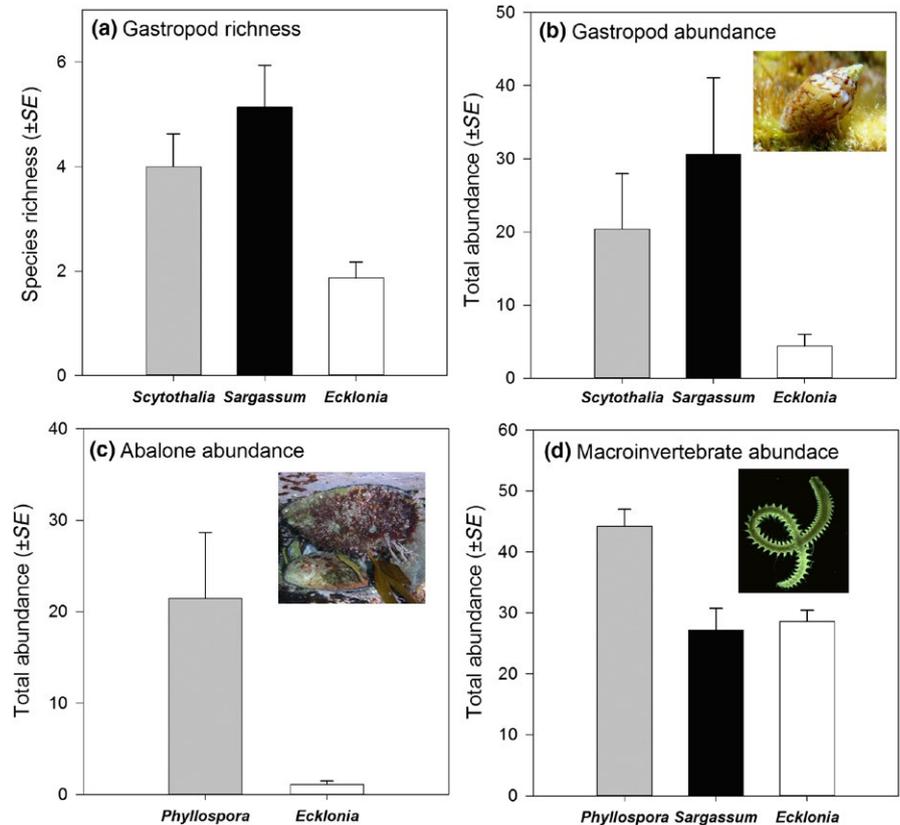


FIGURE 3 *Phyllospora*, *Scytothalia*, and *Sargassum* spp. support unique and diverse associated assemblages relative to co-occurring laminariales (*Ecklonia radiata*). *Scytothalia* and *Sargassum* support higher (a) richness and (b) abundance of gastropods (data re-analyzed from Tuya et al. [2008]). *Phyllospora* supports (c) higher abundances of abalone (data re-analyzed from Marzinelli et al. [2014]), and (d) higher total abundance of infauna in adjacent soft-sediment habitats enriched with detritus from *Ecklonia* and *Sargassum* (data re-analyzed from Bishop et al. [2010])

structuring biodiversity of temperate reefs and should be considered separately, particularly where they occur as dominant monospecific forests (e.g., *Phyllospora* along the east coast of Australia).

Phyllospora and *Scytothalia* occur either as primary constituents of monospecific forests or as components of mixed algal canopies (Goodsell et al., 2004; Irving et al., 2004), whereas *Sargassum* spp. generally occur in mixed stands (Goldberg, 2007; Wernberg & Connell, 2008; Wernberg, Thomsen, et al., 2011). Indeed, even mixed fucalcan/laminarian forests have been shown to provide different abiotic environmental conditions in terms of light, abrasion, and sedimentation (Irving & Connell, 2006; Wernberg et al., 2005) and support unique phytal (Tuya, Wernberg, & Thomsen, 2008; Wernberg et al., 2004), benthic (Goodsell et al., 2004; Irving et al., 2004), and fish (Harman et al., 2003; Tuya, Wernberg, & Thomsen, 2009) communities compared to monospecific laminarian forests. Surprisingly, less is known about the key role these taxa play in supporting biodiversity in monospecific forests despite the prevalence of monospecific fucoid forests around the entire temperate coast of Australia (Connell & Irving, 2008; Wernberg, Thomsen, et al., 2011). Certainly, monospecific forests of *Phyllospora* support unique epifaunal (Marzinelli, Leong, Campbell, Steinberg, & Verges, 2016) and understory communities and greater abundances of economically important species such as abalone (Marzinelli et al., 2014; Figure 3) indicating that they play an important functional role in supporting temperate biodiversity. Interestingly, *Phyllospora* did not support statistically different roving fish communities to the co-dominant *E. radiata*, but it is likely that small and cryptic species may respond to differences in these macrophyte habitats (Marzinelli et al., 2014). No equivalent comparative community-level

studies have been done for *Scytothalia* or *Sargassum*, but studies focused on the gastropod component of epifauna clearly indicate that *Scytothalia* supports different communities compared with the dominant *Ecklonia* (Tuya et al., 2008; Figure 3). Similarly, *Sargassum* spp. can support unique epifaunal communities relative to *Ecklonia* and *Phyllospora* and a greater diversity of epifauna per gram, probably because of its structurally complex form (Marzinelli et al., 2016). Indeed, both natural and experimental losses of *Phyllospora* and *Scytothalia* canopies have been shown to result in significant changes in associated communities (Coleman, Kelaher, et al., 2008; Smale & Wernberg, 2013; Valentine & Johnson, 2004), suggesting that loss and decline of these fucoids will have widespread ecosystem level impacts.

Sargassum (particularly *S. linearifolium*) is a habitat for diverse assemblages of mesograzers and has been used as a model system for plant-herbivore interactions (Poore & Hill, 2005; Poore & Steinberg, 1999; Poore et al., 2013). Some temperate *Sargassum* spp. exhibit tolerance to grazing via compensatory growth (Hay et al. 2011) and temperate *Sargassum* spp. characterized by relatively high levels of phenolics are equally as palatable to tropical fishes as phenolic poor tropical *Sargassum* spp. (Steinberg et al. 1991). This may change, however, under future temperature and acidification scenarios. Palatability of *Sargassum* to amphipods was greater under acidified and elevated temperature conditions, suggesting that the nutritional content or changes in algal growth form may alter trophic dynamics under future ocean conditions (Hay et al. 2011).

Forests of *Scytothalia* and *Phyllospora* also play a role in supporting many important near-shore fisheries and are therefore important economic components of temperate reefs. For example, *Phyllospora*

forests support significantly more abalone than other macroalgal habitats (Marzinelli et al., 2014; Figure 3). Interestingly, the loss of *Phyllospora* from the Sydney region may have exacerbated the failure of abalone to re-establish viable populations in this region following abalone loss through *Perkensis* disease. Furthermore, *Phyllospora*, which is commonly known as “crayweed” is thought to support high densities of adult lobster (pers. obs. MA Coleman) and may also be important in enhancing lobster recruitment and decreasing predation on juveniles (Hinojosa, Green, Gardner, & Jeffs, 2015).

Detached habitat-forming macroalgae play key roles as spatial subsidies, supporting communities in other habitats after being removed from the seafloor following storms (see refs above). *Phyllospora* and *Sargassum* spp. are particularly important spatial subsidies in adjacent soft-sediment communities because the presence of gas-filled vesicles that allow them to float, confer ability to disperse into new and distant areas after being detached. *Phyllospora* is a common component of wrack that washes up in estuarine and beach soft-sediment communities and sediments containing *Phyllospora* detritus support unique infaunal communities and higher total abundance of infauna relative to other species, including *Sargassum* spp. and *Ecklonia radiata* (Bishop et al., 2010; Figure 3). Similarly, floating *Phyllospora* and *Sargassum* wrack supports transient, yet diverse pelagic fish communities (Dempster & Kingsford, 2004) and presumably acts as a dispersal vehicle for a diverse range of marine organisms as is known from other floating seaweeds (Fraser, Nikula, & Waters, 2011). *Scytothalia* and *Sargassum* also play key roles as spatial subsidies to seagrass communities and reefs several kilometers away, where they are rapidly consumed by fauna including herbivorous fish and sea urchins (Vanderklift & Wernberg, 2008). Fucoids are, therefore, key trophic components in near-shore food webs.

4 | THREATS AND DECLINES OF AUSTRALIA'S FUCOID FORESTS

Recent declines, fragmentation, and losses of *Phyllospora*, *Scytothalia*, and *Sargassum* spp. have highlighted the vulnerability of fucoid forests to a range of anthropogenic stressors. Among the most significant losses of fucoid canopies in Australia is the 100 km range retraction of *Scytothalia* from Western Australia following the 2011 marine heatwave (Smale & Wernberg, 2013). During the heatwave, temperatures increased well above the physiologic tolerance of *Scytothalia* for more than 10 weeks. Prior to the heatwave, which also caused a range of other ecological impacts (Pearce et al., 2011; Wernberg, Bennett, et al., 2016), *Scytothalia* was common and highly abundant in Jurien Bay (~30°S). Subsequently, however, it disappeared, contracting south to Wedge Island (Smale & Wernberg, 2013). The loss of *Scytothalia* was associated with substantial changes in habitat and community structure in Jurien Bay (Smale & Wernberg, 2013; Wernberg et al., 2013). A subsequent study has found these changes to correspond to exceedance of the ~2.5°C temperature anomaly (Bennett et al., 2015). Interestingly, this study found populations at the center of their distribution to be equally vulnerable (i.e., to perish under a similar

temperature anomaly) as range edge populations, presumably due to little population connectivity and high ecotypic differentiation.

On the east coast of Australia, *Phyllospora* and *Sargassum* spp. have also undergone similarly significant loss and fragmentation around urban areas (Coleman, Kelaher, et al., 2008; Phillips & Blackshaw, 2011). Herbarium specimens and historical photos demonstrate that *Phyllospora* was once abundant along the entire coastline of metropolitan Sydney, but completely disappeared decades ago leaving a 70 km gap in its distribution (Coleman, Kelaher, et al., 2008). Although the exact cause of its decline is unknown, its loss is spatially and temporally correlated to Sydney's former sewage outfalls which discharged large volumes of sewage directly into the near-shore habitat occupied by *Phyllospora* (Coleman, Kelaher, et al., 2008). This hypothesis is supported by studies demonstrating that *Phyllospora* germlings are more sensitive to sewage effluent than other fucoid species (Burrige et al., 1996). Furthermore, *Phyllospora* disappeared after the installation of a sewage outfall at Ulladulla (May, 1985) and brown algae declined in general with increasing proximity to a sewage outfall in Sydney (Borowitzka, 1972). Although these outfalls have now been moved offshore and water quality in Sydney has greatly improved (Scanes & Phillip, 1995), *Phyllospora* has not returned naturally (Coleman, Kelaher, et al., 2008). Similarly, historic records demonstrate that *Sargassum* spp. have undergone range retractions in southern Queensland, likely due to urbanization (Phillips & Blackshaw, 2011) and failure to recover may be linked to the reliance of adult canopy to ameliorate environmental conditions for recruits (Bennett & Wernberg, 2014) or inability to disperse large distances among rocky headlands (Kendrick & Walker, 1991, 1995). These losses highlight the potential vulnerability of fucoid forests to anthropogenic change and the need for specific monitoring of these key taxa as well as targeted studies to better understand the processes that underpin loss to inform management and conservation initiatives.

Loss and decline of fuclean canopies, regardless of the cause, may itself pose a new threat to marine environments by facilitating proliferation of invasive species. Indeed, both natural and experimental *Phyllospora* canopy removals in Tasmania result in rapid establishment of the invasive kelp, *Undaria pinnatifida* which benefits from available space and increased light following canopy loss (Valentine & Johnson, 2004). Similarly, it is hypothesized that loss of *Phyllospora* in the Sydney region (Coleman, Kelaher, et al., 2008) may have facilitated a local proliferation of the range expanding, *Caulerpa filiformis* which exclusively occupies *Phyllospora*'s former habitat (Glasby, Gibson, West, Davies, & Voerman, 2015). Interestingly, expanding beds of *C. filiformis* can then have cascading effects on nearby *Sargassum* beds, negatively influencing photosynthetic condition (Zhang, Glasby, Ralph, & Gribben, 2014) and decreasing the abundance of epifauna (Lanham, Gribben, & Poore, 2015).

An emerging threat to the long-term persistence of macroalgal forests is the reduction in genetic diversity caused by increased habitat fragmentation and reduced connectivity. Genetic diversity confers adaptive capacity to populations and may allow them to persist through changing environmental conditions (Hughes, Inouye, Johnson, Underwood, & Vellend, 2008; Reusch, Ehlers, Hämmerli, & Worm,

2005; Wernberg et al., in review). Reduced diversity can limit the ability of a population to respond to stressors because fewer genotypes means a limited range of physiologic responses are available to cope with change (Wernberg et al., unpubl. manuscript). This scenario may arise in populations of *Phyllospora* and *Scytothalia* that are isolated either by natural (Coleman, Chambers, et al., 2011; Coleman, Roughan, et al., 2011) or anthropogenic (Coleman, Kelaher, et al., 2008) fragmentation. Indeed, connectivity in macroalgae predicts population persistence with population extirpation being inversely correlated with connectivity (Castorani et al., 2015). Thus, loss and fragmentation of furoid forests can increase the vulnerability of remaining populations because connectivity is often eroded.

The actual physiologic or ecological reasons behind loss of furoid forests are often unknown with losses usually correlated to changes in environmental conditions. This is primarily because losses are often documented post hoc and early warning signs that may hint at the process responsible are missed or unknown. For example, loss of *Phyllospora* from the Sydney region was indirectly correlated with sewage effluent, but it is likely that this sewage directly impacted *Phyllospora* germling survival (Burrige et al., 1996) or may have facilitated disease (Campbell, Verges, & Steinberg, 2014; Peters, 2015). Similarly, the range retraction of *Scytothalia*, while correlated with temperature (Smale & Wernberg, 2013), was likely a direct result of physiologic stress killing adult thalli (Smale & Wernberg, 2013; Xiao et al., 2015) coupled with reproduction and recruitment failure in subsequent warm years (Andrews et al., 2014; Bennett et al., 2015). However, there is some evidence that furoid physiology may be highly plastic and somewhat able to cope with stressors. It has been experimentally demonstrated that *Scytothalia* can acclimate in response to UVB and increased its light absorption efficiency in the UV bands by upregulating synthesis of photoprotective compounds (Xiao et al., 2015). Similarly, *Phyllospora* physiology is also highly plastic and rapidly responds to change in abiotic conditions (Flukes et al., 2015). Certainly, thresholds exist beyond which these species will be unable to compensate, and these thresholds are likely to be determined by a range of factors including dispersal capacity and population connectivity mediating genetic diversity and capacity to adapt (Wernberg et al., in review). Identifying where these thresholds lie may allow better understanding of when and where significant loss of subtidal furoid forests may occur. Determining the direct processes behind loss of these important forests will be key for early detection of loss and, where possible, managing the processes responsible.

5 | THE FUTURE OF AUSTRALIA'S SUBTIDAL FUCOID FORESTS

Given the strong relationship between temperature and performance of *Phyllospora*, *Scytothalia*, and *Sargassum* spp. (see above), species distribution models project substantial future declines in all three taxa as a consequence of ocean warming (Figure 4; Martínez et al., unpubl. manuscript). These models suggest that all three furoids will retreat toward higher latitudes. Projections for 2100 based on the intermediate

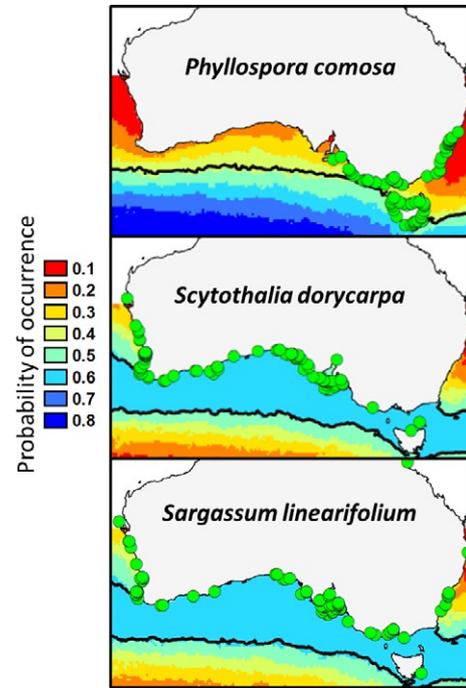


FIGURE 4 Future distribution of *Phyllospora*, *Scytothalia*, and *Sargassum linearifolium* based on species distribution models under the A1B scenario of ocean warming for 2100. The green dots represent confirmed presences (by 2009) as vouchered herbarium specimens. Ocean color represents the probability of occurrence in year 2100. Presence is interpreted as $p > .5$ (black lines; green and blue colors). Data from Martínez et al. (unpubl. manuscript)

A1B carbon emission scenario suggest that *Phyllospora* would be restricted to southwestern Tasmania and would lose 74.6% of its current distribution (Figure 4; Table 1). *Scytothalia*, in contrast, would “only” lose 18.6% of its current distribution along the west coast, whereas populations along the south would remain intact (Figure 4). *Sargassum linearifolium*, one of the most widespread temperate furoids in Australia, would lose 24.3% of its current distribution mainly from its northeastern and northwestern margins (Figure 4; Table 1). The relatively low projected habitat loss by 2100 for *Scytothalia* and *S. linearifolium* are due to their extensive south coast distribution which would remain intact. However, both species would be compressed into a narrow latitudinal range, on the poleward facing edge of the continent where both species would be vulnerable to rapid habitat loss over an extensive area with additional warming.

Predicted (Figure 4) and extant losses of *Phyllospora*, *Scytothalia*, and *Sargassum* spp. (Coleman, Kelaher, et al., 2008; Phillips & Blackshaw, 2011; Smale & Wernberg, 2013; Wernberg, Bennett, et al., 2016) as well as declines in other subtidal furoid forests globally (Airoldi & Beck, 2007; Thibault et al., 2005; Vogt & Schramm, 1991) suggest that management intervention will be critical to the long-term persistence of these key temperate habitats. This could involve passive (habitat protection), active (e.g., restoration), anticipatory (e.g., selective breeding or assisted adaptation) or integrated initiatives to halt further loss, boost the resilience of existing forests or restore areas that have already suffered decline.

TABLE 1 Extent of current and predicted future (2100) distribution for *Phyllospora comosa*, *Scytothalia dorycarpa*, and *Sargassum linearifolium* in temperate Australia

Species	Current distribution (km coastline)	Future distribution (km coastline)	Predicted habitat loss (km coastline)	Predicted habitat loss (% of current distribution)
<i>Phyllospora comosa</i>	5,547	1,409	4,138	74.6
<i>Scytothalia dorycarpa</i>	10,300	8,389	1,911	18.6
<i>Sargassum linearifolium</i>	11,844	8,969	2,874	24.3

Total length of temperate coastline was estimated to be 26,730 km. Data from Martínez et al. (unpubl. manuscript).

Passive approaches have traditionally been employed for managing subtidal macroalgal habitats and include the establishment of MPAs to remove the direct and indirect effects of harvesting pressure. The establishment of MPAs and associated trophic structures has been successful in restoring kelp (Laminariales) habitats to many areas globally, for example, see review by Babcock et al. (2010), but the extent to which this effect extends to furoids is largely unknown because these taxa are often not sampled separately from Laminariales and are simply included within a “canopy-forming” or “kelp” category. There is some evidence for an increase in shallow mixed furoid canopies in MPAs following 24 years of protection in New Zealand (Babcock, Kelly, Shears, Walker, & Willis, 1999). Similarly, Barrett, Buxton, and Edgar (2009) found some species of furoids (*Acrocarpia*) to exhibit more stability within an MPA than fished areas following 10 years of protection, but this pattern was not spatially general. Preliminary sampling of shallow furoid forests in NSW MPAs indicates little change in *Phyllospora* and *Sargassum* abundances after 8 years of protection (Coleman, Palmer-Brodie, & Kelaher, 2013). Although it is likely that this and many other Australian MPAs are still too young for restoration of trophic linkages to be fully realized (Babcock et al., 1999), the experimental demonstration that removal of grazing pressure (urchins) results in an increase in *Phyllospora* (Ling, 2008) warrants specific inclusion of furoids into MPA sampling programs, especially in places where monospecific forests play a key role in temperate ecosystems (e.g., NSW).

Lost furoid forests may be unable to return to their former state even if favorable environmental conditions are restored, for example, see

review by Filbee-Dexter and Scheibling (2014). Thus, where regime shifts have occurred and passive management (e.g., MPAs) has not resulted in recovery of lost habitats, active intervention may be required. For example, complete loss of *Phyllospora* from the Sydney region (Coleman, Kelaher, et al., 2008) and its inability to re-establish after decades despite improvements in water quality (Scanes & Phillip, 1995) and adequate dispersal potential (Coleman & Kelaher, 2009) has demonstrated that active, as opposed to passive management action is required to restore these forests. This has prompted government-funded restoration initiatives (http://www.marine.nsw.gov.au/data/assets/pdf_file/0009/595044/hawkesbury-shelf-discussion-paper.pdf) that are backed by extensive research demonstrating *Phyllospora* is not functionally redundant and warrants restoration (Marzinelli et al., 2014, 2016) and that optimized restoration techniques are successful (Campbell, Marzinelli, et al., 2014). Indeed, initial restoration efforts demonstrated that restored *Phyllospora* populations rapidly become self-sustaining even if transplanted individuals were lost (Campbell, Marzinelli, et al., 2014; Figure 5), thus overcoming a major impediment to many marine macrophyte restoration efforts. Studies on *Scytothalia* and *Sargassum*, however, suggest that facilitation by an adult canopy maybe critical for successful recruitment, particularly at low latitudes (Bennett & Wernberg, 2014) and successful restoration techniques for these species may necessitate the maintenance of donor plants. Regardless, furoid algae may be ideal candidates for restoration due to their life history whereby reproduction can easily be induced during restoration activities, prior to transplanted individuals potentially being lost due to storms or grazing.

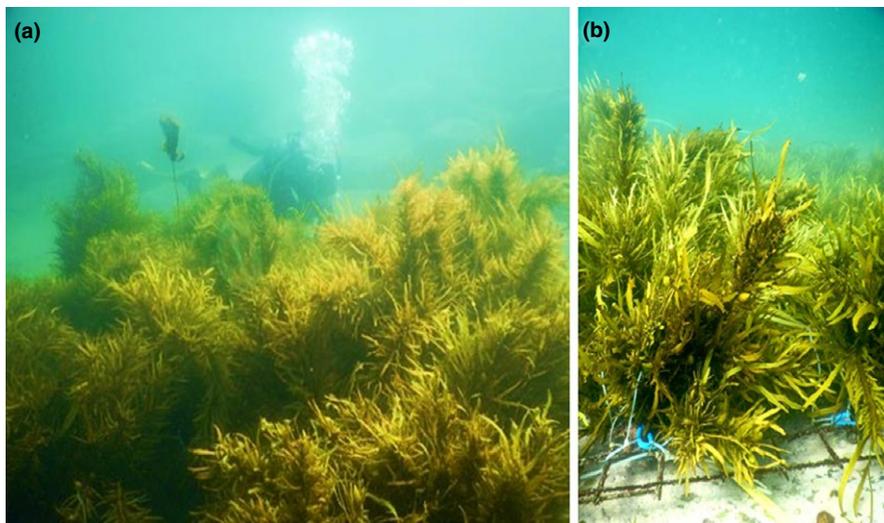


FIGURE 5 Restoration of *Phyllospora* into areas where it was lost in Sydney. Panels showing (a) diver near a 5 × 5 m restored patch and (b) donor plants attached to mesh with rubber tubing. Photos: E. Marzinelli

Integrated approaches to management of marine environments that involve both active and passive initiatives are likely to be most successful in a future of increasing stress. Such approaches acknowledge that we need to not only improve abiotic conditions (e.g., improve water quality) or limit anthropogenic impacts (e.g., MPAs), but it will often be necessary to concurrently actively intervene to restore lost habitat or even anticipate future loss. Integrated approaches to marine management that focus on furoid forests are currently being investigated in NSW (<http://www.marine.nsw.gov.au/key-initiatives/threat-and-risk-assessment-framework>). The Mediterranean, with its long history of anthropogenic use, is a classic example of where such integrated approaches will be required to ensure the long-term persistence of subtidal furoid forests. In this case, MPAs alone are largely ineffective in restoring underwater furoid (*Cystoseira*) forests (Mangialajo et al., 2008) that were lost due to processes including overgrazing (Vergés et al., 2014), beach nourishment, storms, habitat loss, and poor water quality (Perkol-Finkel & Airoldi, 2010). Active intervention (restoration) in combination with improvement in water quality, and MPAs to facilitate dispersal, are suggested to be an effective strategy to bring back these lost forests to the Mediterranean (Airoldi & Beck, 2007; Gianni et al., 2013; Mangialajo et al., 2008). Anticipatory approaches such as selective breeding or assisted adaptation (Aitken & Whitlock, 2013), although potentially controversial, may also provide avenues for boosting the resilience of macroalgal populations against future change and ensure the long-term persistence of these critical habitats.

6 | CONCLUSION

Despite being a unique and important component of temperate reefs in Australia, subtidal furoid forests have been understudied relative to their laminarian counterparts accounting for ~20% of the scientific literature. In Australia, these neglected forests cover over half the continent (~8,000 km coastline, [Bennett et al., 2016]) and play a key role in supporting temperate biodiversity (Bishop et al., 2010; Irving et al., 2004; Marzinelli et al., 2014). Furoid forests play similarly important roles on subtidal rocky reefs in many other parts of the world (Schiel, 1988; Tanaka, Taino, Haraguchi, Prendergast, & Hiraoka, 2012; Thibault et al., 2005; Wikström & Kautsky, 2007) but are rarely studied in their own right, except where these forests are the only habitat formers (i.e., monospecific forests of *Cystosiera* in the Mediterranean or *Fucus* in the Baltic).

Natural and anthropogenic stressors have precipitated recent large-scale declines in subtidal furoid forests globally (Coleman, Kelaher, et al., 2008; Nilsson, Engkvist, & Persson, 2004; Phillips & Blackshaw, 2011; Smale & Wernberg, 2013; Tanaka et al., 2012; Thibault et al., 2005; Vogt & Schramm, 1991). Critically, these declines have led to significant and persistent ecosystem-wide impacts (Bianchelli, Buschi, Danovaro, & Pusceddu, 2016; Wernberg, Bennett, et al., 2016; Wikström & Kautsky, 2007). There is currently a lack of understanding of the long-term ecological implications of these changes and how such ecosystem changes might be reversed.

Although Laminariales appear to respond well to passive forms of conservation (e.g., implementation of MPAs where top down control prevails), the extent to which these strategies confer similar benefit to furoids is unknown and integrating a variety of approaches is likely required. Understanding the specific response of furoids to stressors and the mechanisms facilitating or hindering recovery will be key for designing appropriate and informed management strategies. Furthermore, emerging cutting-edge anticipatory techniques such as assisted adaptation or evolution (Aitken & Whitlock, 2013; van Oppen, Oliver, Putnam, & Gates, 2015) should be investigated as potential avenues to boost resilience of existing populations to change. Addressing the dearth of information on subtidal furoid community ecology, particularly in Australia where furoids dominate canopy diversity of reefs, will be critical for managing subtidal reefs into the future.

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CONFLICT OF INTEREST

None declared.

AUTHOR CONTRIBUTIONS

MAC and TW each contributed equally to all aspects of the concept, research, interpretation, and writing of this manuscript.

REFERENCES

- Airoldi, L., & Beck, M. W. (2007). Loss, status and trends for coastal marine habitats of Europe. *Oceanography and Marine Biology: An Annual Review*, 45, 345–405.
- Aitken, S. N., & Whitlock, M. C. (2013). Assisted gene flow to facilitate local adaptation to climate change. *Annual Review of Ecology, Evolution, and Systematics*, 44, 367–388.
- Andrews, S., Bennett, S., & Wernberg, T. (2014). Reproductive seasonality and early life temperature sensitivity reflect vulnerability of a seaweed undergoing range reduction. *Marine Ecology Progress Series*, 495, 119–129.
- Babcock, R. C., Kelly, S., Shears, N. T., Walker, J. W., & Willis, T. J. (1999). Changes in community structure in temperate marine reserves. *Marine Ecology Progress Series*, 189, 125–134.
- Babcock, R. C., Shears, N. T., Alcalá, A. C., Barrett, N. S., Edgar, G. J., Lafferty, K. D., ... Russ, G. R. (2010). Decadal trends in marine reserves reveal differential rates of change in direct and indirect effects. *Proceedings of the National Academy of Sciences*, 107, 18256–18261.
- Baker, J. L., & Edyvane, K. S. (2003). Subtidal macrofloral survey of St Francis and Fenelon Islands, South Australia. *Transactions of the Royal Society of South Australia*, 127, 177–187.
- Barrett, N. S., Buxton, C. D., & Edgar, G. J. (2009). Changes in invertebrate and macroalgal populations in Tasmanian marine reserves in the decade following protection. *Journal of Experimental Marine Biology and Ecology*, 370, 104–119.
- Bennett, S., & Wernberg, T. (2014). Canopy facilitates seaweed recruitment on subtidal temperate reefs. *Journal of Ecology*, 102, 1462–1470.

- Bennett, S., Wernberg, T., Connell, S. D., Hobday, A. J., Johnson, C. R., & Poloczanska, E. S. (2016). The 'Great Southern Reef': Social, ecological and economic value of Australia's neglected kelp forests. *Marine and Freshwater Research*, *67*, 47–56.
- Bennett, S., Wernberg, T., Joy, B. A., De Bettignies, T., & Campbell, A. H. (2015). Central and rear-edge populations can be equally vulnerable to warming. *Nature Communications*, *6*, 10280.
- Bianchelli, S., Buschi, E., Danovaro, R., & Pusceddu, A. (2016). Biodiversity loss and turnover in alternative states in the Mediterranean Sea: A case study on meiofauna. *Scientific Reports*, *6*, 34544.
- Bishop, M. J., Coleman, M. A., & Kelaher, B. P. (2010). Cross-habitat impacts of species decline: Response of estuarine sediment communities to changing detrital resources. *Oecologia*, *163*, 517–525.
- Bolton, J. J. (2016). What is aquatic botany?—And why algae are plants: The importance of non-taxonomic terms for groups of organisms. *Aquatic Botany*, *132*, 1–4.
- Borowitzka, M. A. (1972). Intertidal algal species diversity and the effect of pollution. *Australian Journal of Marine and Freshwater Research*, *23*, 73–84.
- Burridge, T. R., & Bidwell, J. (2002). Review of the potential use of brown algal ecotoxicological assays in monitoring effluent discharge and pollution in Southern Australia. *Marine Pollution Bulletin*, *45*, 140–147.
- Burridge, T., & Hallam, N. D. (1993). Early development and apical growth in *Phyllospora-Comosa* (Labillardiere) Agardh, C. (Seirococcaceae, Phaeophyta). *Botanica Marina*, *36*, 159–168.
- Burridge, T. R., Lavery, T., & Lam, P. K. S. (1995). Acute toxicity tests using *Phyllospora-Comosa* (Labillardiere) Agardh, C. (Phaeophyta, Fucales) and *Allorchestes Compressa* Dana (Crustacea, Amphipoda). *Bulletin of Environmental Contamination and Toxicology*, *55*, 621–628.
- Burridge, T. R., Portelli, T., & Ashton, P. (1996). Effect of sewage effluents on germination of three marine brown algal macrophytes. *Marine and Freshwater Research*, *47*, 1009–1014.
- Burridge, T. R., & Shir, M. A. (1995). The comparative effects of oil dispersants and oil/dispersant conjugates on germination of the marine macroalga *Phyllospora comosa* (Fucales: Phaeophyta). *Marine Pollution Bulletin*, *31*, 446–452.
- Campbell, A. H., Marzinelli, E. M., Verges, A., Coleman, M. A., & Steinberg, P. D. (2014). Towards restoration of missing underwater forests. *PLoS ONE*, *9*(1), e84106.
- Campbell, A. H., Verges, A., & Steinberg, P. D. (2014). Demographic consequences of disease in a habitat-forming seaweed and impacts on interactions between natural enemies. *Ecology*, *95*, 142–152.
- Castorani, M. C. N., Reed, D. C., Alberto, F., Bell, T. W., Simons, R. D., Cavanaugh, K. C., ... Raimondi, P. T. (2015). Connectivity structures local population dynamics: A long-term empirical test in a large meta-population system. *Ecology*, *96*, 3141–3152.
- Cetina-Heredia, P., Roughan, M., van Sebille, E., & Coleman, M. A. (2014). Long-term trends in the East Australian current separation latitude and eddy driven transport. *Journal of Geophysical Research: Oceans*, *119*, 4351–4366.
- Cetina-Heredia, P., Roughan, M., van Sebille, E., Feng, M., & Coleman, M. A. (2015). Strengthened currents override the effect of warming on lobster larval dispersal and survival. *Global Change Biology*, *21*, 4377–4386.
- Coleman, M. A., & Brawley, S. H. (2005a). Spatial and temporal variability in dispersal and population genetic structure of a rockpool alga. *Marine Ecology Progress Series*, *300*, 63–77.
- Coleman, M. A., & Brawley, S. H. (2005b). Variability in temperature and historical patterns in reproduction in the *Fucus distichus* complex (Heterokontophyta; Phaeophyceae): Implications for speciation and the collection of herbarium specimens. *Journal of Phycology*, *41*, 1110–1119.
- Coleman, M. A., Cetina-Heredia, P., Roughan, M., Feng, M., van Sebille, E., & Kelaher, B. P. (2017). Anticipating changes to future connectivity within a network of marine protected areas. *Global Change Biology*, <https://doi.org/10.1111/gcb.13634>
- Coleman, M. A., Chambers, J., Knott, N. A., Malcolm, H. A., Harasti, D., Jordan, A., & Kelaher, B. P. (2011). Connectivity within and among a network of temperate marine reserves. *PLoS ONE*, *6*(5), e20168.
- Coleman, M. A., Dolman, G., Kelaher, B. P., & Steinberg, P. D. (2008). Characterisation of microsatellite loci in the subtidal habitat-forming alga, *Phyllospora comosa* (Phaeophyceae, Fucales). *Conservation Genetics*, *9*, 1015–1017.
- Coleman, M. A., & Kelaher, B. P. (2009). Connectivity among fragmented populations of a habitat-forming alga, *Phyllospora comosa* (Phaeophyceae, Fucales) on an urbanised coast. *Marine Ecology Progress Series*, *381*, 63–70.
- Coleman, M. A., Kelaher, B. P., Steinberg, P. D., & Millar, A. J. K. (2008). Absence of a large brown macroalga on urbanized rocky reefs around Sydney, Australia, and evidence for historical decline. *Journal of Phycology*, *44*, 897–901.
- Coleman, M. A., & Muhlin, J. F. (2008). Patterns of spatial variability in the morphology of sympatric fucoids. *Northeastern Naturalist*, *15*, 111–122.
- Coleman, M. A., Palmer-Brodie, A., & Kelaher, B. P. (2013). Conservation benefits of a network of marine reserves and partially protected areas. *Biological Conservation*, *167*, 257–264.
- Coleman, M. A., Roughan, M., MacDonald, H. S., Connell, S. D., Gillanders, B. M., Kelaher, B. P., & Steinberg, P. D. (2011). Variation in the strength of continental boundary currents determines continent-wide connectivity in kelp. *Journal of Ecology*, *99*, 1026–1032.
- Coleman, M. A., Vytopil, E., Goodsell, P. J., Gillanders, B. M., & Connell, S. D. (2007). Diversity and depth-related patterns of mobile invertebrates associated with kelp forests. *Marine and Freshwater Research*, *58*, 589–595.
- Connell, S. D., & Irving, A. D. (2008). Integrating ecology with biogeography using landscape characteristics: A case study of subtidal habitat across continental Australia. *Journal of Biogeography*, *35*, 1608–1621.
- Dayton, P. K. (1972). Toward an understanding of community resilience and the potential effects of enrichments to the benthos at McMurdo Sound, Antarctica. In *Proceedings of the colloquium on conservation problems*. Lawrence, KS: Allen Press.
- Dempster, T., & Kingsford, M. J. (2004). Drifting objects as habitat for pelagic juvenile fish off New South Wales, Australia. *Marine and Freshwater Research*, *55*, 675–687.
- Durrant, H. M. S., Barrett, N. S., Edgar, G. J., Coleman, M. A., & Burridge, C. P. (2015). Shallow phylogeographic histories of key species in a biodiversity hotspot. *Phycologia*, *54*, 556–565.
- Edgar, G. J. (1984). General features of the ecology and biogeography of Tasmanian subtidal rocky shore communities. *Papers and Proceedings of the Royal Society of Tasmania*, *118*, 173–186.
- Filbee-Dexter, K., & Scheibling, R. E. (2014). Sea urchin barrens as alternative stable states of collapsed kelp ecosystems. *Marine Ecology Progress Series*, *495*, 1–25.
- Flukes, E. B., Wright, J. T., & Johnson, C. R. (2015). Phenotypic plasticity and biogeographic variation in physiology of habitat-forming seaweed: Response to temperature and nitrate. *Journal of Phycology*, *51*, 896–909.
- Fraser, C. I. (2012). Is bull-kelp kelp? The role of common names in science. *New Zealand Journal of Marine and Freshwater Research*, *46*, 279–284.
- Fraser, C. I., Nikula, R., & Waters, J. M. (2011). Oceanic rafting by a coastal community. *Proceedings of the Royal Society B: Biological Sciences*, *278*, 649–655.
- Gianni, F., Bartolini, F., Airoidi, L., Ballesteros, E., Francour, P., Guidetti, P., ... Mangialajo, L. (2013). Conservation and restoration of marine forests in the Mediterranean Sea and the potential role of Marine Protected Areas. *Advances in Oceanography and Limnology*, *4*, 83–101.
- Glasby, T. M., Gibson, P. T., West, G., Davies, P., & Voerman, S. (2015). Range and habitat associations of the native macroalga *Caulerpa filiformis* in New South Wales, Australia. *Marine and Freshwater Research*, *66*, 1018–1026.
- Goldberg, N. A. (2007). Colonization of subtidal macroalgae in a fucalean-dominated algal assemblage, southwestern Australia. *Hydrobiologia*, *575*, 423–432.
- Goodsell, P. J., Fowler-Walker, M. J., Gillanders, B. M., & Connell, S. D. (2004). Variations in the configuration of algae in subtidal forests: Implications for invertebrate assemblages. *Austral Ecology*, *29*, 350–357.

- Graham, M. H. (2004). Effects of local deforestation on the diversity and structure of southern California giant kelp forest food webs. *Ecosystems*, 7, 341–357.
- Guiry, M. D. (2012). How many species of algae are there? *Journal of Phycology*, 48, 1057–1063.
- Harman, N., Harvey, E. S., & Kendrick, G. A. (2003). Differences in fish assemblages from different reef habitats at Hamelin Bay, south-western Australia. *Marine and Freshwater Research*, 54, 177–184.
- Hinojosa, I. A., Green, B. S., Gardner, C., & Jeffs, A. (2015). Settlement and early survival of southern rock lobster, *Jasus edwardsii*, under climate-driven decline of kelp habitats. *ICES Journal of Marine Science*, 72, 59–68.
- Hay, K. B., Poore, A. G. B., & Lovelock, C. E. (2011). The effects of nutrient availability on tolerance to herbivory in a brown seaweed. *Journal of Ecology*, 99, 1540–1550.
- Hirst, A. J. (2006). Influence of taxonomic resolution on multivariate analyses of arthropod and macroalgal reef assemblages. *Marine Ecology Progress Series*, 324, 83–93.
- Hobday, A. J., & Pecl, G. T. (2014). Identification of global marine hotspots: Sentinels for change and vanguards for adaptation action. *Reviews in Fish Biology and Fisheries*, 24, 415–425.
- Hughes, A. R., Inouye, B. D., Johnson, M. T. J., Underwood, N., & Vellend, M. (2008). Ecological consequences of genetic diversity. *Ecology Letters*, 11, 609–623.
- Huisman, J. M. (2000). *Marine plants of Australia*. Nedlands, WA: University of Western Australia Press.
- Irving, A. D., & Connell, S. D. (2006). Physical disturbance by kelp abrades erect algae from the understorey. *Marine Ecology Progress Series*, 324, 127–137.
- Irving, A. D., Connell, S. D., & Gillanders, B. M. (2004). Local complexity in patterns of canopy-benthos associations produces regional patterns across temperate Australasia. *Marine Biology*, 144, 361–368.
- James, N. P., Reid, C. M., Bone, Y., Levings, A., & Malcolm, I. (2013). The macroalgal carbonate factory at a cool-to-warm temperate marine transition, Southern Australia. *Sedimentary Geology*, 291, 1–26.
- Kendrick, G. A. (1994). Effects of propagule settlement density and adult canopy on survival of recruits of *Sargassum* spp. (Sargassaceae, Phaeophyta). *Marine Ecology Progress Series*, 103, 129–140.
- Kendrick, G. A., & Walker, D. I. (1991). Dispersal distances for propagules of sargassum-spinuligerum (Sargassaceae, Phaeophyta) measured directly by vital staining and venturi suction sampling. *Marine Ecology Progress Series*, 79, 133–138.
- Kendrick, G. A., & Walker, D. I. (1994). Role of recruitment in structuring beds of *Sargassum* spp. (Phaeophyta) at Rottneest Island, Western-Australia. *Journal of Phycology*, 30, 200–208.
- Kendrick, G. A., & Walker, D. I. (1995). Dispersal of propagules of *Sargassum* spp. (Sargassaceae, Phaeophyta) – Observations of local patterns of dispersal and consequences for recruitment and population-structure. *Journal of Experimental Marine Biology and Ecology*, 192, 273–288.
- Krumhansl, K. A., & Scheibling, R. E. (2012). Production and fate of kelp detritus. *Marine Ecology Progress Series*, 467, 281–302.
- Lanham, B. S., Gribben, P. E., & Poore, A. G. B. (2015). Beyond the border: Effects of an expanding algal habitat on the fauna of neighbouring habitats. *Marine Environmental Research*, 106, 10–18.
- Ling, S. D. (2008). Range expansion of a habitat-modifying species leads to loss of taxonomic diversity: A new and impoverished reef state. *Oecologia*, 156, 883–894.
- Mangialajo, L., Gianni, F., Airoldi, L., Bartolini, F., Francour, P., Meinesz, A., ... Ballesteros, E. (2008). Conservation and restoration of *Cystoseira* forests in the Mediterranean Sea: The role of marine protected areas. *Rapport Commission Internationale Mer Mediterranee*, 40, 2013.
- Marzinelli, E. M., Campbell, A. H., Verges, A., Coleman, M. A., Kelaher, B. P., & Steinberg, P. D. (2014). Restoring seaweeds: Does the declining fucoid *Phyllospora comosa* support different biodiversity than other habitats? *Journal of Applied Phycology*, 26, 1089–1096.
- Marzinelli, E. M., Leong, M. R., Campbell, A. H., Steinberg, P. D., & Verges, A. (2016). Does restoration of a habitat-forming seaweed restore associated faunal diversity? *Restoration Ecology*, 24, 81–90.
- May, V. (1985). Observation on algal floras close to 2 sewerage outlets. *Cunninghamia*, 1, 385–394.
- May, D. I., & Clayton, M. N. (1991). Oogenesis, the formation of oogonial stalks and fertilization in *Sargassum-Vestitum* (Fucales, Phaeophyta) from southern Australia. *Phycologia*, 30, 243–256.
- Millar, A. J. K., & Kraft, G. T. (1993). Catalogue of marine and freshwater red algae (Rhodophyta) of New South Wales, including Lord Howe Island, South-western Pacific. *Australian Systematic Botany*, 6, 1–90.
- Muhlin, J. F., Coleman, M. A., Rees, T. A. V., & Brawley, S. H. (2011). Modeling of reproduction in the intertidal macrophyte *Fucus vesiculosus* and implications for spatial subsidies in the nearshore environment. *Marine Ecology Progress Series*, 440, 79–94.
- Nilsson, J., Engkvist, R., & Persson, L. E. (2004). Long-term decline and recent recovery of *Fucus* populations along the rocky shores of southeast Sweden, Baltic Sea. *Aquatic Ecology*, 38, 587–598.
- van Oppen, M. J. H., Oliver, J. K., Putnam, H. M., & Gates, R. D. (2015). Building coral reef resilience through assisted evolution. *Proceedings of the National Academy of Sciences*, 112, 2307–2313.
- Pearce, A., Lenanton, R., Jackson, G., Moore, J., Feng, M., & Gaughan, D. (2011). The “marine heat wave” off Western Australia during the summer of 2010/11. *Fisheries Research Report*. Western Australia: Government of Western Australia, Department of Fisheries.
- Pearson, G. A., & Serrão, E. A. (2006). Revisiting synchronous gamete release by fucoid algae in the intertidal zone: Fertilization success and beyond? *Integrative and Comparative Biology*, 46, 587–597.
- Perkol-Finkel, S., & Airoldi, L. (2010). Loss and recovery potential of marine habitats: An experimental study of factors maintaining resilience in subtidal algal forests at the Adriatic Sea. *PLoS ONE*, 5, e10791.
- Peters, T. A. (2015). *Patterns, mechanisms and consequences of disease in a habitat forming macroalga*. PhD, University of New South Wales.
- Phillips, J. A. (2001). Marine macroalgal biodiversity hotspots: Why is there high species richness and endemism in southern Australian marine benthic flora? *Biodiversity & Conservation*, 10, 1555–1577.
- Phillips, J. A., & Blackshaw, J. K. (2011). Extirpation of macroalgae (*Sargassum* spp.) on the subtropical east Australian coast. *Conservation Biology*, 25, 913–921.
- Phillips, J. C., Kendrick, G. A., & Lavery, P. S. (1997). A test of a functional group approach to detecting shifts in macroalgal communities along a disturbance gradient. *Marine Ecology Progress Series*, 153, 125–138.
- Poore, A. G. B., Graba-Landry, A., Favret, M., Brennand, H. S., Byrne, M., & Dworjanyn, S. A. (2013). Direct and indirect effects of ocean acidification and warming on a marine plant-herbivore interaction. *Oecologia*, 173, 1113–1124.
- Poore, A. G. B., & Hill, N. A. (2005). Spatial associations among palatable and unpalatable macroalgae: A test of associational resistance with a herbivorous amphipod. *Journal of Experimental Marine Biology and Ecology*, 326, 207–216.
- Poore, A. G. B., & Steinberg, P. D. (1999). Preference-performance relationships and effects of host plant choice in an herbivorous marine amphipod. *Ecological Monographs*, 69, 443–464.
- Reusch, T. B. H., Ehlers, A., Hämmerli, A., & Worm, B. (2005). Ecosystem recovery after climatic extremes enhanced by genotypic diversity. *Proceedings of the National Academy of Sciences of the United States of America*, 102, 2826–2831.
- Scanes, P. R., & Phillip, N. (1995). Environmental impact of deepwater discharge of sewage off Sydney, NSW, Australia. *Marine Pollution Bulletin*, 31, 343–346.
- Schiel, D. R. (1988). Algal interactions on shallow subtidal reefs in northern New Zealand: A review. *New Zealand Journal of Marine and Freshwater Research*, 22, 481–489.

- Shepherd, S. A., & Edgar, G. J. (2013). Large Brown Algae: The Fucoids. In S. A. Shepherd & G. J. Edgar (Eds.), *Ecology of Australian temperate reefs* (pp. 91–110).
- Shepherd, S. A., & Womersley, H. B. S. (1971). Pearson Island expedition 1969–7. The subtidal ecology of benthic algae. *Transactions. Royal Society of South Australia*, 93, 155–167.
- Smale, D. A., Kendrick, G. A., Waddington, K. I., van Niel, K. P., Meeuwig, J. J., & Harvey, E. S. (2010). Benthic assemblage composition on subtidal reefs along a latitudinal gradient in Western Australia. *Estuarine Coastal and Shelf Science*, 86, 83–92.
- Smale, D. A., & Wernberg, T. (2013). Extreme climatic event drives range contraction of a habitat-forming species. *Proceedings of the Royal Society B-Biological Sciences*, 280, 20122829.
- Steinberg, P. D., Edyvane, K., de Nys, R., Birdsey, R., & van Altena, I. A. (1991). Lack of avoidance of phenolic-rich brown algae by tropical herbivorous fish. *Marine Biology*, 109, 335–343.
- Steneck, R. S., Graham, M. H., Bourque, B. J., Corbett, D., Erlandson, J. M., Estes, J. A., & Tegner, M. J. (2002). Kelp forest ecosystems: Biodiversity, stability, resilience and future. *Environmental Conservation*, 29, 436–459.
- Steneck, R. S., & Johnson, C. R. (2013). Kelp forests: Dynamic patterns, processes, and feedbacks. In M. D. Bertness, J. F. Bruno, B. R. Silliman & J. J. Stachowicz (Eds.), *Marine community ecology* (pp. 315–336). Sunderland, MA: Sinauer Associates.
- Tanaka, K., Taino, S., Haraguchi, H., Prendergast, G., & Hiraoka, M. (2012). Warming off southwestern Japan linked to distributional shifts of subtidal canopy-forming seaweeds. *Ecology and Evolution*, 2, 2854–2865.
- Thibault, T., Pinedo, S., Torras, X., & Ballesteros, E. (2005). Long-term decline of the populations of Fucales (*Cystoseira* spp. and *Sargassum* spp.) in the Albères coast (France, North-western Mediterranean). *Marine Pollution Bulletin*, 50, 1472–1489.
- Thomsen, M. S., Wernberg, T., Staehr, P. A., & Pedersen, M. F. (2006). Spatio-temporal distribution patterns of the invasive macroalga *Sargassum muticum* within a Danish Sargassum-bed. *Helgoland Marine Research*, 60, 50–58.
- Thomson, D. P., Babcock, R. C., Vanderklift, M. A., Symonds, G., & Gunson, J. R. (2012). Evidence for persistent patch structure on temperate reefs and multiple hypotheses for their creation and maintenance. *Estuarine Coastal and Shelf Science*, 96, 105–113.
- Turner, D. J., & Cheshire, A. C. (2003). Encounter 2002 expedition to the Isles of St Francis, South Australia: Structure and productivity of benthic macroalgal communities. *Transactions of the Royal Society of South Australia*, 127, 153–166.
- Tuya, F., Wernberg, T., & Thomsen, M. S. (2008). The spatial arrangement of reefs alters the ecological patterns of fauna between interspersed algal habitats. *Estuarine Coastal and Shelf Science*, 78, 774–782.
- Tuya, F., Wernberg, T., & Thomsen, M. S. (2009). Habitat structure affect abundances of labrid fishes across temperate reefs in south-western Australia. *Environmental Biology of Fishes*, 86, 311–319.
- Valentine, J. P., & Johnson, C. R. (2004). Establishment of the introduced kelp *Undaria pinnatifida* following dieback of the native macroalga *Phyllospora comosa* in Tasmania, Australia. *Marine and Freshwater Research*, 55, 223–230.
- Vanderklift, M. A., & Wernberg, T. (2008). Detached kelps from distant sources are a food subsidy for sea urchins. *Oecologia*, 157, 327–335.
- Verges, A., Steinberg, P. D., Hay, M. E., Poore, A. G. B., Campbell, A. H., Ballesteros, E., ... Wilson, S. K. (2014). The tropicalization of temperate marine ecosystems: Climate-mediated changes in herbivory and community phase shifts. *Proceedings of the Royal Society B-Biological Sciences*, 281, 20140846.
- Vergés, A., Tomas, F., Cebrian, E., Ballesteros, E., Kizilkaya, Z., Dendrinos, P., ... Sala, E. (2014). Tropical rabbitfish and the deforestation of a warming temperate sea. *Journal of Ecology*, 102, 1518–1527.
- Vogt, H., & Schramm, W. (1991). Conspicuous decline of *Fucus* in Kiel Bay (Western Baltic): What are the causes? *Marine Ecology Progress Series*, 69, 189–194.
- Weigner, K. 2016. *Facilitating modern genetic analysis of the habitat forming macroalga, *Phyllospora comosa**. BSc (Honours), Southern Cross University.
- Wernberg, T., Bennett, S., Babcock, R. C., de Bettignies, T., Cure, K., Depczynski, M., ... Wilson, S. (2016). Climate-driven regime shift of a temperate marine ecosystem. *Science*, 353, 169–172.
- Wernberg, T., Coleman, M., Fairhead, A., Miller, S., & Thomsen, M. (2003). Morphology of *Ecklonia radiata* (Phaeophyta: Laminariales) along its geographic distribution in south-western Australia and Australasia. *Marine Biology*, 143, 47–55.
- Wernberg, T., & Connell, S. D. (2008). Physical disturbance and subtidal habitat structure on open rocky coasts: Effects of wave exposure, extent and intensity. *Journal of Sea Research*, 59, 237–248.
- Wernberg, T., de Bettignies, T., Bijo, A. J., & Finnegan, P. (2016). Physiological responses of habitat-forming seaweeds to increasing temperatures. *Limnology and Oceanography*, 61, 2180–2190.
- Wernberg, T., Kendrick, G. A., & Phillips, J. C. (2003). Regional differences in kelp-associated algal assemblages on temperate limestone reefs in south-western Australia. *Diversity and Distributions*, 9, 427–441.
- Wernberg, T., Kendrick, G. A., & Toohey, B. D. (2005). Modification of the physical environment by an *Ecklonia radiata* (Laminariales) canopy and implications for associated foliose algae. *Aquatic Ecology*, 39, 419–430.
- Wernberg, T., Russell, B. D., Moore, P. J., Ling, S. D., Smale, D. A., Campbell, A., ... Connell, S. D. (2011). Impacts of climate change in a global hotspot for temperate marine biodiversity and ocean warming. *Journal of Experimental Marine Biology and Ecology*, 400, 7–16.
- Wernberg, T., Smale, D. A., Tuya, F., Thomsen, M. S., Langlois, T. J., de Bettignies, T., ... Rousseaux, C. S. (2013). An extreme climatic event alters marine ecosystem structure in a global biodiversity hotspot. *Nature Climate Change*, 3, 78–82.
- Wernberg, T., Thomsen, M. S., Staehr, P. A., & Pedersen, M. F. (2004). Epibiota communities of the introduced and indigenous macroalgal relatives *Sargassum muticum* and *Halidrys siliquosa* in Limfjorden (Denmark). *Helgoland Marine Research*, 58, 154–161.
- Wernberg, T., Thomsen, M. S., Tuya, F., & Kendrick, G. A. (2011). Biogenic habitat structure of seaweeds change along a latitudinal gradient in ocean temperature. *Journal of Experimental Marine Biology and Ecology*, 400, 264–271.
- Wikström, S. A., & Kautsky, L. (2007). Structure and diversity of invertebrate communities in the presence and absence of canopy-forming *Fucus vesiculosus* in the Baltic Sea. *Estuarine, Coastal and Shelf Science*, 72, 168–176.
- Womersley, H. B. S. (1987). *The marine benthic flora of Southern Australia. Part II. Adelaide, SA, Australia: Government Printer.*
- Xiao, X., De Bettignies, T., Olsen, Y. S., Agusti, S., Duarte, C. M., & Wernberg, T. (2015). Sensitivity and acclimation of three canopy-forming seaweeds to UVB radiation and warming. *PLoS ONE*, 10, e0143031.
- Zhang, D., Glasby, T. M., Ralph, P. J., & Gribben, P. E. (2014). Mechanisms influencing the spread of a native marine alga. *PLoS ONE*, 9(4), e94647.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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