New perspectives on Western Australian seagrass and macroalgal biogeography

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Abstract

The widespread adoption of new methodologies, especially molecular techniques, has dramatically changed our understanding of how species of seagrasses and macroalgae are classified and distributed. One consequence of this new paradigm is increased uncertainty regarding biogeographic studies based on pre-molecular species records. The question "how does one delineate an individual species?" has changed and differing interpretations may alter how previous assessments are viewed. In some instances, specimens previously regarded as a single species have been shown to represent multiple genetic lineages. An extreme example is that of the red alga *Portiera hornemannii*, now thought to include 21 cryptic species in the Philippines alone, and possibly up to 96 species in the wider Indo-Pacific. Reworking and reclassification of species based on DNA analyses have sunk many species into one, or combined or reorganized genera. These changes in taxonomic concepts have implications for conservation and biogeographical assessments, but our understanding of many groups is still in its infancy and requires further work. In order to address these mounting challenges, significant investment and a commitment to taxonomic research will be required in the coming decades.

Keywords: seagrass, macroalgae, taxonomy, biogeography, molecular sequencing

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INTRODUCTION

Seagrasses and macroalgae are important marine primary producers that provide significant structural habitat in coastal waters (Walker & Bellgrove 2017; Bellgrove *et al.* 2018), and support diverse faunal communities (van der Heide *et al.* 2012). Western Australia is well-known as a centre of biodiversity for seaweeds and seagrasses, with numerous species recorded and a particularly high percentage of endemic taxa. Several recent publications have included detailed descriptions of the state's marine flora (seagrasses in Larkum *et al.* 2018; macroalgae in Huisman 2015, 2018) and this paper does not reiterate those works. Rather, we will describe the history of marine plant biodiversity knowledge in Western Australia, then discuss how new methodologies, especially molecular techniques, have made dramatic changes to our understanding of how species of seagrasses and macroalgae are classified and distributed. The implications of these changes may be significant, with real impacts on marine biodiversity assessments, and potential impacts on environmental legislation.

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SEAGRASSES

Western Australian waters are rich in seagrass species, both in diversity and areal extent. The history of seagrass collectors and collections are summarised in Figure 1. The state's 26 currently recognized seagrass species represent almost 40% of the world's approximately 70+ known species (Kilminster *et al.* 2018; Larkum *et al*. 2018; Waycott *et al.* 2014), a concentrated diversity not found in any other region. Western Australian seagrasses are widely distributed across coastal areas and estuaries (Carruthers *et al.* 2007) and a variety of habitats, although they are most commonly found associated with shallow, sandy substrata. Most of the Western Australia's temperate species are endemic, while those occurring in tropical waters are more widely distributed across the Indo-Pacific region. A list of currently recognised species across all of the Western Australian coast (Table 1) is divided into three major regions (South West, South-Coast, and Tropical WA) with dominant species life history strategies (colonising, opportunistic or persistent, sensu Kilminster *et al.* 2015) also indicated.

The published patterns of distribution and biogeography have changed little from the earlier historical records summarised in Walker (1991). The historical and present-day drivers shaping biogeography patterns are explored and distributional changes due to

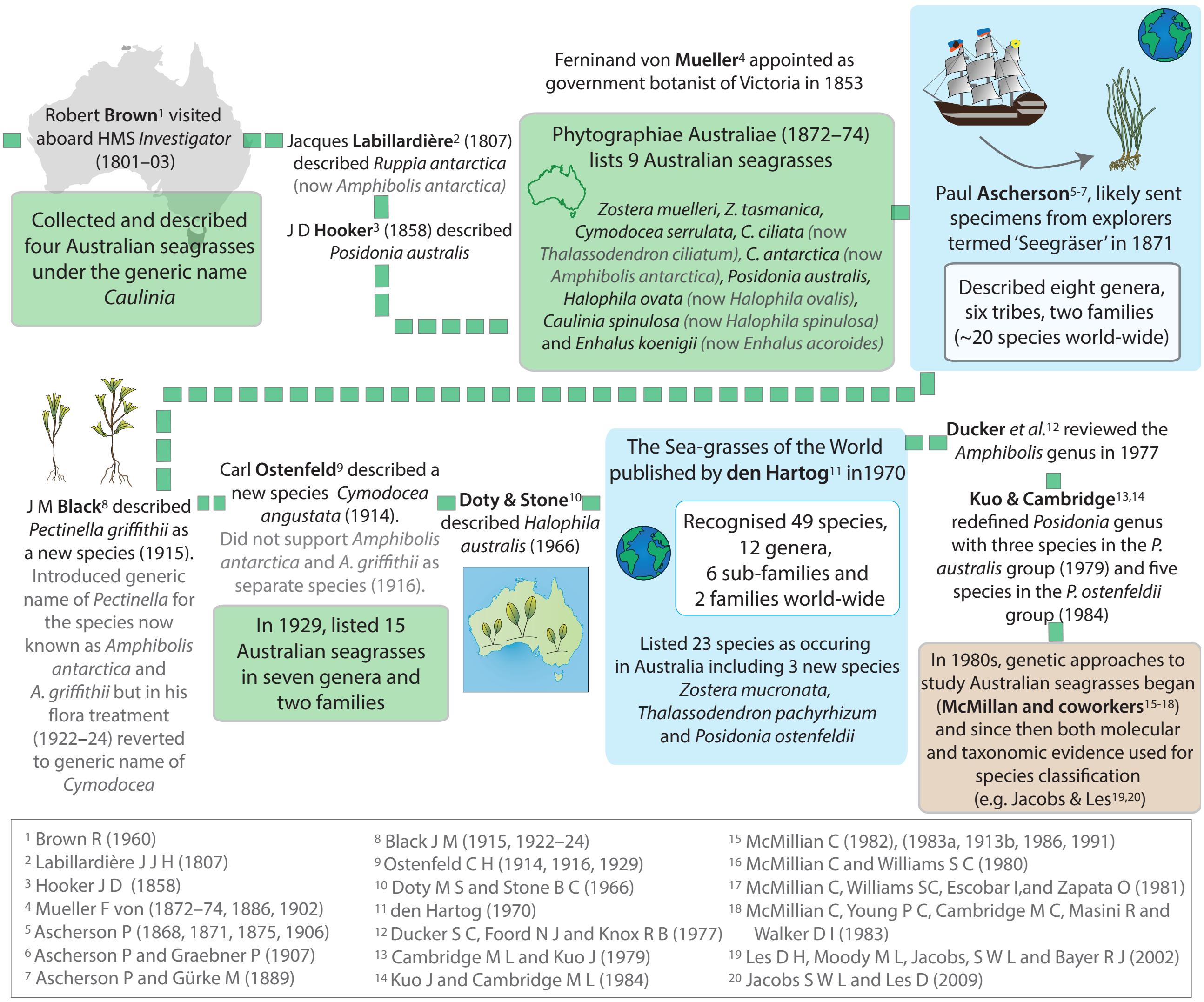

Figure 1. A selection of notable botanists and their contributions to Australian seagrass knowledge from 1800–2010.

anthropogenic and climate impacts for the south-west of Western Australia are reported in Kilminster *et al.* (2018).

Recent seagrass research in Western Australia has primarily focused on ecophysiological aspects or studies of recruitment and population structure. Many of the ecophysiological studies have shifted in focus to the roots and rhizomes of seagrasses, specifically exploring relationships between sediment biogeochemistry, seagrass health and the microbes that inhabit the seagrass rhizosphere (Fraser *et al.* 2017; Kilminster *et al.* 2014; Martin *et al.* 2019; Martin *et al.* 2018; Olsen *et al.* 2018). A conservation and restoration agenda has driven the studies of recruitment and population structure, with enhanced understanding of the potential of seed-based restoration, recruitment-bottlenecks and genetic connectivity between populations (Kendrick *et al.* 2017; McMahon *et al.* 2017; McMahon *et al.* 2018; Sinclair *et al.* 2018; Statton *et al.* 2017a; Statton *et al.* 2017b). Most of these areas of new knowledge were initiated in response to the broad-scale threat that climate-change and extreme events pose in the region; e.g. the wide-scale losses of the seagrass in Shark Bay as a response to the 2011 marine heatwave (Ariaz-Ortiz *et al.* 2018; Kilminster *et al.* 2018). It is likely that climate-driven changes will alter the biogeography of seagrasses in the region in decades to come.

Over the last decade, 10 new species have been added to the Australian seagrass flora (Larkum *et al.* 2018), but several of these are reclassifications of existing records and their validity is the subject of much debate (Waycott *et al.* 2018). Kuo (2005) found that *Heterozostera* was not a monotypic genus but consisted of at least three Australian species. He redefined *H. tasmanica* and described two new species, *H. nigricaulis* J. Kuo and *H. polychlamys* J. Kuo, in the process removing *H. tasmanica* from the Western Australia flora. Jacobs & Les (2009) formally rejected *Heterozostera* as a genus and transferred the two new described *Heterozostera* species into the genus *Zostera* as *Zostera nigricaulis* (Kuo) S.W.L Jacobs & Les and *Zostera polychlamys* (Kuo) S.W.L Jacobs & Les.

Molecular studies (Les *et al.* 1997) appeared to support the recognition of only one genus instead of two

Table 1

Seagrass species list by three major Western Australian regions indicating dominant species life history. Small symbols indicate the species exhibit cross-over traits whereas the large symbols indicate the dominant life form.

Australian Region	Genus	Species	Species life history C	O	P
Southwest					
19 species total	*Amphibolis*	*A. antarctica*		◆	◆ (small)
		A. griffitthi		◆	◆ (small)
	Halodule	*H. uninervis*	◆	◆ (small)	
	Syringodium	*S. isoetifolium*		◆	
	Thalassodendron	*T. pachyrhizum*			◆
	Posidonia	*P. angustifolia*			◆
		P. australis			◆
		P. sinuosa			◆
		P. ostenfeldii		◆ (small)	◆
		P. coriacea			◆
		P. denhartogii			◆
		P. kirkmanii			◆
		P. robertsoniae			◆
	Halophila	*H. australis*	◆		
		H. decipiens	◆		
		H. ovalis	◆		
	Zostera/	*Z. muelleri*	◆ (small)	◆	
	Heterozostera	*H. nigricaulis*	◆ (small)	◆	
		H. polychlamus	◆ (small)	◆	
South Coast					
17 species total	*Amphibolis*	*A. antarctica*		◆	◆ (small)
		A. griffitthi		◆	◆ (small)
	Thalassodendron	*T. pachyrhizum*			◆
	Posidonia	*P. angustifolia*			◆
		P. australis			◆
		P. sinuosa			◆
		P. ostenfeldii			◆
		P. coriacea		◆ (small)	◆
		P. denhartogii			◆
		P. kirkmanii			◆
		P. robertsoniae			◆
	Halophila	*H. australis*	◆		
		H. decipiens	◆		
		H. ovalis	◆		
	Zostera/	*Z. muelleri*	◆ (small)	◆	
	Heterozostera	*H. nigricaulis*	◆ (small)	◆	
		H. polychlamus	◆ (small)	◆	
Tropical					
10 species total	*Cymodocea*	*C. serrulata*		◆	
		C. rotundata		◆	
	Halodule	*H. uninervis*	◆	◆ (small)	
	Syringodium	*S. isoetifolium*		◆	
	Thalassodendron	*T. ciliatum*			◆
	Enhalus	*E. acoroides*			◆
	Halophila	*H. ovalis*	◆		
		H. decipiens	◆		
		H. spinulosa	◆		
	Thalassia	*T. hemprichii*			◆

Notes: Information within this table is derived from Kilminster *et al*. (2015, supp. table 1), Kilminster *et al*. (2018) and IUCN Redlist website (www.iucnredlist.org)

Southwest = Shark Bay to Cape Leeuwin, South-Coast = Cape Leeuwin to Great Australia Bight, Tropical is north of Shark Bay to the Northern Territory border.

Dominant life history: C = colonising, O = opportunistic and P = persistent (sensu Kilminster *et al.* 2015).

genera in the Australian Zosteraceae. However, other taxonomists who focused primarily on morphological characteristics (Den Hartog & Kuo 2006; Kuo 2011) retained both genera, *Heterozostera* and *Zostera*.

Agreement on how many species of seagrass exist has proved elusive. There is currently significant disagreement between species lists described using morphological traits (Kuo *et al.* 2018) and those derived from molecular studies (Coyer *et al*. 2013; Les *et al.* 2002; Waycott *et al.* 2018). Seagrasses are notably plastic in their morphological characteristics; in particular, attributes such as leaf width and leaf thickness can vary dramatically with environmental conditions, a testament to their ability to adapt to a variety of underwater environments. This plasticity may present challenges for identifying species with traditional taxonomy (although species differentiation by reproductive traits has generally proved stable with both taxonomic and molecular agreement). With the recent use of molecular tools for examining seagrass populations, and indeed studies sequencing whole genomes (Lee *et al.* 2016, 2018), it is anticipated that significant progress will soon be made towards resolving these controversies.

MACROALGAE

As is probably true of most marine taxa, knowledge of the diversity and distribution of the Western Australian macroalgae has historically accumulated erratically, with major advances primarily associated with individual collectors and taxonomists (Fig. 2). Some of the earliest algal specimens were collected by Archibald Menzies in 1791 on HMS Discovery and later by Robert Brown, who was the botanist accompanying Mathew Flinders during 1801–03 on HMS Investigator. Dawson Turner described these algae, all from King George Sound, but the collections included only five species. The first resident collector was Johann August Ludwig Preiss, who lived in the Swan River colony from December 1838 to January 1842, making a large collection that included about 3000–4000 species, from an area extending from about 100 km north of Perth south to Albany and east to the vicinity of Cape Riche. Sonder (1845, 1846–1848) described more than 80 new species of algae based on the Preiss specimens, but unfortunately the precise collection localities were deemed unnecessary and only 'occidentales Novae Hollandiae' [Western Australia] was given. Undoubtedly, the phycologist with the greatest impact historically was the Irish botanist William Henry Harvey, who visited Australia in 1854–1855, arriving in Western Australia where he made collections from the Fremantle region and the south-west coast, before moving to Victoria, Tasmania and New South Wales. Harvey was a fervent collector, amassing a staggering 20 000 specimens during his 18 months in Australia. Womersley (1984) calculated that on many days he must have collected and prepared well over 100 specimens, and Harvey reported from King George Sound "In one day I collected and preserved 700 specimens, some being new kinds." Harvey's Western Australian collections were described primarily in a paper written 'at sea', en route to Victoria (Harvey 1855).

Following Harvey, documentation of the Western Australian marine flora essentially languished for over a century, at which time the South Australian phycologist H.B.S (Bryan) Womersley embarked on a life-long study to document the marine flora of southern Australia, a region that nominally extended to Cape Naturaliste in south-west Western Australia, but also included species records from further north. Womersley's studies culminated in the six volume series 'The Marine Benthic Flora of Southern Australia' (Womersley 1984, 1987, 1994, 1996, 1998, 2003), undoubtedly one of the most significant contributions to documenting Australia's algal diversity. Western Australia was also visited by phycologists from other parts of Australia (e.g. Gerry Kraft, Bill Woelkerling), but it was not until late in the 1980s that resident phycologists (JMH & DIW) began making significant contributions to macroalgal biodiversity assessments for Western Australia.

The focus of Harvey, Womersley and most visitors has been the southern and central coasts, leaving the

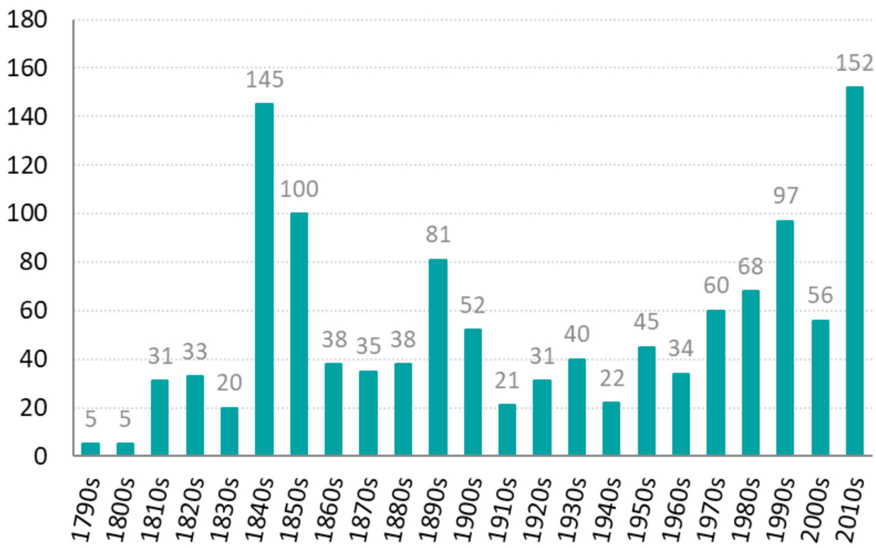

Figure 2. Species descriptions per decade of Western Australian macroalgae.

tropics virtually untouched and unknown. Recent expeditions mounted by the Western Australian Museum to examine the marine biodiversity of the north-west coast have enabled the collection of seagrass and macroalgal specimens throughout the tropics. Numerous publications have resulted, with much of the macroalgal information collated in two volumes in the 'Algae of Australia' series (Huisman 2015, 2018). These included 522 species (351 red algae, 110 green algae and 61 brown algae), of which 92 were new to science.

RECENT ADVANCES

Two methodological advances have had a significant impact on our understanding of marine plant taxonomy and biogeography, namely DNA sequence analysis and the use of 'big data'. DNA sequence analyses have facilitated both species identification through the establishment of 'barcodes', and phylogenetic assessments. 'Barcoding' can ensure accurate identification, the proviso being that the reference sequence used for comparison is indeed representative of the named species. One clear trend arising from molecular analyses is that in most cases there are more species than have previously been named. An extreme example was highlighted by the studies of the red algal genus *Portieria* by Payo *et al*. (2012) and Leliaert *et al*. (2018), who tested species boundaries based on mitochondrial, plastid and nuclear encoded loci, using a general mixed Yule-coalescent (GMYC) model-based approach and a Bayesian multilocus species delimitation method. They found that the then current morphology-based assumption that the genus includes a single, widely distributed species in the Indo-West Pacific (*Portieria hornemannii*), was not supported, and they recognized 21 species within the Philippines alone. Species distributions were found to be highly structured with most species restricted to island groups. Leliaert *et al.* (2018) subsequently broadened the Payo (2013) study to include specimens collected from additional localities in the Indo-Pacific, and reported a staggering 92 species-level lineages. Similar studies of other seemingly widespread species have also revealed previously unrecognized species diversity. The brown alga *Lobophora variegata*, for example, also regarded as morphologically variable, may encompass over 100 species (Vieira *et al*. 2014).

Molecular methods have also impacted our understanding of individual species. In south-western Australia lives a species of the otherwise almost wholly tropical green algal genus *Halimeda.* Originally described from South Africa as *Halimeda cuneata*, the species was recorded for south-west Australia by Womersley (1956, 1984) based on convincing morphological evidence. Cremen *et al.* (2016) undertook a detailed morphological and molecular study of '*Halimeda cuneata*', their DNA sequence analyses demonstrating that specimens identified by morphology as *H. cuneata* in fact formed several species-level lineages, including two from South Africa and one from south-west Australia. Thus the Australian taxon could no longer be identified as *H. cuneata*, and the name *Halimeda versatilis* J. Agardh, based on a specimen from Cape Riche, was restored from synonymy.

Conversely, molecular methods have also demonstrated the presence of seemingly introduced species in Western Australian seas. Recently, a species of the green alga *Codium* was collected from the Walpole/ Nornalup estuary on the south coast. This alga was initially thought to be a new species (Huisman *et al.* 2011), but DNA sequence analyses indicated conspecificity with the South African species *Codium tenue* (Huisman *et al.* 2015). Remarkably, this species is rare in Western Australia where it is known only from muddy estuarine locations, a habitat mirrored precisely by the equally rare species in South Africa. How *Codium tenue* came to be established in southwest Australia can only be speculated on.

Molecular methods have thus led to the recognition of cryptic and pseudocryptic species: those that cannot be distinguished by morphology and those with diagnostic features only recognized following guidance by molecular analyses, respectively. This process has been described as 'molecular assisted alpha taxonomy' (Saunders 2005) and has been adopted in most recent studies. However, traditional taxonomy cannot be ignored as appropriate names have to be applied to barcode sequences. There is still a need for the field-biologist to be able to identify what species they are working on, recognizing in the case of some algae this may be an impossible task. Given the presence of cryptic species, it becomes imperative that barcode sequences are generated from type material or at the least putatively authentic material from the type locality. The commonly held belief that many species are widespread and encompass considerable morphological diversity can no longer be regarded as indisputable. Past species records based on morphology, particularly of seemingly widespread taxa, will need to be reassessed. In many cases this will not be achievable, particularly for the countless records based on formalin-preserved specimens, a preservation that renders them useless for DNA analysis. Even if methodologically feasible, it is unlikely that resources will be directed towards barcoding entire herbarium collections. Undoubtedly, DNA barcoding will ultimately result in taxonomic clarity, but the road to enlightenment might be long and arduous. Clearly, the first target should be establishing a barcode reference library based on sequences obtained from type material, or if unavailable then authentic specimens collected from the type locality, their identities verified by an experienced taxonomist.

The second major advance is the use 'big' data. All information pertaining to plant specimens (including the algae) housed in the Western Australian Herbarium (DBCA) is recorded in a database and made available through the Herbarium's portal 'FloraBase' and, combined with records from other Herbaria, additionally through the 'Australasian Virtual Herbarium' and the 'Atlas of Living Australia'. The ready availability of these records (which includes names, localities, dates etc.), potentially allows for assessment of range shifts and local extinctions, assuming the initial records are comprehensive enough to permit such assessments.

While the methodological advances described above will clearly enhance our taxonomic knowledge, and ultimately provide tools to enable rapid identification of specimens, their impact on biodiversity assessments and marine conservation efforts must also be considered. Visual field surveys lacking vouchers, already unreliable due to the difficulty in identifying all but the common species (see Fig. 3 for example), will potentially underestimate the actual biodiversity by orders of magnitude. Conservation efforts must take into account the possibility of small-range endemics and not assume that marine species are resilient based on an assumed large geographical range.

RANGE SHIFTS

The availability of historical, geolocated specimen records, if adequate and used appropriately (Huisman & Millar 2013), can enable assessments of range shifts due to climate variation and other factors. The west coast, with its essentially north–south alignment and latitudinal (= temperature) gradient, provides an ideal setting for assessing the susceptibility of marine species to variations in sea temperature. Range shifts along the coast of Western Australia are not a recent phenomenon, with species undoubtedly impacted by historical variations in the strength of the southerly flowing warm Leeuwin Current. An interesting example was provided by Harvey, who in 1855 described the essentially tropical green alga *Penicillus nodulosus* (as *P. arbuscula*) as "abundant, on shallow sand covered reefs at Rottnest". This species has not been observed at Rottnest in recent times. The presence in south-western and southern Australia of tropical species (e.g. *Acrosymphyton taylorii* I.A. Abbott) or endemic species of otherwise tropical genera (e.g. *Gibsmithia womersleyi* Kraft), also suggests past periods or influxes of warmer water and the establishment and maintenance of these species in refugia.

A dramatic example of the impact of elevated sea temperatures was the recent decline of the temperate fucalean brown alga *Scytothalia dorycarpa* (Turner) Grev. from the Jurien Bay region, following an extreme warming event (Smale & Wernberg 2013; Wernberg *et al.* 2013), leading to a shift in community structure towards a depauperate state. Similarly, the recent loss of large tracts of habitat forming seagrass from Shark Bay released an estimated 2–9 million metric tonnes of carbon dioxide into the atmosphere within three years (Arias-Ortiz *et al.* 2018) and the seagrasses are showing little sign of recovery (Nowicki *et al.* 2017). It is of course hoped that such declines are isolated and temporary, but given future scenarios describing higher temperatures and more frequent extreme events this is unlikely.

Changing species names present a practical problem for non-taxonomic specialist users. Environmental managers are particularly at risk of not knowing how to access the changing information, as they are required to be across a substantial breadth of information and often need to make decisions quickly (Lynch *et al.* 2015). For example, *Cladophora montagneana* Kütz. was the main nuisance green macroalga in the eutrophic Peel Inlet and was so dominant that algae was removed by bulldozers from shorelines and the shallow waters in 1970s and 1980s. This species has recently undergone a name change based on molecular analyses (Boedeker *et al.* 2016) and is now known as *Willeella brachyclados* (Montagne) M.J. Wynne (Wynne 2016). In years to come, managers could wrongly assume there was a shift in algal species composition in the Peel–Harvey estuary. This example presents other potential difficulties. The type locality of *W. brachyclados* is Cuba, yet the samples used to represent this species in the molecular analyses of Boedeker *et al.* (2016) were collected from Western Australia and New Zealand. Given the very real possibility of cryptic species, basing a name change on results derived from specimens collected from different oceans and hemispheres could be misleading.

Similarly, historical Western Australian records of the seagrass *Heterozostera tasmanica* must now be interpreted

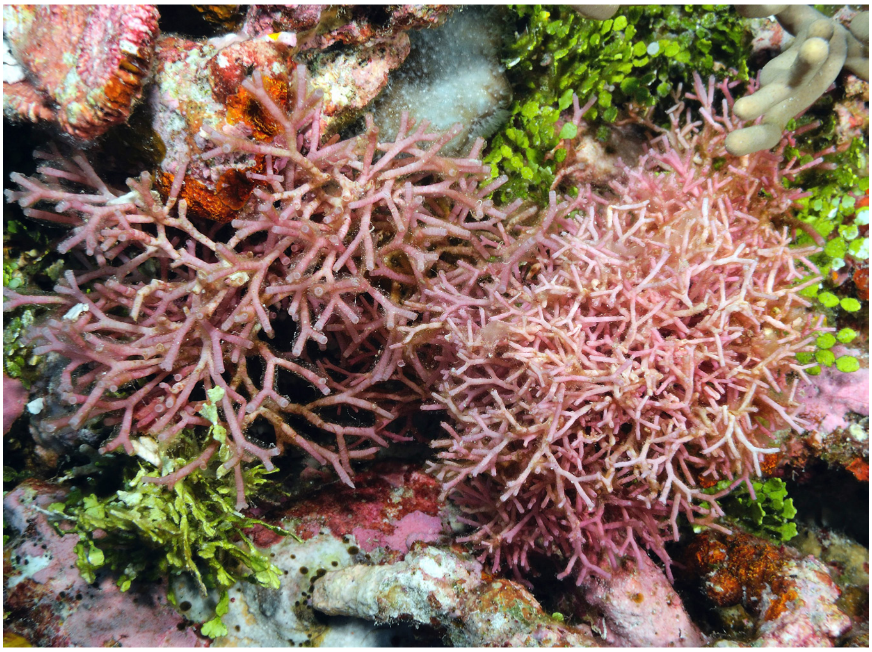

Figure 3. The similar looking red algae *Galaxaura pacifica* (left) and *Tricleocarpa fastigiata* (right) at Hibernia Reef, illustrating the difficulty in identifying species in situ.

as either *Heterozostera nigricaulis* or *H. polychlamys* as *H. tasmanica* is now not considered to occur in Western Australian waters. If relevant voucher specimens were not retained, it will be impossible to assess which of the two species the earlier records refer.

Worldwide, conservation policies and legislation also rely on species names to list for protection. For example, the Australian Environment Protection and Biodiversity Conservation Act 1999 (EPBC Act) contains a list of threatened species and ecological communities. Species listed are considered in categories of critically endangered, vulnerable, conservation dependent, extinct in the wild, and extinct, and includes as 'species' sub-species and distinct populations at the Minister's discretion for the purposes of the Act. For the marine flora, currently no species are considered conservation dependent or extinct in the wild, but the vast majority of species (certainly in the macroalgae) are data deficient and their true conservation status is unknown. Many species of algae are under-collected—their apparent rarity most likely due to historical disinterest or logistical difficulties—potentially leading to unsupportable assumptions regarding their status. It remains important for conservation to know whether something is locally endemic, or more widely distributed, and rapidly evolving taxonomies (with concomitant name changes) may not be reflected in legislation leading to either over-conservative, or inadequate conservation measures.

CONCLUSION

The marine flora of Western Australia is highly diverse, yet despite significant advances in molecular tools that can complement traditional taxonomy, the task of accurately assessing the diversity and biogeography remains problematic. The advances in barcoding molecular samples will lead us to very different and unexpected understandings as whole ecosystem assessments may be assessed using environmental DNA or "bar coding water samples". These challenges are not faced by WA alone—although the physical size of the marine environment (relative to the number of active research scientists) makes our challenge potentially greater.

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REFERENCES

Arias-Ortiz A, Serrano O, Masqué P, Lavery P S, Mueller U, Kendrick G A, Rozaimi M, Esteban A, Fourqurean J W, Marbà N, Mateo M A, Murray K, Rule M J & Duarte C M 2018. A marine heatwave drives massive losses from the world's largest seagrass carbon stocks. *Nature Climate Change* **8**, 338–344.

Ascherson P 1868. Vorabeiten zu einer Ubersicht der phanerogamen Meergewächse. *Linnaea* **35**, 152–208.

Ascherson P 1871. Die geographische Verbreitung der Seegräser. *in* Petermann's *Geographische Mitteilungen* **17**, 241–248.

Ascherson P 1875. Die geographische Verbreitung der Seegräser. pp. 359–373 *in* Neumayer G, editor, *Anleitung zu wissenschaftlichen Beobachtungen auf Reisen, mit besondere Rücksicht auf die Bedürfnisse der kaiserlichen Marine*, Robert Oppenheim Verlag, Berlin.

Ascherson P 1906. Die geographische Verbreitung der Seegräser. pp. 389–413 *in* Neumayer G, editor, *Anleitung zu wissenschaftlichen Beobachtungen auf Reisen*. 3rd Edition, Band 2, Dr. Max Jänecke Verlagsbuchhandlung, Hannover.

Ascherson P & Graebner P 1907. Potamogetonaceae *in* Engler A, editor, *Das Pflanzenreich Heft* **31**, 1–184. W. Engelmann, Leipzig.

Ascherson P & Gürke M 1889. Hydrocharitaceae *in* Engler A & Prantl K, editors, Die natürlichen Pflanzenfamilien **2**, 238–258. W. Engelmann, Leipzig.

Black J M 1915. Additions to the flora of South Australia, No. 8. *Transactions of the Royal Society of South Australian* **39**, 94–97.

Black J M 1922–24. The Flora of South Australia. Government Printer, Adelaide.

Boedeker C, Leliaert F & Zuccarello G C 2016. Molecular phylogeny of the Cladophoraceae (Cladophorales, Ulvophyceae) with the resurrection of *Acrocladus* Nägeli & W Børgesen, and the description of *Lurbica* gen. nov. and *Pseudorhizoclonium* gen. nov. *Journal of Phycology* **52**, 905–928.

Brown R 1960. (Facsimile edition). *Prodromus Florae Novae Hollandiae et Insulae Van-Diemen* 1810, *Supplementum primum* 1830 by Robert Brown with an introduction by William T. Stearn. Hafner, New York.

Cambridge M L & Kuo J 1979. Two new species of seagrasses from Australia, *Posidonia sinuosa* and *P. angustifolia* (Posidoniaceae). *Aquatic Botany* **6**, 307–328.

Carruthers T J B, Dennison W C, Kendrick G, Waycott M, Walker D & Cambridge M 2007. Seagrasses of south-west Australia, A conceptual synthesis of the world's most diverse and extensive seagrass meadows. *Journal of Experimental Marine Biology and Ecology* **350**, 21–45.

Coyer J A, Hoarau G, Kuo J, Tronholm A, Veldsink J & Olsen J L 2013. Resolution and temporal divergence of the Zosteraceae using one nuclear and three chloroplast loci. *Systematics and Biodiversity* **11**, 271–284.

Cremen M C M, Huisman J M, Marcelino V R & Verbruggen H 2016. Taxonomic revision of *Halimeda* (Bryospidales, Chlorophyta) in south-western Australia. *Australian Systematic Botany* **29**, 41–54.

Den Hartog C 1970. *The Sea-Grasses of the World*. North Holland, Amsterdam.

Den Hartog C & Kuo J 2006. Seagrass taxonomy and biogeography. pp. 1–23 *in* Larkum A W D, Orth R J & Duarte C M, editors, *Seagrasses, Biology, Ecology and Conservation*, Springer, Dordrecht, The Netherlands.

Den Hartog C 1970. The Sea-Grasses of the World. North Holland, Amsterdam.

Doty M S & Stone B C 1966. Two new species of *Halophila* (Hydrocharitaceae). *Brittonia* **18**, 303–306.

Ducker S C, Foord N J & Knox R B 1977. Biology of Australian seagrasses, the genus *Amphibolis* C. Agardh (Cymodoceaceae). *Australian Journal of Botany* **25**, 67–95.

Fraser, M W & Kendrick, G A 2017. Belowground stressors and long-term seagrass declines in a historically degraded seagrass ecosystem after improved water quality. *Scientific Reports* **7**, 14469.

Harvey W H 1855. Some account of the marine botany of the colony of Western Australia. *Transactions of the Royal Irish Academy* **22** (Science), 525–566.

Hooker J D 1858. The botany of the Antarctic voyage of HM Discovery Ships *Erebus* and *Terror* in the years 1839–1843, under command of Captain Sir James Clark Ross. III. Flora Tasmaniae. Vol. 2 (Monocotyledons). Lovell Reeve, London.

Huisman J M & Millar A J K 2013. Australian Seaweed Collections: Use and Misuse. *Phycologia* **52**, 2–5.

Huisman J M 2015. Algae of Australia: Marine Benthic Algae of North-western Australia, 1. Green and Brown Algae. ABRS, Canberra; CSIRO Publishing, Melbourne.

Huisman J M 2018. Algae of Australia: Marine Benthic Algae of North-western Australia, 2. Red Algae. ABRS, Canberra; CSIRO Publishing, Melbourne.

Huisman J M, Dixon R R M, Hart F N, Verbruggen H & Anderson R J 2015. The South African estuarine specialist *Codium tenue* (Bryopsidales, Chlorophyta) discovered in a south-western Australian estuary. *Botanica Marina* **58**, 511–521.

Huisman J M, Kendrick A J & Rule M J 2011. Benthic algae and seagrasses of the Walpole and Nornalup Inlets Marine Park, Western Australia. *Journal of the Royal Society of Western Australia* **94**, 29–44.

Jacobs S W L & Les D 2009. New combination in *Zostera* (Zosteraceae). *Telopea* **12**, 419–423.

Kendrick G A, Orth R J, Statton J, Hovey R, Ruiz Montoya L, Lowe R J, Krauss S L & Sinclair E A 2017. Demographic and genetic connectivity: the role and consequences of reproduction, dispersal and recruitment in seagrasses. *Biological Reviews* **92**, 921–938.

Kilminster K, Forbes V & Holmer M 2014. Development of a 'sediment-stress' functional-level indicator for the seagrass *Halophila ovalis*. *Ecological Indicators* **36**, 280–289.

Kilminster K, Hovey R, Waycott M & Kendrick G A 2018. Seagrasses of southern and south-western Australia. pp. 61–89 *in* Larkum A W D, Kendrick G A & Ralph P J, editors, *Seagrasses of Australia: Structure, Ecology and Conservation*, Springer International Publishing, Switzerland.

Kilminster K, McMahon K, Waycott M, Kendrick G, Scanes P, Mckenzie L, O'Brien K R, Lyons M, Ferguson A, Maxwell P, Glasby T & Udy J 2015. Unravelling complexity in seagrass systems for management: Australia as a microcosm. *Science of the Total Environment* **534**, 97–109.

Kuo J 2005. A revision of the genus *Heterozostera* (Setchell) den Hartog (Zosteraceae). *Aquatic Botany* **81**, 97–140.

Kuo J 2011. *Enhalus*, *Thalassia*, *Halophila* and Posidoniaceae, Cymodoceaceae, Zosteraceae. p. 32–44; 111–120; 120–134; 135–143 *in* Wilson A, editor, *Flora of Australia*. Vol. 39, Alismatales to Arales ABRS, Canberra.

Kuo J & Cambridge M 1984. A taxonomic study of the *Posidonia ostenfeldii* complex (Posidoniaceae) with description of four new Australian seagrasses. *Aquatic Botany* **20**, 267–295.

Kuo J, Kanamoto Z, Iizumi, H & Mukai H 2006. Seagrasses the genus *Halophila* Thouars (Hydrocharitaceae) from Japan. *Acta Phytotaxonomica et Geobotanica* **57**, 129–154.

Kuo J, Cambridge M L, McKenzie L G & Coles, R G 2018. Taxonomy of Australian Seagrasses. pp. 765–786 *in* Larkum A W D, Kendrick G A & Ralph P J, editors, *Seagrasses of Australia: Structure, Ecology and Conservation*, Springer International Publishing, Switzerland.

Labillardière J J H 1807. Novae Hollandiae Plantarum Specimen 2: 131 pp. (p.126, Pl. 264).

Larkum A W, Kendrick G A & Ralph, P J 2018. *Seagrasses of Australia: Structure, Ecology and Conservation*. Springer.

Lee H, Golicz A A, Bayer P E, Jiao Y, Tang H, Paterson A H, Sablok G, Krishnaraj R R, Chan, C-K K, Batley J, Kendrick G A, Larkum A W D, Ralph P J & Edwards D 2016. The genome of a Southern Hemisphere seagrass species (*Zostera muelleri*). *Plant Physiology* **172**, 272–283.

Lee H, Golicz A A, Bayer P E, Severn-Ellis A, Kenneth Chan C-K, Batley J, Kendrick G A & Edwards D 2018. Genomic comparison of two independent seagrass lineages reveals habitat-driven convergent evolution. *Journal of Experimental Botany* **69**, 3689–3702

Leliaert F, Payo D A, Gurgel C F D, Schils T, Draisma S G A, Saunders G W, Kamiya M, Sherwood A R, Lin S-M, Huisman J M, Le Gall L, Anderson R J, Bolton J J, Mattio L, Zubia M, Spokes T, Vieira C, Payri C E, Coppejans E, D'Hondt S, Verbruggen H & De Clerck O 2018. Patterns and drivers of species diversity in the Indo-Pacific red seaweed *Portieria*. *Journal of Biogeography* **45**, 2299–2313.

Les D H, Cleland M A & Waycott M 1997. Phylogenetic studies in Alismatids, II. Evolution of marine angiosperms (seagrasses) and hydrophily. *Systematic Botany* **22**, 443–463.

Les D H, Moody M L, Jacobs S W L & Bayer R J 2002. Systematics of seagrasses (Zosteraceae) in Australia and New Zealand. *Systematic Botany* **27**, 468–484.

Lynch A J J, Thackway R, Specht A, Beggs P J, Brisbane S, Burns E L, Byrne M, Capon S J, Casanova M T, Clarke P A, Davies J M, Dovers S, Dwyer R G, Ens E, Fisher D O, Flanigan M, Garnier E, Guru S M, Kilminster K, Locke J, Mac Nally R, McMahon K M, Mitchell P J, Pierson J C, Rodgers E M, Russell-Smith J, Udy J & Waycott M 2015. Transdisciplinary synthesis for ecosystem science, policy and management: The Australian experience. *Science of the Total Environment* **534**, 173–184.

Martin B C, Bougoure J, Ryan M H, Bennett W W, Colmer T D, Joyce N K, Olsen Y S & Kendrick G A 2019. Oxygen loss from seagrass roots coincides with colonisation of sulphide-oxidising cable bacteria and reduces sulphide stress. *The ISME Journal* **13**, 707–719.

Martin B C, Gleeson D, Statton J, Siebers, A R, Grierson P, Ryan M H & Kendrick G A 2018. Low light availability alters root exudation and reduces putative beneficial microorganisms in seagrass roots. *Frontiers in microbiology* **8**: 2667.

McMahon K, Sinclair E A, Sherman C D, van Dijk K-j, Hernawan U E, Verduin J. & Waycott M 2018. Genetic Connectivity in Tropical and Temperate Australian Seagrass Species, pp. 155–194 *in* Larkum A W D, Kendrick G A & Ralph P J, editors, *Seagrasses of Australia: Structure, Ecology and Conservation*. Springer International Publishing, Switzerland.

McMahon K M, Evans R D, van Dijk K-j, Hernawan U, Kendrick G A, Lavery P S, Lowe R, Puotinen M & Waycott M 2017. Disturbance is an important driver of clonal richness in tropical seagrasses. *Frontiers in plant science* **8,** 2026.

McMillan C 1982. Isozymes in seagrasses. *Aquatic Botany* **14**, 231–243.

McMillan C 1983a Sulfated flavonoids and leaf morphology of the *Halophila ovalis-H. mino*r complex (Hydrocharitaceae) in the Pacific Islands and Australia. *Aquatic Botany* **16**, 337–347.

McMillan C 1983b. Morphological diversity under controlled conditions for the *Halophila ovalis-H. minor* complex and the *Halodule uninervis* complex from Shark Bay, Western Australia. *Aquatic Botany* **17**, 29–42.

McMillan C 1986. Sulfated flavonoids and leaf morphology in the *Halophila ovalis–H. minor* complex (Hydrocharitaceae) of the Indo-Pacific Ocean. *Aquatic Botany* **25**, 63–72.

McMillan C 1991. Isozymes patterning in marine spermatophytes. pp. 193–200 *in* Triest L, editor, *Isozymes in Water Plants*, National Botanic Garden of Belgium, Meise.

McMillan C & Williams S C 1980. Systematic implications of isozymes in *Halophila* section *Halophila*. *Aquatic Botany* **9**, 21–31.

McMillan C, Williams S C, Escobar I & Zapata O 1981. Isozymes, secondary compounds and experimental cultures of Australian seagrasses in *Halophila*, *Halodule*, *Zostera*, *Amphibolis* and *Posidonia*. *Australian Journal of Botany* **29**, 249–260.

McMillan C, Young P C, Cambridge M C, Masini R, & Walker D I 1983. The status of an endemic Australian seagrass, *Cymodocea angustata* Ostenfeld. *Aquatic Botany* **17**, 231–241.

Mueller F von 1872–74. Phytographiae Australiae. Government Printer, Melbourne.

Mueller F von 1886. Fragmenta phytographiae Australiae. Government Printer, Melbourne, 6, 198–199.

Mueller F von 1902. List of extra-tropic Western Australian Plants'. Revised and arranged by A. Morrison – Western Australian Year Book for 1900–1901. Vol. 1 (Perth).

Nowick R J, Thomson J A, Burkholder D A, Fourqurean J W & Heithaus M R 2017. Predicting seagrass recovery times and their implications following an extreme climate event. *Marine Ecology Progress Series* **567**, 79–93. DOI: 10.3354/meps12029

Olsen, Y S, Fraser, M W, Martin, B C, Pomeroy, A, Lowe, R, Pedersen, O & Kendrick, GA 2018. In situ oxygen dynamics in rhizomes of the seagrass *Posidonia sinuosa*: impact of light, water column oxygen, current speed and wave velocity. *Marine Ecology Progress Series* **590**, 67–77.

Ostenfeld C H 1914 On the geographical distrbution of the seagrasses. A preliminary communication. *Proceedings of the Royal Society of Victoria* **27**, 179–191.

Ostenfeld C H 1916. Contributions to Western Australian Botany. Part 1. *Danish Botanical Ark* **2**, 1–44.

Ostenfeld C H 1929. A list of Australian sea-grasses. *Royal Society of Victoria* **42** (1), 1–4.

Payo D A, Leliaert F, Verbruggen H, D'Hondt S, Calumpong H P & De Clerck O 2013. Extensive cryptic species diversity and fine-scale endemism in the marine red alga *Portieria* in the Philippines. *Proceedings of the Royal Society B* **280** (1753):20122660.

Saunders G W 2005. Applying DNA barcoding to red macroalgae: a preliminary appraisal holds promise for future applications. *Philosophical Transactions of the Royal Society B* **360**, 1879–1888.

Sinclair E A, Ruiz-Montoya L, Krauss S L, Anthony, J M, Hovey R K, Lowe R J & Kendrick G A 2018 Seeds in motion: genetic assignment and hydrodynamic models demonstrate concordant patterns of seagrass dispersal. *Molecular Ecology* **27** (24), 5019–5034.

Smale D A & Wernberg T 2013. Extreme climatic event drives range contraction of a habitat-forming species. *Proceedings of the Royal Society B* **280**, 20122829.

Sonder O G W 1845. Nova algarum genera et species, quas in itinere ad oras occidentales Novae Hollandiae, collegit L. Priess, Ph. Dr. *Botanische Zeitung* **3**, 49–57.

Sonder O G W 1846–1848. Algae *in* Lehmann C, Plantae Preissianae … quas in Australasia occidentali et meridionali-occidentali annis 1838–1841 collegit Ludovicus Preiss. 2, 148–160 (1846), 161–195 (1848). Hamburg.

Statton J, Montoya L R, Orth R J, Dixon K W & Kendrick, G A 2017a. Identifying critical recruitment bottlenecks limiting seedling establishment in a degraded seagrass ecosystem. *Scientific Reports* **7** (1), 14786.

Statton J, Sellers R, Dixon K W, Kilminster K, Merritt D J & Kendrick G A 2017b. Seed dormancy and germination of *Halophila ovalis* mediated by simulated seasonal temperature changes. *Estuarine, Coastal and Shelf Science* **198**, 156–162.

van der Heide T, Covers L L, De Fouw J, Olaf H, van der Geest M, van Katwijk M M, Piersma T, van de Koppel J, Silliman B R, Smolders J P & van Gils, J A, 2012. A Three-Stage Symbiosis Forms the Foundation of Seagrass Ecosystems. *Science* **336**, Issue 6087, 1432–1434.

Vieira C, D'Hondt S, De Clerck O & Payri C E 2014. Toward an inordinate fondness for stars, beetles and *Lobophora*? Species diversity of the genus *Lobophora* (Dictyotales, Phaeophyceae) in New Caledonia. *Journal of Phycology* **50**, 1101–1119.

Walker D I 1991. The effect of sea temperature on seagrasses and algae on the Western Australian coastline. *Journal of the Royal Society of Western Australia* **74**, 71–77.

Walker D I & Bellgrove A 2017. Physical threats to macrophytes as ecosystem engineers. pp. 259–272 *in* Olafsson, E, editor, *Marine macrophytes as foundation species*, CRC Press, Boca Raton, Florida.

Waycott M, Biffin E & Les D H 2018. Systematics and Evolution of Australian Seagrasses in a Global Context. pp. 129–154 *in* Larkum A W D, Kendrick G A & Ralph P J, editors, *Seagrasses of Australia: Structure, Ecology and Conservation*, Springer International Publishing, Switzerland.

Waycott M, McMahon K & Lavery P 2014. *A guide to southern temperate seagrasses*. CSIRO Publishing, Collingwood, Victoria.

Wernberg T, Smale D A, Tuya F, Thomsen M S, Langlois T J, de Bettignies T, Bennett S & Rousseaux C S 2013. An extreme climatic event alters marine ecosystem structure in a global biodiversity hotspot. *Nature Climate Change Letters* **3**, 7882. DOI: 10.1038/NCLIMATE1627

Womersley H B S 1956. A critical survey of the marine algae of southern Australia. I. Chlorophyta. *Australian Journal of Marine and Freshwater Research* **7**, 343–383.

Womersley H B S 1984. The Marine Benthic Flora of Southern Australia, Part I. Flora and Fauna Handbooks Committee, Adelaide.

Womersley H B S 1987. The Marine Benthic Flora of Southern Australia, Part II. Flora and Fauna Handbooks Committee, Adelaide.

Womersley H B S 1994. The Marine Benthic Flora of Southern Australia. Rhodophyta – Part IIIA. ABRS, Canberra.

Womersley H B S 1996. The Marine Benthic Flora of Southern Australia. Rhodophyta – Part IIIB. ABRS, Canberra.

Womersley H B S 1998. The Marine Benthic Flora of Southern Australia. Rhodophyta – Part IIIC. State Herbarium of South Australia, Adelaide.

Womersley H B S 2003. The Marine Benthic Flora of Southern Australia. Rhodophyta – Part IIID. ABRS, Canberra; State Herbarium of South Australia, Adelaide.

Wynne M J 2016. The proposal of *Willeella brachyclados* (Montagne) M.J.Wynne comb. nov. (Ulvophyceae). *Notulae algarum* **18**, 1–3.