Swainsona 30: 33–40 (2018)

The marine benthic algae of South Australia

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Abstract: The status of phycological (primarily taxonomic) studies concerning the marine benthic algae in South Australia is reviewed, including a brief history highlighting the contributions of H.B.S. Womersley that culminated in his six volume *The marine benthic flora of southern Australia* (1984–2003). The impact of the advent of molecular methods is discussed, with examples of recent changes resulting from the adoption of these methods in taxonomic studies. A case is made for the continued relevance of herbaria and taxonomy, particularly in light of the on-line provision of identification guides and specimen data, the latter directly pertinent to biogeographical analyses and the surveillance of introduced and pest species. However, the recent decline in support for taxonomy will undoubtedly negatively impact on the education and mentoring of future phycologists, and ultimately the maintenance and quality of data.

Keywords: algae, seaweeds, South Australia, taxonomy, botanical history, H.B.S. Womersley

Introduction

Seaweeds play a part of the utmost importance in the scheme of Nature, and incidentally may be of great direct service to Man.

Lucas (1936: 13)

Seaweeds, or marine benthic algae in the more formal sense, which excludes sea grasses, are a major component of the Australian coastal biota and play an important role in near-shore ecology, as they provide habitat, food, and substratum stabilization. Australia, in particular the temperate southern coast, is well-known as a global hotspot of seaweed diversity, with a large number of species recorded in a broad range of higher taxa and a particularly high percentage of endemic taxa. (Phillips 2001; Kerswell 2006; Hommersand 2007).

History

The number of Algae dispersed along the Australian coast may perhaps be estimated at nearly 1000: the number actually known is about 800.

Harvey (1858: vii)

The early history of phycological studies in Australia has been reviewed by several authors and only those major contributions that advanced knowledge of the seaweeds of South Australia will be specifically addressed in this paper. For a more general treatise we refer the reader to the excellent accounts by Womersley (1984), Ducker (1979, 1981a, b, c, 1988) and Cowan & Ducker (2007 and references therein).

Several figures loom particularly large in the history of phycological studies in South Australia, although one never actually set foot in the State. The first was Baron Ferdinand von Mueller, who lived in Adelaide for four years (late 1847–1852) and collected numerous algae from the Lefevre Peninsula, Holdfast Bay, and Encounter Bay, with other collectors providing specimens from Kangaroo Island and Port Lincoln. These collections were sent to and described by several European phycologists, primarily Sonder (1853), and records based on Mueller collections made up the bulk of those recorded for South Australia in a subsequent compendium of all known Australian algae (Harvey 1858–1863).

William Henry Harvey was an Irish phycologist 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

Published online: 7 Nov. 2018 • flora.sa.gov.au/swainsona

ISSN 2206-1649 (Print) • ISSN 2206-1657 (Online)

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" (Anonymous 1869). Harvey subsequently described his collections (and those of others) in several publications, but undoubtedly his greatest contribution to Australian phycology is his five volume *Phycologia Australica* (1858–1863), wherein 300 species of algae were depicted in detailed colour lithographs (engraved by Harvey) (see Fig. 1). While Harvey did not visit South Australia, he did receive specimens from local collectors, primarily David Curdie and Clara Wehl (Mueller's sister). Harvey (1863), in his 'Synoptic Catalogue' listing all Australian species, included the species described by Sonder based on Mueller's South Australian collections, but acknowledged that they "have not come into my hands, and several of the species named by Sonder remain unknown to me" (Harvey 1863).

Subsequent additions to the South Australian algal flora were made by Reinbold (1897, 1898, 1899), who was sent specimens collected from Lacepede and Guichen Bay by Dr A. Engelhardt, and from Investigator Strait by Miss Nellie Davey. Jessie Hussey sent collections from Port Elliot to J. Agardh, some of which were

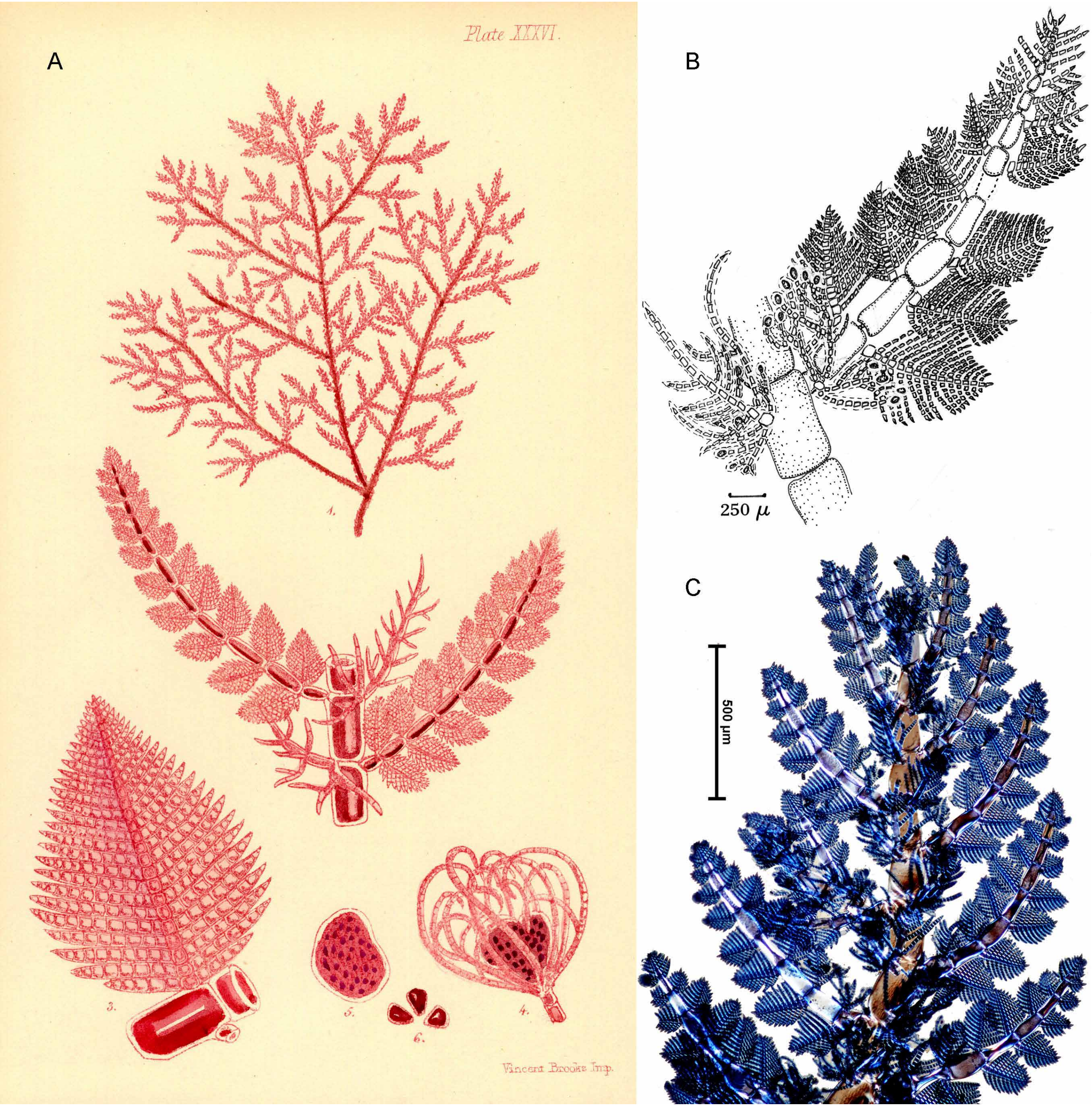

Fig. 1. *Inkyuleea ballioides* (Sonder) H.-G.Choi, Kraft & G.W.Saunders. The species was first described as *Callithamnion ballioides* by Sonder (1853) from collections by Ferdinand von Mueller from Guichen Bay, near Robe (S.A.). **A** The species as depicted in Harvey (1858: pl. XXXVI), as *Ballia robertiana* Harv.; **B** Line-drawing in Womersley & Wollaston (1998: 155); **C** Microscopic image, specimen stained with aniline blue (photo: R.N. Baldock).

described as new genera and species (Agardh 1897, 1901). The first attempts at an algal flora just for South Australia did not appear until sometime later, after an extended fallow period where very little progress was made. *Seaweeds of South Australia* comprised two volumes, the first by Lucas (1936) describing the green algae, the second by Lucas & Perrin (1947) describing the red algae. As noted by Womersley (1984: 36) the latter, completed after Lucas's death, contained little original work and relied heavily on reproductions of Harvey's plates from *Phycologia Australica*. However, it was readily available, it included English descriptions and keys, as well as figures, and was most likely the first resource consulted by Australian phycologists leading up to the latter part of the 20th century.

As with most under-appreciated groups, understanding of the taxonomy of the marine benthic algae has progressed sporadically, with periods of elevated activity almost entirely due to the contributions of individuals or small groups of dedicated taxonomists. In many respects South Australia has been blessed, as the State not only supports an extremely diverse macroalgal flora, but additionally several dedicated taxonomists that have spent the major parts of their lifetimes endeavouring to comprehensively describe this flora.

One person must be singled out, Professor H.B.S. (Bryan) Womersley (1922–2011) of The University of Adelaide and the State Herbarium of South Australia. Professor Womersley (see Fig. 2), initially an ecologist, realized quite early how little was known about the southern Australian marine flora and from that moment made it his life's work to remedy this lack of knowledge. Aided by several co-workers and students, many of whom went on to equally highly productive taxonomic careers (Gerry Kraft, Bill Woelkerling, Murray Parsons), Womersley's studies culminated in a series of six books under the general banner of *The marine benthic flora of southern Australia*. The first of these (Womersley 1984) described the green algae and seagrasses, the second (1987) the brown algae, then followed four volumes dedicated to the red algae (1994, 1996, 1998, 2003). Final species tallies were presented in the last volume (2003: 4): "Chlorophyta 123 (plus 3 unrecorded in Part I), Phaeophyta 231 (plus 6–8 unrecorded in Part II) and *Vaucheria* 5 and Rhodophyta 778 (plus about 40 unrecorded), giving a total of 1137 recorded species and about 50 still to be described". The southern Australian algal flora then clearly exceeded Harvey's prediction for the entire continent. The Womersley Flora is justly regarded as a pinnacle of alpha taxonomy and will undoubtedly remain the primary source of taxonomic knowledge for decades. The algal diversity of very few regions worldwide is as well documented as that of southern Australia. As noted by Kraft (2011), in a tribute to Professor Womersley, "In the over 60 years of his active research, he and his students have elevated the broad coastal expanse of southern Australia from a virtual *terra incognita* of enormous algal biodiversity to the status of being among the best taxonomically understood stretches of richly endowed coastline in the world."

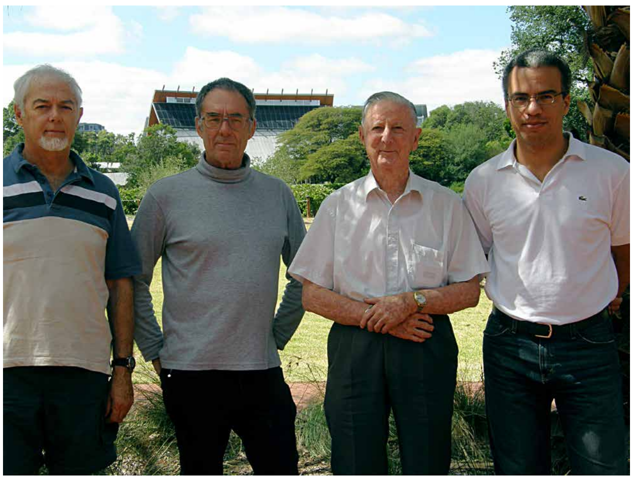

Fig. 2. Prominent phycologists from the State Herbarium of South Australia, L to R: Bob Baldock, Gerry Kraft, Bryan Womersley, Fred Gurgel.

Given these plaudits, one might reasonably conclude 'job done' and move on. However, as was regularly acknowledged by Womersley, that is certainly not the case. Many groups require further study, particularly in the red algae. When he passed away, Womersley still had 6 green, 13 brown and 44 red algae on his list of 'things to do'.

The molecular revolution

Seaweeds are often morphologically relatively simple organisms and convergent evolution of thallus forms, plus morphological plasticity, has resulted in often considerable difficulty in identification and classification. As such, the group is well-suited to the use of molecular methods in assessing relationships and the application of correct names. For southern Australia, the next major undertaking will be the evaluation and refinement of Womersley's taxonomic concepts based on DNA sequence analyses. This was initiated by Carlos (Fred) Gurgel during his tenure at the State Herbarium of South Australia (2008–2013) and resulted in several taxonomic revisions (e.g. Sun *et al.* 2012; Belton *et al.* 2014; Dixon *et al.* 2014; Schmidt 2016), but the process is far from complete. Undoubtedly some well-known groups will remain unchanged, but, based on the results and implications of recent studies, major revisions can also be expected.

For example, the first red algal volume (Womersley 1994) included the order Nemaliales, which at the time comprised two families, the Liagoraceae and Galaxauraceae (Huisman & Womersley 1994). The Nemaliales has been the subject of considerable scrutiny in subsequent years and studies employing molecular methods have seen the recognition of a further four families: the Scinaiaceae Huisman, J.T.Harper & G.W.Saunders, Nemaliaceae (Farlow) De Toni & Levi, Yamadaellaceae Showe M.Lin, Rodr.-Prieto & Huisman and the Liagoropsidaceae Showe M.Lin, Rodr.-Prieto & Huisman (Huisman *et al.* 2004; Lin *et al.* 2015), of which at least two have southern Australian representatives. Moreover, some putatively widespread species have been shown to encompass considerable species diversity. *Nemalion elminthoides* (Velley) Batters, with a type locality in England, was recorded for southern Australia based on morphological congruence by Womersley (1994, as *N. helminthoides*). Le Gall & Saunders (2010) undertook molecular analyses of this species based on specimens from a variety of locations worldwide. Their results resolved five divergent clades, one of which included a Tasmanian specimen that they suggested most likely represented a new species. Authentic *N. elminthoides* is therefore probably restricted to Europe. A similar study by Lindstrom *et al.* (2015) revealed that the Australian species previously identified as *Nothogenia fastigiata* (Bory) P.G.Parkinson (Huisman & Womersley 1992, 1994, 2006) was actually a sister taxon of that species and they resurrected from synonymy a Harvey species described from Tasmania, as *Nothogenia lingula* (Harv.) S.C.Lindstr. & Hughey. Further studies in the Nemaliales have resulted in additional revisions of southern Australian taxa, with species transferred from *Liagora* to *Ganonema* (Huisman & Kraft 1994) and from *Galaxaura* to *Dichotomaria* (Huisman *et al.* 2004). Of the 22 southern Australian species included in the Nemaliales in Part IIIA of the Flora (Womersley 1984; Huisman & Womersley 1994), nine have undergone a name change and eight have been transferred to other families (Table 1).

Revisions of this type are not restricted to the Nemaliales. In the green algae, Cremen *et al.* (2016) recently highlighted the significant genetic diversity in specimens attributed to *Halimeda cuneata* Hering, a South African species recorded from numerous localities worldwide, including western and south-western Australia (Womersley 1984; Huisman 2000). Cremen *et al.* (2016) concluded that the Australian taxon differed from specimens from the South African type locality and resurrected *Halimeda versatilis* J.Agardh (type locality Cape Riche, Western Australia) from synonymy.

In the brown algae, Dixon *et al.* (2012) undertook a morphological and molecular study of the common genus *Sargassum*, their results leading to the recognition of *Sargassum* subg. *Phyllotricha* at genus level and the transfer of several southern Australian species to the recently resurrected genus *Sargassopsis*. Echoing the *Nemalion elimthoides* study mentioned above, the supposedly widespread brown alga *Lobophora variegata* (J.V.Lamour.) E.C.Oliveira was thought to occur in Australia on most coasts except for those of cold-temperate Tasmania. However, the recent study by Sun *et al.* (2012), based on comparative morphology and molecular analyses, recognised considerable species-level variation and resulted in the description of four new species and another resurrected from synonymy. Two species were attributed to southern Australia, *L. nigrescens* J.Agardh and *L. australis* Z.Sun, Gurgel & H.Kawai, where previously only *L. variegata* was thought to occur (Womersley 1987).

The preceding are but a few examples of where taxonomy is heading and highlight the spectacular impact that the advent of molecular techniques has made, and will undoubtedly continue to make, on algal taxonomy. Indeed, some authors are suggesting that "all [new] species descriptions must be accompanied by representative DNA reference sequences of the type specimen" (De Clerck *et al.* 2013), a requirement already implemented by some journals (e.g. the *Journal of Phycology*).

Table 1. Recent taxonomic and nomenclatural changes in the southern Australian Nemaliales.

Womersley 1984; Huisman & Womersley 1994	Current	Reference
Liagoraceae	*Liagoraceae* *Nemaliaceae*	Lin *et al.* (2015)
Galaxauraceae	*Galaxauraceae* *Scinaiaceae*	Huisman *et al.* (2004)
Nemalion helminthoides	*Nemalion* possible sp. nov.	Le Gall & Saunders (2010)
Liagora farinosa	*Ganonema farinosum*	Huisman & Kraft (1994)
Liagora codii	*Ganonema codii*	Huisman & Kraft (1994)
Scinaia australis	*Scinaia acuta Wynne*	Wynne (2005)
Nothogenia fastigiata	*Nothogenia lingula*	Lindstrom *et al.* (2015)
Galaxaura obtusata	*Dichotomaria obtusata*	Huisman *et al.* (2004)
Galaxaura marginata	*Dichotomaria australis* *Dichotomaria spathulata*	Kurihara & Huisman (2006) Kurihara & Huisman (2006)
Tricleocarpa cylindrica	*Tricleocarpa australiensis*	Huisman *et al.* (2018)

Biogeography

As our knowledge of the flora improves, so ecological and biogeographical studies will be better based.
Womersley (1984: 37)

As with all specimens held in Australian herbaria, the information connected to algal specimens is being databased and made available on-line as part of 'The Australasian Virtual Herbarium' (AVH 2018). These data include identities, location, collector and date of collection, plus occasionally habitat descriptions. The availability of this information and the tools to analyse it has led to a several projects wherein the biogeography of the algae is being assessed based on data associated with specimens in herbaria (e.g. Waters *et al.* 2010). Studies such as these considerably enhance the value of herbarium collections and enable specimen records to be used in a broader variety of studies, including conservation assessments, analyses of range shifts, tracking disease and pest vectors, biological invasions and species distributions through time and space (Guerin 2013).

Of particular note are the collections made by Edyvane and Baker in the determination of the Integrated Marine and Coastal Regionalisation of Australia and validated by Womersley, which reside in the State Herbarium of South Australia. Regionally, Baker & Gurgel (2011) described algal assemblages in Gulf St Vincent based on herbarium data. However, conclusions generated solely from such studies need to be approached with caution and should consider the many biases that might affect the results (Huisman & Millar 2013). In the past, algal specimens (certainly most of those lodged in Australian herbaria) were collected primarily for taxonomic studies and only secondarily for range assessments. Thus, background information, such as location, was of secondary importance. The collection effort was almost certainly never at such a level that specimens covering entire distribution ranges and time periods were collected. In fact, in some cases, only "good" specimens (those with reproductive or characteristic features) have been archived. Initially, these were from the intertidal, shallow water and drift plants. As a consequence, assessing rarity can be similarly problematic if based on herbarium records and Womersley preferred the phrase "species for which there are few records".

However, South Australia may have been more fortunate than other States in that, in the past, symbiotic relationships existed between marine taxonomists and SCUBA divers of the South Australian Museum, the Department of Fisheries and latterly, South Australian Research and Development Institute (SARDI), which allowed extensive deeper water collections of algae, particularly by Scoresby Shepherd (see Shepherd 2016, for a personal historical account; Womersley & Baldock 2003 and Baldock & Womersley 2005, for collections at Isles of St Francis and Althorpe Islands, respectively). Scoresby Shepherd's collections were the basis of many new taxa, for example the remarkable *Palmoclathrus stipitatus* Womersley (Fig. 3) which featured on the cover of Womersley (1984). Over time, enough specimens have been accumulated that some general conclusions regarding distributions can be made, but assessing any changes in distribution requires further field work, wider collecting efforts, and a commitment by collectors to provide voucher specimens for archiving in State herbaria.

Fig. 3. *Palmoclathrus stipitatus* Womersley. Photo: K.L. Branden.

Pest seaweeds

Currently, several invasive seaweeds present a real or potential threat to South Australia. Three 'trigger list' species (i.e., those that are having, or are likely to have, a significant impact on local marine ecosystems and require a response) have become established. The green alga *Caulerpa taxifolia* (Vahl) C.Agardh, native to southern Queensland, but introduced in numerous locations worldwide due to its use as an aquarium decoration, was found in West Lakes and the Port River near the Jervois Bridge in March 2002. It was subsequently eradicated from West Lakes, but the infestation in the Port River and Barker Inlet persists and is now regarded as ineradicable. *Codium fragile* subsp. *fragile* (Suringar) Har. (formerly subsp. *tomentosoides* (Goor) P.C.Silva) was also introduced to West Lakes (see Womersley 2003: 499) and *Caulerpa cylindracea* Sond. (formerly *C. racemosa* var. *cylindracea* (Sond.) M.Verlaque, Huisman & Boudour.) first recorded by photo by Baldock (pers. obs., 2002) is present in Port Adelaide and at O'Sullivan Beach (Wiltshire *et al.* 2010). In addition to these species, several others are regarded as having been introduced, but their current status is poorly known (Wiltshire *et al.* 2010), with many not recollected since the original record. The most significant potential threat to South Australia is the kelp *Undaria pinnatifida* (Harv.) Suringar (also known as 'Japanese kelp' or 'wakame'), which is now well established in Tasmania and Victoria (as well as New Zealand and numerous other countries). This species most likely spreads via hull fouling and, given the proximity to South Australia of known populations, would appear to pose a serious threat to the State. Continued surveillance for these pest species is crucial, in the hope that any new outbreaks can be eradicated before becoming established.

The future

Given the firm grounding provided by the alpha taxonomic studies of the 20th century and the exciting prospects afforded by the advent of molecular methods and online analytical tools, the future would seem to be bright for phycology in Australia. Yet at this point in time the phycological taxonomic workforce in Australia is perhaps at its lowest ebb for the last 50 years (if based on the standard gauge of 'full time equivalents'). The golden era of the late 20th century, when phycologists were employed at the majority of Australia's universities and herbaria, is becoming a distant memory. Job prospects are gloomy and the pursuit of pure scientific research seemingly a thing of the past, or is undertaken only by volunteers or retirees.

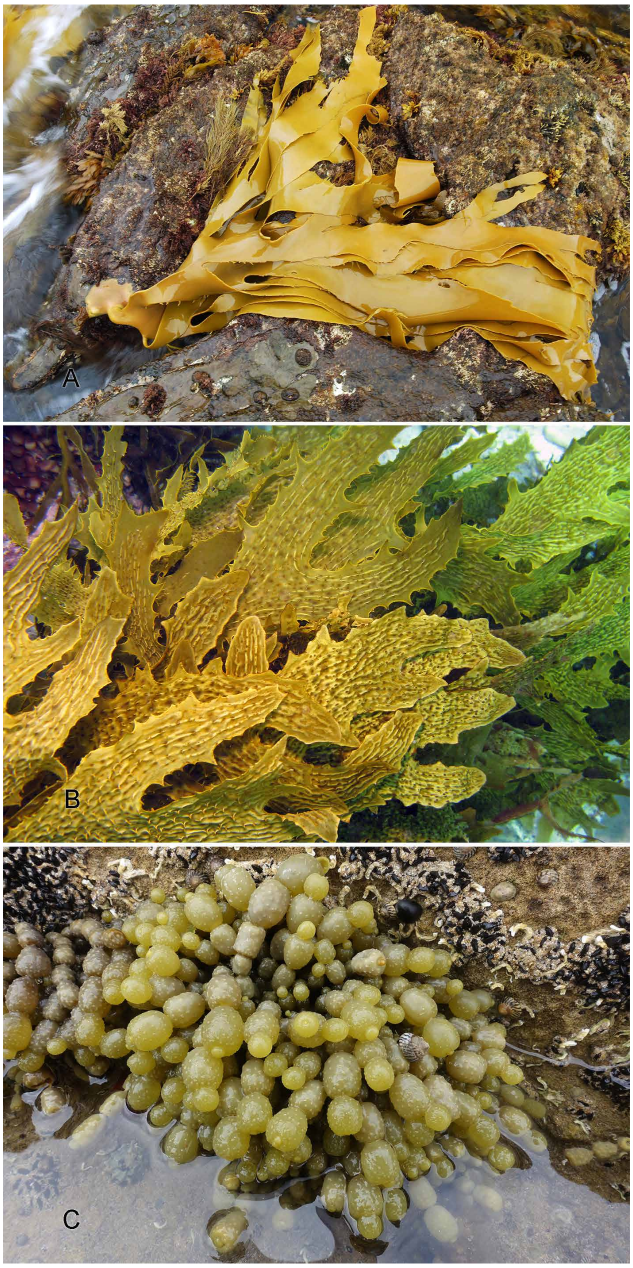

Fig. 4. Potential indicator species. **A** *Durvillaea potatorum* (Labill.) Aresch.; **B** *Ecklonia radiata* (C.Agardh) J.Agardh; **C** *Hormosira banksii* (Turner) Decaisne. Photos: J.M. Huisman.

However, there are some promising alternatives to the traditional research avenues. The last twenty or so years have seen the profile of marine plants raised considerably, initially through the appearance of field guides incorporating colour photography (Fuhrer *et al.* 1981 and Huisman 2000, both now out-of-print, the broader marine publication of Edgar 2008 and the regional Coffin Bay field guide of Saunders 2009 in which algae form a small section). More recently on-line resources such as Algaebase (Guiry & Guiry 2018), FloraBase (Western Australian Herbarium 1998–), and the eFlora of South Australia, including 'Algae Revealed' (Baldock 2005–) have become available. The last aims to make information from the wealth of material arising from the Womersley era more accessible to the public, without compromising its accuracy or prime use in research. Each of these resources aims to provide an entry point to the often difficult process of seaweed identification and, perhaps as importantly, hopes to raise the public perception of seaweeds from the rotting, smelly drift on the beach to that of attractive, ecologically valuable plants. The incorporation of seaweeds into the Australian diet has also flourished, although primarily through Asian cuisine and using non-Australian species, but the potential for increased use of Australian produce is clear, especially given the vast range of available species (Tinellis 2015). In addition, the introduction and spread of invasive pest species such as *Undaria pinnatifida*, *Caulerpa taxifolia*, and *Codium fragile* subsp. *fragile* has raised awareness of the ecological importance of seaweeds in the marine environment.

Given this increased awareness and on-line profile, the opportunities for citizen-based science are many. Distribution records, whether based on specimens or verifiable sightings, can be contributed for recognizable species. Potential indicator species, such as *Durvillaea potatorum* (Labill.) Aresch., *Ecklonia radiata* (C.Agardh) J.Agardh, and *Hormosira banksii* (Turner) Decne. (Fig. 4) could be monitored at sensitive sites and range extremities, the information then uploaded to the 'Atlas of Living Australia' (ALA 2018).

However promising these alternative avenues for phycological research might be, it would be unrealistic to expect that they might replace traditional institution-based research. As with all fields of scientific study, validation of information, education and mentoring are vitally important if Australia's taxonomic capacity is to be maintained. At present, with few taxonomic phycologists in secure employment in Australia, the future is looking particularly bleak. Herbaria as depositories of specimens should at least remain as storehouses of priceless biological information for future and essential pure research in less economically stringent times.

References

Agardh, J.G. (1897). Analecta algologica. Continuatio IV. *Lunds Universitets Års-Skrift, Andra Afdelningen, Kongl. Fysiografiska Sällskapets i Lund Handlingar* 33: 1–106, plates 1–2.

Agardh, J.G. (1901). *Species genera et ordines algarum*, Vol. 3, Part 4. (C.W.K. Gleerup: Lund).

Anonymous (1869). *Memoir of W.H. Harvey, M.D., F.R.S., etc., etc. Late professor of Botany, Trinity College, Dublin. With selections from his journal and correspondence*. (Bell & Daldy: London).

Atlas of Living Australia [ALA] (2018). (CSIRO: Canberra). http://www.ala.org.au. [accessed: 17 October 2018].

AVH (2018). *The Australasian Virtual Herbarium* (Council of Heads of Australasian Herbaria). http://avh.chah.org.au [accessed: 17 October 2018].

Baldock, R.N. (2005–). Algae Revealed. In: *eFloraSA: Electronic Flora of South Australia*. (State Herbarium of South Australian: Adelaide). http://flora.sa.gov.au/algae_revealed/index.shtml [accessed: 1 Aug. 2017].

Baldock, R.N. & Womersley, H.B.S. (2005). Marine benthic algae of the Althorpe Islands, South Australia. *Transactions of the Royal Society of South Australia* 129: 116–127.

Baker, J.L. & Gurgel, C.F.D. (2011). *Biodiversity and conservation of macroalgae in the Adelaide and Mount Lofty Ranges NRM Region, including an assessment of biodiversity and distribution of macroalgae in the Gulf St Vincent Region*. Report to Adelaide & Mt Lofty Ranges Natural Resources Management Board. (Adelaide & Mt Lofty Ranges Natural Resources Management Board: Adelaide). http://www.naturalresources.sa.gov.au/files/sharedassets/adelaide_and_mt_lofty_ranges/coast_and_marine/macroalgae-rep.pdf

Belton, G.S., Prud'homme van Reine, W.F., Huisman, J.M., Draisma, S.G.A. & Gurgel, C.F.D. (2014). Resolving phenotypic plasticity and species designation in the morphologically challenging *Caulerpa racemosa–peltata* complex (Chlorophyta, Caulerpaceae). *Journal of Phycology* 50: 32–54.

Cowan, R.A. & Ducker, S.C. (2007). A history of systematic phycology in Australia. In: McCarthy, P.M. & Orchard, A.E. (eds), *Algae of Australia: Introduction*, pp. 1–65. (Australian Biological Resources Study & CSIRO Publishing: Canberra & Melbourne).

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

De Clerck, O., Guiry, M.D., Leliaert, F., Samyn, Y. & Verbruggen, H. (2013). Algal taxonomy: A road to nowhere? *Journal of Phycology* 49: 215–225.

Dixon, R.R.M., Huisman, J.M., Buchanan, J., Gurgel, C.F. & Spencer, P. (2012). A morphological and molecular study of austral *Sargassum* (Fucales, Phaeophyceae) supports the recognition of *Phyllotricha* at genus level, with further additions to the genus *Sargassopsis*. *Journal of Phycology* 48: 1119–1129.

Dixon, R.R.M., Mattio, L., Huisman, J.M., Payri, C.E., Bolton, J.J. & Gurgel, C.F. (2014). North meets south - Taxonomic and biogeographic implications of a phylogenetic assessment of *Sargassum* subgenera *Arthrophycus* and *Bactrophycus*. *Phycologia* 53: 15–22.

Ducker, S.C. (1979). History of Australian phycology: The significance of early French explorations. *Brunonia* 2: 19–42.

Ducker, S.C. (1981a). Australian phycology: The German influence. In: Carr, D.J. & Carr, S.G.M. (eds), *People and plants in Australia*, pp. 116–138. (Academic Press: Sydney).

Ducker, S.C. (1981b). History of Australian phycology: Early German collectors and botanists. In: Wheeler, A. & Price, J.H. (eds), *History in the service of systematics*, pp. 43–51. (Society for the Bibliography of Natural History: London). [*Special Publication* no. 1].

Ducker, S.C. (1981c). A history of Australian marine phycology. In: Clayton, M.N. & King, R.J. (eds), *Marine botany: an Australasian perspective*, pp. 1–14. (Longman Cheshire: Melbourne).

Ducker, S.C. (1988). *The contented botanist: letters of W.H. Harvey about Australia and the Pacific*. (Melbourne University Press: Melbourne).

Edgar, G.J. (2008). *Australian marine life: The plants and animals of temperate waters*. (Reed New Holland: Sydney).

Fuhrer, B., Christianson, I.G., Clayton, M.N. & Allender, B.M. (1981). *Seaweeds of Australia*. (Reed: Sydney).

Guerin, G.R. (2013). The value of herbaria to diverse collections-based research. *Australasian Systematic Botany Society Newsletter* 157: 43–44.

Guiry, M.D. & Guiry, G.M. (2018). *AlgaeBase*. World-wide electronic publication. (National University of Ireland: Galway). http://www.algaebase.org [accessed: 17 October 2018].

Harvey, W.H. (1858). *Phycologia Australica*, Vol. 1. (Lovell Reeve & Co.: London).

Harvey, W.H. (1859). *Phycologia Australica*, Vol. 2. (Lovell Reeve & Co.: London).

Harvey, W.H. (1860). *Phycologia Australica*, Vol. 3. (Lovell Reeve & Co.: London).

Harvey, W.H. (1862). *Phycologia Australica*, Vol. 4. (Lovell Reeve & Co.: London).

Harvey, W.H. (1863). *Phycologia Australica*, Vol. 5. (Lovell Reeve & Co.: London).

Hommersand, M.H. (2007). Global biogeography and relationships of the Australian marine macroalgae. In: McCarthy, P.M. & Orchard A.E. (eds), *Algae of Australia: Introduction*, pp. 511–542. (Australian Biological Resources Study & CSIRO Publishing: Canberra & Melbourne).

Huisman, J.M. (2000). *Marine Plants of Australia*. (University of Western Australia Press: Perth).

Huisman, J.M., Boo, G.H., Boo, S.M. & Lin, S.-M. (2018). Galaxauraceae. In: Huisman, J.M., *Algae of Australia: Marine benthic algae of north-western Australia, 2. Red Algae*, pp. 30-49. (Australian Biological Resources Study & CSIRO Publishing: Canberra & Melbourne).

Huisman, J.M., Harper, J.T. & Saunders, G.W. (2004). Phylogenetic study of the Nemaliales (Rhodophyta) based on large-subunit ribosomal DNA sequences supports segregation of the Scinaiaceae fam. nov. and resurrection of *Dichotomaria* Lamarck. *Phycological Research* 52: 224–234.

Huisman, J.M. & Kraft, G.T. (1994). Studies of the Liagoraceae (Rhodophyta) of Western Australia: *Gloiotrichus fractalis* gen. et sp. nov. and *Ganonema helminthaxis* sp. nov. *European Journal of Phycology* 29: 73–85.

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

Huisman, J.M. & Womersley, H.B.S. (1992). Cystocarp development in the red alga *Nothogenia fastigiata* (Galaxauraceae, Rhodophyta). *Phycologia* 31: 359–364.

Huisman, J.M. & Womersley, H.B.S. (1994). Family Galaxauraceae Parkinson. In: Womersley, H.B.S., *The marine benthic flora of southern Australia* IIIA: 99–118. (Australian Biological Resources Study: Canberra).

Huisman, J.M. & Womersley, H.B.S. (2006). *Nothogenia*. In: Huisman, J.M., *Algae of Australia: Nemaliales*, pp. 91–93. (Australian Biological Resources Study & CSIRO Publishing: Canberra & Melbourne).

Kerswell, A.P. (2006). Global biodiversity patterns of benthic marine algae. *Ecology* 87: 2479–2488.

Kraft, G.T. (2011). In Memoriam: Tribute to Professor Hugh Bryan Spencer Womersley (19 November 1922–16 January 2011). *Phycologia* 50: 439–441.

Kurihara, A. & Huisman, J.M. (2006). The *Dichotomaria marginata* assemblage in Australia. In: Huisman, J.M., *Algae of Australia: Nemaliales*, pp. 120–122, 134–136. (Australian Biological Resources Study & CSIRO Publishing: Canberra & Melbourne).

Le Gall, L. & Saunders, G.W. (2010). Establishment of a DNA-barcode library for the Nemaliales (Rhodophyta) from Canada and France uncovers overlooked diversity in the species *Nemalion helminthoides* (Velley) Batters. *Cryptogamie Algologie* 31: 403–421.

Lin, S.-M., Rodríguez-Prieto, C., Huisman, J.M., Guiry, M.D., Payri, C., Nelson, W.A. & Liu, S.-L. (2015). A phylogenetic re-appraisal of the family Liagoraceae *sensu lato* (Nemaliales, Rhodophyta) based on sequence analyses of two plastid genes and post-fertilization development. *Journal of Phycology* 51: 546–559.

Lindstrom, S.C., Gabrielson, P.W., Hughey, J.R., Macaya, E.C. & Nelson, W.A. (2015). Sequencing of historic and modern specimens reveals cryptic diversity in *Nothogenia* (Scinaiaceae, Rhodophyta). *Phycologia* 54: 97–108.

Lucas, A.H.S. (1936). *The seaweeds of South Australia*, Part I. *Introduction and the green and brown seaweeds*. (Government Printer: Adelaide).

Lucas, A.H.S. & Perrin, F. (1947). *The seaweeds of South Australia*, Part II. *The red seaweeds*. (Government Printer: Adelaide).

Phillips, J.A. (2001). Marine macroalgal biodiversity hotspots: why is there high species richness and endemism in southern Australian marine benthic flora? *Biodiversity and Conservation* 10: 1555–1577.

Reinbold, T. (1897). Die Algen der Lacepede und Guichen Bay und deren näherer Umgebung (Süd Australien), gesammelt von Dr. A. Engelhart-Kingston. *Nuova Notarisia* 8: 41–62.

Reinbold, T. (1898). Die Algen der Lacepede und Guichen Bay (Süd Australien) und deren näherer Umgebung, gesammelt von Dr. A. Engelhart-Kingston. II. *Nuova Notarisia* 9: 33–54.

Reinbold, T. (1899). Meeresalgen von Investigator Street (Süd-Australien), gesammelt von Miss Nellie Davey (Waltham, Honiton). *Hedwigia* 38: 39–51.

Saunders, B. (2009). *Shores and shallows of Coffin Bay: An identification guide*. (Eyre Peninsula Natural Resources Management Board: Coffin Bay).

Schmidt, W.E., Gurgel, C.F.D. & Fredericq, S. (2016). Taxonomic transfer of the red algal genus *Gloiosaccion* to *Chrysymenia* (Rhodymeniaceae, Rhodymeniales), including the description of a new species, *Chrysymenia pseudoventricosa*, for the Gulf of Mexico. *Phytotaxa* 243(1): 54–70.

Shepherd, S.A. (2016). *Paradise is under water: Memoir of a marine biologist*. (Zeus Publications: Burleigh).

Sonder, O.G. (1853). Plantae Muellerianae. Algae. *Linnaea* 25: 657–703.

Sun, Z., Hanyuda, T., Lim, P.-E., Tanaka, J., Gurgel, C.F.D. & Kawai, H. (2012). Taxonomic revision of the genus *Lobophora* (Dictyotales, Phaeophyceae) based on morphological evidence and analyses [of] *rbc*L and *cox3* gene sequences. *Phycologia* 51: 500–512.

Tinellis, C. (2015). *Coastal chef*. (Harbour Publishing House: Ulladulla).

Waters, J.M., Wernberg, T., Connell, S.D., Thomsen, M.S., Zuccarello, G.C., Kraft, G.T., Sanderson, J.C., West, J.A. & Gurgel, C.F.D. (2010). Australia's marine bioregions revisited: back to the future? *Austral Ecology* 35: 988–992.

Western Australian Herbarium (1998–). *FloraBase—the Western Australian Flora*. (Department of Parks and Wildlife: Perth). https://florabase.dpaw.wa.gov.au/ [accessed: 22 June 2016].

Wiltshire, K., Rowling, K. & Deveney, M. (2010). *Introduced marine species in South Australia: a review of records and distribution mapping*. (South Australian Research and Development Institute, Aquatic Sciences: Adelaide). [*SARDI Publication* No. F2010/000305-1; *SARDI Research Report Series* No. 468]. http://pir.sa.gov.au/__data/assets/pdf_file/0003/232068/No_468_Introduced_marine_species_in_South_Australia_a_review_of_records_and_distribution_mapping.pdf

Womersley, H.B.S. (1984). *The marine benthic flora of southern Australia*, Part I. *Introduction; Seagrasses; Chlorophyta and Charophyta*. (South Australian Government Printing Division: Adelaide).

Womersley, H.B.S. (1987). *The marine benthic flora of southern Australia*, Part II. *Phaeophyta and Chrysophyta (Vaucheria)*. (South Australian Government Printing Division: Adelaide).

Womersley, H.B.S. (1994). *The marine benthic flora of southern Australia*, Part IIIA. *Rhodophyta: Bangiophyceae and Florideophyceae (Acrochaetiales, Nemaliales, Gelidiales, Hildenbrandiales and Gigartinales (sensu lato)*. (Australian Biological Resources Study: Canberra). [*Flora of Australia Supplementary Series* 1].

Womersley, H.B.S. (1996). *The marine benthic flora of southern Australia*, Part IIIB. *Rhodophyta: Gracilariales, Rhodymeniales, Corallinales and Bonnemaisoniales*. (Australian Biological Resources Study: Canberra). [*Flora of Australia Supplementary Series* 5].

Womersley, H.B.S. (1998). *The marine benthic flora of southern Australia*, Part IIIC. *Rhodophyta: Ceramiales – Ceramiaceae, Dasyaceae*. (State Herbarium of South Australia: Adelaide).

Womersley, H.B.S. (2003). *The marine benthic flora of southern Australia*, Part IIID. *Rhodophyta: Ceramiales – Delessariaceae, Sarcomeniaceae, Rhodomelaceae*. (Australian Biological Resources Study & State Herbarium of South Australia: Canberra & Adelaide). [*Flora of Australia Supplementary Series* 18].

Womersley, H.B.S. & Baldock, R.N. (2003). The Encounter 2002 Expedition to the Isles of St. Francis, South Australia: marine benthic algae. *Transactions of the Royal Society of South Australia* 127: 141–151.

Womersley, H.B.S. & Wollaston, E.M. (1998). Tribe Pterothamnieae Athanasiadis 1996: 44. In: Womersley, H.B.S., *The marine benthic flora of southern Australia* IIIC: 132–156. (State Herbarium of South Australia: Adelaide).

Wynne, M.J. (2005). *Scinaia acuta*, a new name proposed for *Scinaia australis* (Rhodophyta). *Contributions from the University of Michigan Herbarium* 24: 227 –228.