Review

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From Tasmania to the world: long and strong traditions in seaweed use, research, and development

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Abstract: Tasmania is an island state in south-eastern Australia that has a long and rich history of seaweed use, research, and development. It is a cool-temperate system with 750 macroalgal species currently described. Tasmanian Aboriginal peoples have lived on this land for at least 40,000 years utilising seaweed as food, shelter, water carriers and medicine, as well as for ceremonial reasons. Modern taxonomic investigations began with French naturalist Jacques-Julien Houtou de La Billardière in 1791, and there are 184 type specimens of seaweeds originating from Tasmania. Ecological and physiological studies of seaweed in Tasmania have focussed on the dominant large brown seaweeds (Laminariales and Fucales) and have contributed significantly to the global understanding of these systems, particularly related to community resilience, seaweed-urchin interactions, their habitat-forming role for other species, responses to global change, and restoration of lost habitat. Ocean warming and changing oceanography have caused a 95% decline in surface canopy cover of *Macrocystis pyrifera* in eastern Tasmania since the 1950s and led to a focus on restoring these lost forests. Tasmanian seaweed communities have a uniquely high proportion (up to ~90%) of seaweeds that rely solely on CO_2 for photosynthesis, which has implications for responses to ocean acidification. Tasmania has industries that use brown seaweeds for fucoidan extraction and beach-cast harvest for alginates, fertilisers, and feeds for agriculture. New aquaculture initiatives include integrated multi-trophic aquaculture, offshore kelp mariculture and *Asparagopsis* cultivation for bioactive products to reduce methane emissions in ruminants, as and the development of unexploited species including *Caulerpa* spp. for food.

Keywords: aquaculture; ecology; ocean global change; physiology; seaweeds; taxonomy.

1 Introduction

Tasmania is an island state (68,400 km^2) in south-eastern Australia, characterised as a cool temperate region with relatively oligotrophic waters (Thompson et al. 2009, see Figure 1 which indicates key oceanic currents around Tasmania and the locations referred to in the text). It has a diverse seaweed (marine macroalgae) flora, and a strong history of seaweed use, research, and development. This review synthesises current knowledge and understanding of the unique contributions that Tasmania has made to global seaweed research, identifies knowledge gaps that may impede research progress, and proposes future research directions. The review is split into six sections, in which we chronicle seaweed use and research in Tasmania: 1. Tasmanian Aboriginal peoples' use of seaweed, 2. Systematics and biogeography, 3. Ecology, 4. Physiology, 5. Anthropogenic impacts, and 6. Applications and industry. We focus on published literature but acknowledge that there are numerous commissioned reports and theses, many of which

we list in an appendix to illustrate how Tasmanian research has contributed to the global body of knowledge on seaweeds.

2 Tasmanian Aboriginal peoples' use of seaweed

Aboriginal peoples have lived in Australia for at least 70,000 years, with oral histories that document the rise and fall of sea levels, including the opening of the Bass Strait that currently separates Tasmania from mainland Australia ~14,000 years ago (Lambeck and Chappell 2001), and the formation of the current Great Barrier Reef which is 6000–8000 years old (Nunn and Reid 2016). Across temperate southern Australia, seaweeds played an important role in Indigenous Australian culture and tradition and continue to do so today (reviewed by Thurstan et al. 2018). Seaweed is mentioned in the mythology of some groups (Clarke 1995). Archival records of seaweed use by Indigenous Australians
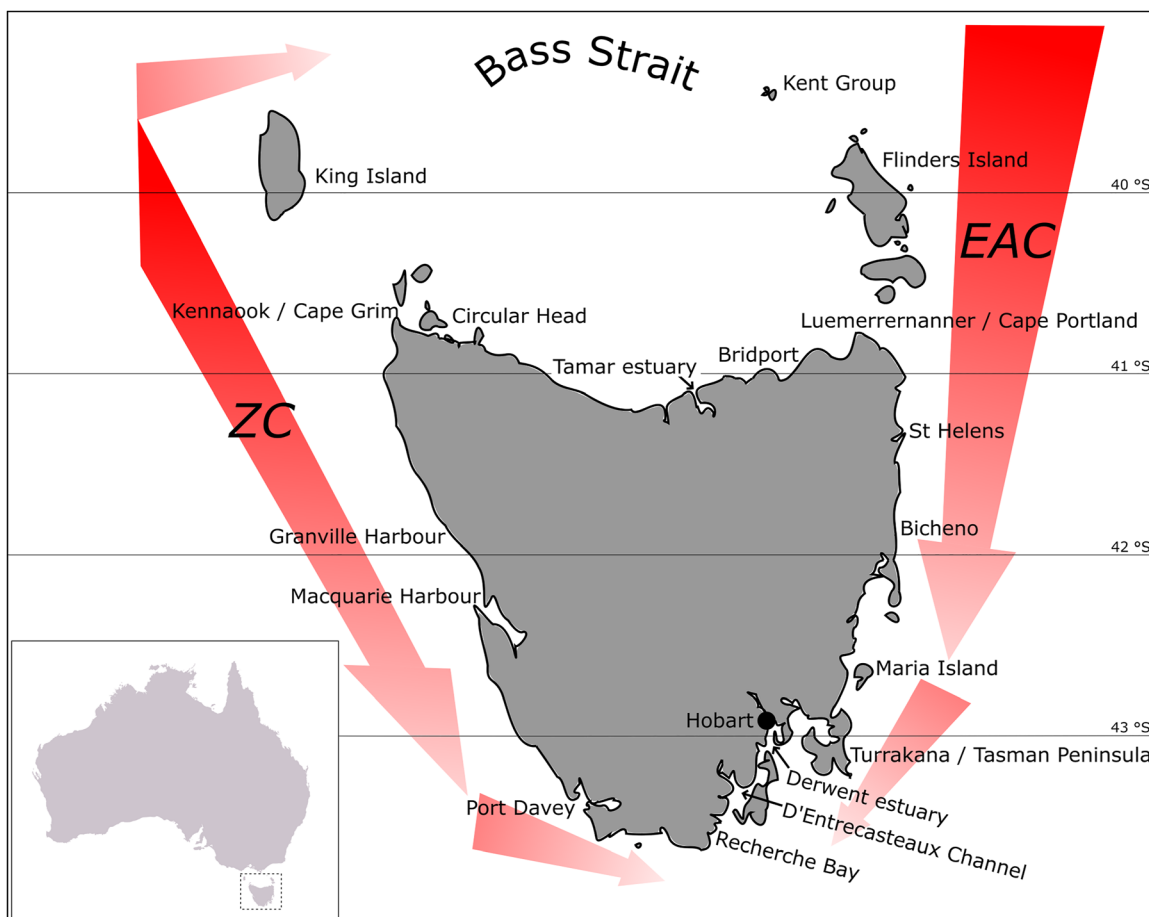

Figure 1: Map of Tasmania with regional oceanographic currents, and locations referred to in the text and Table 1, including the East Australian Current (EAC) and Zeehan Current (ZC).

(Thurstan et al. 2018 and sources therein) include ceremonial and medicinal practices (e.g. of red seaweeds, kelps), and uses as clothing (e.g. shoes made from *Durvillaea* spp.), food (e.g. *Durvillaea* spp., *Chaetomorpha coliformis*, *Cystophora* spp., *Hormosira banksii*, *Porphyra/Pyropia* spp., *Ulva* spp.), shelter (e.g. *Durvillaea* spp.), and as domestic devices such as water carriers. Indeed, the specific name of *Durvillaea potatorum* means 'potable' or 'container of water', and the species was described by the French naturalist Jacques-Julien La Billardière after he observed Indigenous Tasmanians carrying food and water using containers made from the seaweed in the late 18th century (Gough 2018).

In Tasmania, the destruction of Aboriginal peoples, and their knowledge and understanding, during European colonisation was particularly systematic and extensive (Ryan 2012). Nevertheless, much cultural knowledge and practice has been maintained by Tasmanian Aboriginal groups. This includes the use of *Durvillaea* spp. in making water carriers (Gough 2018; Thurstan et al. 2018) and contemporary artistic practices (e.g. sculpting and painting), and also 'shell-stringing' by Aboriginal women, which is the making of culturally significant necklaces using maireener shells (Gastropoda, *Phasianotrochus* spp.) that are collected from seaweeds and seagrasses (Cameron 2006; NMA 2020). Some Indigenous Tasmanian language names have also been retained and include *reigoua* or *regaa* (South East Nation) for *Durvillaea* spp., and also *myerlee* (Oyster Bay Nation) for seaweed in general (Aunty Patsy Cameron pers. comm). Kelp forests and other seaweed dominated ecosystems also acted as rich larders for Tasmanian Aboriginals, and women divers would collect abalone (*Haliotis* spp.), periwinkles (*Lunella undulata*) and crayfish (*Jasus edwardsii*).

3 Systematics and biogeography

3.1 Seaweed diversity

Tasmania has a rich marine-algal flora that includes some of the earliest-named seaweeds in Australia. A search of AlgaeBase (Guiry and Guiry 2022) revealed ~750 species of green, brown and red seaweeds recorded from Tasmania. Womersley (1990, 2004; Wright et al. 2022) documents 1137–1155 species for the whole of southern Australia, from the Perth region to southern New South Wales and around Tasmania, meaning that 65% of that total is reported from Tasmania. The order Fucales, which originated in the Australian region has a particularly high diversity, but they are understudied in terms of their physiology and ecological roles (Coleman and Wernberg 2017). In contrast there are very few members of the order Laminariales (*Ecklonia radiata*, *Lessonia corrugata*, *Macrocystis pyrifera*, and the invasive *Undaria pinnatifida*) but these are comparatively well studied. Of particular interest are the 184 species and 18 genera based on type specimens from Tasmania, of which 11 genera and 22 species are endemic. Table 1 catalogues the type specimens that are the focus of this section which synthesises how our knowledge of the Tasmanian macroalgal flora has evolved since the first taxonomic collections in 1791.

The Tasmanian Herbarium (HO, Tasmanian Museum and Art Gallery) holds some 16,000 specimens of algae including micro- and macroalgae sourced from terrestrial, freshwater, and marine habitats. Approximately 80% of these now have a digital record that is accessible through the Australasian Virtual Herbarium (AVH 2022). Of the algal specimens archived at HO, 8835 (~55%) are Tasmanian; the remainder were sourced from (other) Australian and global localities. There is a strong history of renowned algal collectors who contributed to the HO archives. Of the early collectors, R.C. Gunn (1840s) archived 80 specimens, W.H. Harvey (1850s) 2, L.A. Meredith (1870s) 92, A.H.S. Lucas and F. Perrin (1920s–1930s) 3867, and H.B.S. Womersley (1940s–1990s) 667. With the advent of SCUBA, further noteworthy contributions were made by S.A. Shepherd (1970s) 142, J.C. Sanderson (1980s) 303, G.J. Edgar (1980s–1990s) 92, N.S. Barrett (1990s) 46, G.T. Kraft (1980s–2022) 2068, and F.J. Scott (1980s–2022) 4655. Here we highlight significant explorers and taxonomists who have contributed to our understanding of the Tasmanian flora, whose archived material will assist future research using molecularly assisted alpha taxonomy (MAAT).

The earliest taxonomic samples in Tasmania were collected by French naturalist Jacques-Julien Houtou de La Billardière, a member of the D'Entrecasteaux expedition of 1791–1794. From April to May 1792 one of its ships anchored in Recherche Bay, and La Billardière became the first person to collect and later (1807) publish on the specimens that he took to Europe. The next collector was Robert Brown, a botanist aboard Matthew Flinders' ship H.M.S. *Investigator* that stopped at the Kent Islands, Bass Strait. He collected species of green (two *Caulerpa* spp.), brown (including *Xiphophora*, *Sargassum* and *Cystophora*), and red (including *Callophyllis*, *Hymenocladia* and *Laurencia*) seaweeds that all appeared as *Fucus* in Turner's 1811 four volumes titled "Fuci" (Turner 1808, 1809, 1811, 1819). Large and common brown seaweeds featured prominently in most of the earliest Tasmanian collections. Irish botanist William H. Harvey, a leading seaweed taxonomist of the 19th century, named many Australian, including Tasmanian, seaweeds. In the 20th century, H.B.S. Womersley made a major contribution to knowledge of the Australian flora, producing six volumes of The Marine Benthic Flora of Southern Australia, Parts I

Table 1: Macroalgal taxa based on type material collected in Tasmania.

#	Original name	Author	Type locality	Collector	Current name	Remarks
	I. Green algae					
1	Conferva coliformis	Montagne	Tasmania		Chaetomorpha coliformis (Mont.) Kützing	
2	Chaetomorpha billardierii	Kützing	Southern Tasmania		Chaetomorpha billardierii Kützing	
3	Conferva valida	Hooker et Harvey	Georgetown, Tamar estuary	Gunn	Chaetomorpha valida (Hooker et Harvey) Kützing	
4	Cladophora feredayi	Harvey	Georgetown, Tamar estuary	Harvey	Lychaete feredayi (Harvey) M.J. Wynne	
5	Codium perriniae	Lucas	Low Head, Tamar estuary	Lucas	Codium perriniae Lucas	One of the first Tasmanian species named by an Australian
6	Caulerpa selago var. brownii	C. Agardh	Kent Group of Islands, Bass Strait	R. Brown	Caulerpa brownii (C. Agardh) Endlicher	
7	Caulerpa sedoides	Harvey	Kent Group of Islands, Bass Strait	R. Brown	Caulerpa sedoides Harvey	
8	Caulerpa annulata	Lucas (nom. illeg.)	Port Arthur, Tasman Peninsula	Perrin et Lucas	Caulerpa lucasii Prud'homme, Draisma et Belton	
9	Fucus simpliciuscula	R. Brown ex Turner	Kent Group of Islands, Bass Strait	R. Brown	Caulerpa simpliciuscula (R. Br. ex Turner) C. Agardh	One of the first Tasmanian algae named
	II. Brown algae					
10	Cladophora ferruginea	Harvey	Safety Cove, Port Arthur, Tasman Peninsula	Harvey	Asteronema ferrugineum (Harvey) Delépine et Asensi	On Hormosira banksii; easy to mistake for a Cladophora when non-reproductive
11	Ectocarpus sordidus	Harvey	Georgetown, Tamar estuary	Probably Harvey	Hincksia sordida (Harvey) P.C. Silva	
12	Liebmannia harveyana	J. Agardh	Georgetown, Tamar estuary	Harvey	Suringariella harveyana (J. Agardh) Womersley et Bailey	The generitype species
13	Mesogloiopsis tasmanica	Womersley et Bailey	Eaglehawk Neck, Tasman Peninsula	Gordon	Mesogloiopsis tasmaica Womersley et Bailey	A Tasmanian endemic genus and species
14	Liebmannia australis	Harvey	Georgetown, Tamar estuary	Probably Harvey	Tinocladia australis (Harvey) Kylin	
15	Sphacelaria reinkei	Sauvageau	Georgetown, Tamar estuary		Sphacelaria reinkei Sauvageau	
16	Dictyota diemensis	Kützing	Georgetown, Tamar estuary	Harvey	Dictyota diemensis Kützing	
	Dictyota nigricans	J. Agardh	Orford, mid-east coast	Meredith	Dictyota nigricans J. Agardh	Until recently known as Glossophora nigricans (J. Agardh) Womersley; Womersley (1987) says the authority is (J. Ag.) Womersley
17	Haliseris acrostichoides	J. Agardh	Tasmania	Gunn	Dicyopteris acrostichoides (J. Agardh) Bornet (fide AlgaeBase)	
18	Stylophora(?) australis	Harvey	Georgetown, Tamar estuary	Gunn	Austronereia australis (Harvey) Womersley	The type species of the genus
19	Sporochnus apodus	Harvey	Georgetown, Tamar estuary	Harvey	Sporochnus apodus Harvey	
20	Fucus caudatus	Labillardière	Southeast Tasmania		Perithalia caudata (Labillardière) Womersley	Generitype species (as the synonymous Perithalia inermis (Turner) J. Agardh
21	Lessonia corrugata	Lucas	Port Arthur, Tasman Peninsula	Lucas	Lessonia corrugata Lucas	Endemic species
22	Fucus potatorum	Labillardière	Recherche Bay	Labillardière	Durvillaea potatorum (Labillardière) Areschoug	"Bull Kelp", one of the earliest discovered and named Australian algae

Table 1: (continued)

#	Original name	Author	Type locality	Collector	Current name	Remarks
23	*Durvillaea amatheiae*	Weber, Edgar, Banks, Waters *et* Fraser	Sisters Bay, D'Entrecasteaux Channel	Burridge	*Durvillaea amatheiae* Weber, Edgar, Banks, Waters *et* Fraser	Most recent addition to the brown flora
24	*Fucus gladiatus*	Labillardière	Recherche Bay	Labillardière	*Xiphophora gladiata* (Labilliardière) Montagne ex Kjellman	Generitype (as the synonymous *X. bill-ardierei* Montagne)
25	*Fucus chondrophyllus*	R. Brown *ex* Turner	Port Dalrymple, Tamar estuary	R. Brown	*Xiphophora chondrophylla* (R. Br. ex Turn.) Montagne ex Harvey	
26	*Fucus comosus*	Labillardière	Recherche Bay	Labillardière	*Phyllospora comosa* (Labilliardière) C. Agardh	Known as "cray-weed," one of the dominant large browns
27	*Fucus axillaris*	R. Brown *ex* Turner	Tamar estuary		*Seirococcus axillaris* (R. Brown ex Turner) Greville	Among the earliest Australian marine algae named
28	*Fucus cephalornithos*	Labillardière	Recherche Bay	Labillardière	*Caulocystis cephalornithos* (Labilliardière) Areschoug	Name means "bird-headed"
29	*Fucus paniculatus*	Turner	Kent Group of Islands, Bass Strait	R. Brown	*Acrocarpia paniculata* (Turner) Areschoug	Another of Tasmania's large browns
30	*Cystophora xiphocarpa*	Harvey	Port Arthur, Tasman Peninsula	Harvey	*Cystophora xiphocarpa* Harvey	Endemic species with distinctive morphology
31	*Fucus torulosus*	R. Brown *ex* Turner	Kent Group of Islands, Bass Strait	R. Brown	*Cystophora torulosa* (R. Brown ex Turner) J. Agardh	
32	*Fucus retroflexus*	Labillardière	Recherche Bay	Labilliardière	*Cystophora retroflexa* (Labilliardière) J. Agardh	
33	*Fucus subfarcinatus*	Mertens	Tasmania		*Cystophora subfarcinatus* (Mertens) J. Agardh	Most common *Cystophora* in southern Australia
34	*Fucus confluens*	R. Brown *ex* Turner	Port Dalrymple, Tamar estuary	R. Brown	*Carpoglossum confluens* (R. Brown ex Turner) Kützing	
35	*Myriodesma integrifolium*	Harvey	Georgetown, Tamar estuary	Harvey	*Myriodesma integrifolium* Harvey	Deep-water species
36	*Sargassum heteromorphum*	J. Agardh	Georgetown, Tamar estuary	Gunn	*Sargassopsis heteromorphum* (J. Agardh) R. Dixon et Huisman	Mostly only vegetative basal parts collected
37	*Fucus paradoxus*	R. Brown *ex* Turner	Kent Group of Islands, Bass Strait	R. Brown	*Sargassum paradoxum* (R. Brown ex Turner) Hooker et Harvey	Biggest *Sargassum* in southern Australia
38	*Fucus vestitus*	R. Brown *ex* Turner	Kent Group of Islands, Bass Strait	R. Brown	*Sargassum vestitum* (R. Brown ex Turner) C. Agardh	
39	*Fucus lacerifolius*	Turner	Port Dalrymple, Tamar estuary mouth	R. Brown	*Sargassum lacerifolium* (Turner) C. Agardh	Most widely distributed *Sargassum* in southern Australia
			III. Red algae			
40	*Porphyra woolhouseae*	Harvey	Tasmania on *Macrocystis*		*Porphyra woolhousiae* Harvey	
41	*Ballia hirsuta*	Wollaston	Catamaran, Recherche Bay	Wollaston *et* Mitchell	*Camontagnea hirsuta* (Wollaston) Woelkerling *et* Womersley	
42	*Nemastoma ? densa*	Harvey	Georgetown, Tamar estuary	Gunn?	*Helminthocladia densa* (Harvey) Schmitz *et* Hauptfleisch	

Table 1: (continued)

#	Original name	Author	Type locality	Collector	Current name	Remarks
43	Sphaerococcus asper	C. Agardh	Recherche Bay	Labillardière	Gelidium asperum (C. Agardh) Greville	
44	Acropeltis phyllophora	Hooker et Harvey	Port Arthur, Tasman Peninsula	Jeannerett	Carpopeltis phyllophora (Hooker et Harvey) Schmitz	
45	Halymenia kraftii	Womersley et J. A. Lewis	Port Arthur, Tasman Peninsula		Halymenia kraftii Womersley et J. Lewis	
46	Grateloupia tasmanica	Womersley et J. A. Lewis	Taroona, D'Entrecasteaux Channel	Sanderson	Polyopes tasmanicus (Womersley et J. Lewis) Kawaguichi et J. Lewis	
47	Dasyphloea insignis	Montagne	"Probably Tasmania"		Dasyphloea insignis Montagne	
48	Kallymenia cribrogloea	Womersley et R. Norris	Bruny Island, D'Entrecasteaux Channel	Shepherd	Austrokallymenia cribrogloea (Womersley et R. Norris) Huisman et G.W. Saunders	
49	Kallymenia tasmanica	Harvey	Georgetown, Tamar estuary	Harvey?	Croisettea tasmanica (Harvey) Wynne	
50	Kallymenia polycoelioides	J. Agardh	Orford, mid-east coast	Meredith	Rhipidomenia polycoelioides (J. Agardh) G.W. Saunders	
51	Thamnophyllis lacerata	Womersley et R. Norris	Bruny Island, D'Entrecasteaux Channel	Shepherd	Stauromenia lacerata (Womersley et R. Norris) G.W. Saunders	
52	Callophyllis harveyana	J. Agardh	Orford, mid-east coast	Meredith	Austrophyllis harveyana (J. Agardh) Womersley et R. Norris	
53	Fucus rangiferinus	R. Brown ex Turner	Kent Group of Islands, Bass Strait	R. Brown	Callophyllis rangiferina (R Brown ex Turner) Womersley	Womersley says the type locality is Georgetown and Gunn, which AlgaeBase disputes
54	Ahnfeltiopsis fastigiata	J. Lewis et Womersley	Bridport	Gunn	Ahnfeltiopsis fastigiata J. Lewis et Womersley	A replacement name for the invalid Gymnogongrus fastigiatus Harvey
55	Nemastoma feredayae	Harvey	Georgetown, Tamar estuary	Fereday	Tsengia feredayae (Harvey) Womersley et Kraft	
56	Gigartina brachiata	Harvey	Georgetown, Tamar estuary	Harvey	Gigartina brachiata Harvey	
57	Gigartina recurva	Edyvane et Womersley	Bicheno	Womersley	Gigartina recurva Edyvane et Womersley	Endemic to the east coast. This species was long known as G. ancistroclada J. Agardh
58	Fucus concinnus	R. Brown ex Turner	Kent Group of Islands, Bass Strait	R. Brown	Trematocarpus concinnus (R. Brown ex Turner) De Toni	
59	Chrysymenia coccinea	Harvey	Georgetown, Tamar estuary	Gunn	Rhabdonia coccinea (Harvey) Hooker et Harvey	
60	Rhabdonia verticillata	Harvey	Georgetown, Tamar estuary	Harvey?	Rhabdonia verticillata Harvey	
61	Fucus congestus	Turner	Kent Group of Islands, Bass Strait	R. Brown	Areschougia congesta (Turner) J. Agardh	
62	Areschougia stuartii	Harvey	Southport, D'Entrecasteaux Channel	Stuart	Areschougia stuartii Harvey	
63	Rhabdonia nigrescens	Harvey in Hooker et Harvey	Georgetown, Tamar estuary	Gunn	Antrocentrum nigrescens (Harvey in Hooker et Harvey) Kraft et Min-Thein	One of many reds starting out life as the brown alga Fucus
64	Plocamium dilatatum	J. Agardh	Tasmania		Plocamium dilatatum J. Agardh	

Table 1: (continued)

#	Original name	Author	Type locality	Collector	Current name	Remarks
65	Plocamium leptophyllum	Kützing	Georgetown, Tamar estuary	Gunn	Plocamium leptophyllum Kützing	
66	Phacelocarpus complanatus	Harvey	Southport, D'Entrecasteaux Channel	Stuart	Phacelocarpus complanatus Harvey	One of the earliest Australian species named
67	Fucus pepercarpus	Poiret	Probably Recherche Bay	Probably Labillardière	Phacelocarpus pepercarpus (Poiret) Wynne, Ardré et Silva	
68	Hypnea planicaulis	Harvey	Georgetown, Tamar estuary	Harvey?	Calliblepharis planicaulis (Harvey) Kylin	
69	Halymenia membranacea	Harvey	Georgetown, Tamar estuary	Gunn	Rhodophyllis membranacea (Harvey) Hooker et Harvey	
70	Rhodophyllis multipartita	Harvey	Port Arthur, Tasman Peninsula	Harvey?	Rhodophyllis multipartita Harvey	
71	Mychodea carnosa	Hooker et Harvey	Georgetown, Tamar estuary	Gunn	Mychodea carnosa Hooker et Harvey	Type species of Australia's largest endemic algal genus
72	Mychodea membranacea	Hooker et Harvey	Georgetown, Tamar estuary	Gunn	Mychodea membranacea Hooker et Harvey	
73	Mychodea terminalis	Harvey	Georgetown, Tamar estuary	Gunn	Mychodea terminalis Harvey	
74	Mychodea pseudoacicular	G.W. Saunders et Kraft	Georgetown, Tamar estuary	G.W. Saunders et Dixon	Mychodea pseudoaciculare G.W. Saunders et Kraft	Endemic species, based on molecular evidence
75	Mychodea hamata	Harvey	Port Arthur, Tasman Peninsula	Harvey	Mychodea hamata Harvey	
76	Mychodea disticha	Harvey	Georgetown, Tamar estuary	Gunn	Mychodea disticha Harvey	
77	Acrothesaurum gemilliferum	Kraft et G.W. Saunders	Wynyard, northern Tasmania	G.W. Saunders et Dixon	Acrothesaurum gemilliferum Kraft et G.W. Saunders	Monotypic endemic genus and species
78	Ostiophyllum sonderopeltae	Kraft	Eaglehawk Neck, Tasman Peninsula	Kraft et Sanderson	Ostiophyllum sonderopeltae Kraft	Type species of monotypic genus
79	Entwisleia bella	Scott, G.W. Saunders et Kraft	Blackmans Bay, Derwent estuary	Scott et Mitchell	Entwisleia bella F.J. Scott, G.W. Saunders et Kraft	Type species of monotypic genus
80	Fucus obtusata	Labillardière	Recherche Bay	Labillardière	Melanthalia obtusata (Labillardière) J. Agardh	Early named, widespread red
81	Gloiosaccion brownii	Harvey	Georgetown, Tamar estuary	Harvey	Chrysymenia brownii (Harvey) De Toni	Generitype of the recently merged genus Gloiosaccion
82	Webervanbossea tasmanensis	Womersley	Ninepin Point, D'Entrecasteaux Channel	Thomas et Womersley	Webervanbossea tasmanensis Womersley	
83	Rhodymenia prolificans	Zanardini	Georgetown, Tamar estuary	Miss Goodwin	Rhodymenia prolificans Zanardini	Few of Zanardini's species are unchanged
84	Epymenia halymenioides	J. Agardh	Orford, mid-east coast	Meredith	Halopeltis cuneata (Harvey) G.W. Saunders	
85	Rhodymenia cuneata	Harvey	Eastern Tasmania	Gunn	Halopeltis cuneata (Harvey) G.W. Saunders	
86	Horea polycarpa	Harvey	Eastern Tasmania	Gunn	Gloiodadia polycarpa (Harvey) Womersley	
87	Fucus usneus	R. Brown ex Turner	Kent Group of Islands, Bass Strait	R. Brown	Hymenocladia usnea (R. Brown ex Turner) J. Agardh	Generitype of Hymenocladia

Table 1: (continued)

#	Original name	Author	Type locality	Collector	Current name	Remarks
88	*Champia insignis*	Lucas	Sandy Bay, Derwent estuary	Lucas	*Champia insignis* Lucas	Endemic species
89	*Chylocladia affinis*	Hooker et Harvey	Georgetown, Tamar estuary	Gunn	*Champia affinis* (Hooker et Harvey) J. Agardh	
90	*Mastophora canaliculata*	Harvey	Tasmania		*Mastophoropsis canaliculata* (Harvey) Woelkerling	Type species of monotypic genus
91	*Phymatolithon masonianum*	Wilks et Woelkerling	Ninepin point, D'Entrecasteaux channel	Kraft et Scott	*Phymatolithon masonianum* Wilks et Woelkerling	
92	*Pneophyllum submersiporum*	Penrose	Safety Cove, Port Arthur, Tasman Peninsula	Platt et Woelkerling	*Pneophyllum submersiporum* Penrose	
93	*Spongites tunicatus*	Penrose	Variety Bay, Bruny Island, D'Entrecasteaux channel	Woelkerling, Platt et Brown	*Spongites tunicatus* Penrose	
94	*Delisea hypneoides*	Harvey	Georgetown, Tamar estuary	Fereday	*Delisea hypneoides* Harvey	
95	*Delisea elegans*	Lamouroux	Probably southeast Tasmania		*Delisea elegans* Lamouroux	
96	*Fucus conferta*	R. Brown ex Turner	Kent Group of Islands, Bass Strait	R. Brown	*Leptophyllis conferta* (R. Brown ex Turner) J. Agardh	
97	*Ptilonia australasica*	Harvey	Georgetown, Tamar estuary	Harvey	*Ptilonia australasica* Harvey	
98	*Callithamnion comosum*	Harvey	Georgetown, Tamar estuary	Gunn	*Warrenia comosa* (Harvey) Harvey ex Schmitz et Hauptfleisch	
99	*Wrangelia plumosa*	Harvey	Georgetown, Tamar estuary	Gunn	*Wrangelia plumosa* Harvey	
100	*Wrangelia nobilis*	Hooker et Harvey	Georgetown, Tamar estuary	Gunn	*Wrangelia nobilis* Hooker et Harvey	
101	*Crouania brunyana*	Wollaston	Simpson Bay, Bruny Island, D'Entrecasteaux channel	Shepherd	*Crouania brunyana* Wollaston	Endemic species
102	*Crouania gracilis*	J. Agardh	Tasmania	Gunn	*Ptilocladia gracilis* (J. Agardh) Womersley	
103	*Dasya crouanioides*	Sonder	Tasmania	Stuart	*Ptilocladia crouanioides* (Sonder) Womersley	
104	*Bornetia? meredithiana*	J. Agardh	Orford, mid-east coast	Meredith	*Involucrana meredithiana* (J. Agardh) Baldock et Womersley	Type species of genus
105	*Wrangelia crassa*	Hooker et Harvey	Georgetown, Tamar estuary	Gunn	*Involucrana crassa* (Hooker et Harvey) Gordon	
106	*Wrangelia mucronata*	Harvey	Tasmania	Gunn	*Wollastoniella mucronata* (Harvey) Gordon	
107	*Antithamnion biarmatum*	Athanasiadis	Bicheno	Kraft	*Antithamnion biarmatum* Athanasiadis	
108	*Spyridia pellucida*	Harvey	Georgetown, Tamar estuary	Gunn	*Macrothamnion pellucidum* (Harvey) Wollaston	Generitype of *Macrothamnion*
109	*Macrothamnion pectenellum*	Wollaston	South Arm, Derwent estuary	Wollaston	*Macrothamnion pectenellum* Wollaston	
110	*Glandothamnus acicularis*	Wollaston	Taroona, Derwent estuary	Shepherd	*Pterothamnion acicularis* (Wollaston) Athanasiadis et Kraft	Endemic species
111	*Glandothamnus manifestus*	Wollaston	Satellite I., D'Entrecasteaux Channel	Shepherd	*Pterothamnion manifestum* (Wollaston) Athanasiadis et Kraft	Endemic species

Table 1: (continued)

#	Original name	Author	Type locality	Collector	Current name	Remarks
112	*Glandothamnus ramulentus*	Wollaston	Georgetown, Tamar estuary	Harvey	*Pterothamnion ramulentum* (Wollaston) Athanasiadis et Kraft	Type species of monotypic genus
113	*Callithamnion fastigiatum*	Harvey	Georgetown, Tamar estuary	Gunn	*Leptoklonion fastigiatum* (Harvey) Womersley	
114	*Callithamnion dispar*	Harvey	Eastern Tasmania	Gunn	*Elisiella dispar* (Harvey) Womersley	Type species of genus
115	*Tetrathamnion lineatum*	Wollaston	White Beach, Wedge Bay	Wollaston et Mitchell	*Tetrathamnion lineatum* Wollaston	
116	*Spermothamnion pinnatum*	Gordon	Southport	Wollaston et Mitchell	*Spermothamnion pinnatum* Gordon	
117	*Callithamnion violaceum*	Harvey	Georgetown, Tamar estuary	Harvey	*Callithamnion violaceum* Harvey	
118	*Callithamnion byssoides* var. *caulescens*	J. Agardh	Tasmania	Gunn	*Callithamnion caulescens* (J. Agardh) Womersley	
119	*Callithamnion angustatum*	Hooker et Harvey	Georgetown, Tamar estuary	Gunn	*Hirsutithallia angustata* (Hooker et Harvey) Wollaston et Womersley	
120	*Thamnocarpus gunnianus*	Harvey in W.J. Hooker	Port Arthur, Tasman Peninsula	Gunn	*Carpothamnion gunnianum* (Harvey) Kützing	Type species of monotypic genus
121	*Callithamnion latissimum*	Harvey	Georgetown, Tamar estuary	Gunn	*Dasythamniella latissima* (Harvey) Womersley	
122	*Corynospora arachnoidea*	Harvey	Georgetown, Tamar estuary	Gunn	*Mazoyerella arachoidea* (Harvey) Gordon-Mills et Womersley	Type species of genus
123	*Griffithsia gunniana*	J. Agardh	Georgetown, Tamar estuary	Gunn	*Griffithsia gunniana* J. Agardh	
124	*Griffithsia crinita*	Kützing	Tasmania	Gunn	*Anotrichium crinitum* (Kützing) Baldock	
125	*Callithamnion elongatum*	Harvey	Georgetown, Tamar estuary	Harvey	*Anotrichium elongatum* (Harvey) Baldock	
126	*Thamnocarpus ptilota*	Hooker et Harvey	Port Arthur, Tasman Peninsula	Jeannerett	*Diapse ptilota* (Hooker et Harvey) Kylin	Type species of monotypic genus
127	*Spyridia filamentosa* var. *tasmanica*	Kützing	Tasmania	Gunn	*Spyridia tasmanica* (Kützing) J. Agardh	
128	*Ceramium monacanthum*	J. Agardh	Georgetown, Tamar estuary	Gunn	*Ceramium monacanthum* J. Agardh	
129	*Ceramium excellens*	J. Agardh	Tamar River mouth	Oakden	*Ceramium excellens* J. Agardh	
130	*Trichoceras tasmanicum*	Kützing	Tasmania	Gunn	*Ceramium tasmanicum* (Kützing) Womersley	
131	*Dasya villosa*	Harvey	Georgetown, Tamar estuary	Gunn	*Dasya villosa* Harvey	
132	*Dasya ceramioides*	Harvey	Georgetown, Tamar estuary	Gunn	*Dasya ceramioides* Harvey	
133	*Dasya hapalathrix*	Harvey	Rapid Point, Tamar estuary	Harvey	*Dasya hapalathrix* Harvey	
134	*Dasya quadrispora*	Parsons et Womersley	Bridport	Womersley et Parsons	*Dasya quadrispora* Parsons et Womersley	
135	*Dasya naccarioides*	Harvey	Georgetown, Tamar estuary	Gunn	*Dasya naccarioides* Harvey	
136	*Dasya crescens*	Parsons et Womersley	Port Sorell, northern Tasmania	Womersley	*Dasya crescens* Parsons et Womersley	
137	*Dasya capillaris*	Hooker et Harvey in Harvey	Georgetown, Tamar estuary	Gunn	*Dasya capillaris* Hooker et Harvey in Harvey	

Table 1: (continued)

#	Original name	Author	Type locality	Collector	Current name	Remarks
138	*Polysiphonia gunniana*	Harvey	Georgetown, Tamar estuary	Gunn	*Heterosiphonia gunniana* (Harvey) Reinbold	
139	*Polysiphonia lawrenciana*	Harvey	Georgetown, Tamar estuary		*Heterosiphonia lawrenciana* (Harvey) Parsons	
140	*Delesseria frondosa*	Hooker et Harvey	Tasmania	Gunn	*Hemineura frondosa* (Hooker et Harvey) Harvey	Type species of *Hemineura*. Work by G.W. Saunders points to several species hidden in it.
141	*Delesseria spathulata*	Sonder	Georgetown, Tamar estuary	Harvey	*Apoglossum spathulatum* (Sonder) Womersley et Shepley	
142	*Delesseria similans*	J. Agardh	Georgetown, Tamar estuary	Harvey	*Halicnide similns* (J. Agardh) J. Agardh	Type species of monotypic genus
143	*Nitospinosa tasmanica*	Womersley	Arch Rock, Ninepin Point, D'Entrecasteaux Channel	Andrews	*Nitospinosa tasmanica* Womersley	
144	*Nitophyllum gunnianum*	Hooker et Harvey	Georgetown, Tamar estuary	Gunn	*Myriogramme gunniana* (Hooker et Harvey) Kylin	
145	*Schizoseris tasmanica*	S.M-Lin et Kraft	Ninepin Point, D'Entrecasteaux Channel	Kraft et Sanderson	*Schizoseris tasmanica* S.M-Lin et Kraft	Endemic species
146	*Nitophyllum perriniae*	Lucas	Georgetown, Tamar estuary	Perrin et Lucas	*Schizoseris perriniae* (Lucas) Womersley	Endemic species
147	*Nitophyllum hymenena*	Zanardini	Near Hobart	Hannaford	*Schizoseris hymenena* (Zanardini) Womersley	
148	*Aglaophyllum crispum*	Kützing	Georgetown, Tamar estuary	Gunn	*Nitophyllum crispum* (Kützing) J. Agardh	
149	*Nitophyllum affine*	Harvey	Georgetown, Tamar estuary	Gunn	*Hymenena affinis* (Harvey) Kylin	
150	*Nitophyllum multipartitum*	Hooker et Harvey	Georgetown, Tamar estuary	Gunn	*Hymenena multipartita* (Hooker et Harvey) Kylin	
151	*Delesseria endiviaefolia*	Hooker et Harvey	Georgetown, Tamar estuary	Gunn	*Hymenena endiviaefolia* (Hooker et Harvey) Womersley	
152	*Polysiphonia mollis*	Hooker et Harvey ex Harvey	Tasmania	Gunn	*Polysiphonia mollis* Hooker et Harvey ex Harvey	
153	*Polysiphonia perriniae*	Womersley	Low Head, Tamar estuary	Perrin	*Polysiphonia perriniae* Womersley	
154	*Polysiphonia succuleta*	Harvey	Georgetown, Tamar estuary	Gunn	*Polysiphonia succuleta* Harvey	
155	*Polysiphonia crassiuscula*	Harvey	Eastern Tasmania	Gunn	*Polysiphonia crassiuscula* Harvey	
156	*Polysiphonia abscissoides*	Womersley	Oyster Bay, Swansea	Skinner	*Polysiphonia abscissoides* Womersley	
157	*Polysiphonia adamsiae*	Womersley	Prosser Bay, Orford, mid-east coast	Shepherd	*Polysiphonia adamsiae* Womersley	
158	*Polysiphonia hystrix*	Hooker et Harvey	Georgetown, Tamar estuary	Gunn	*Echinothamnion hystrix* (Hooker et Harvey) Kylin	Type species of *Echinthamnion*
159	*Polysiphonia hookeri*	Harvey	Georgetown, Tamar estuary	Gunn	*Echinothamnion hookeri* (Harvey) Kylin ex Silva	
160	*Polysiphonia ericoides*	Harvey *in* Hooker et Harvey	"Tasmania"	Ewing	*Perrinia ericoides* (Harvey *in* Hooker et Harvey) Womersley	Type species of monotypic genus

Table 1: (continued)

#	Original name	Author	Type locality	Collector	Current name	Remarks
161	*Acanthophora tasmanica*	Sonder	Georgetown, Tamar estuary	Stuart	*Pityophycos tasmanica* (Sonder) Papenfuss	Type species of monotypic genus
162	*Acanthophora arborea*	Harvey	Georgetown, Tamar estuary	Harvey	*Chiracanthia arborea* (Harvey) Falkenberg *in* Schmitz *et* Falkenberg	Type species of *Chiracanthia*
163	*Dasya feredayae*	Harvey	Georgetown, Tamar estuary	Harvey	*Micropeuce feredayae* (Harvey) Kylin *ex* Silva	
164	*Dasya bolbochaete*	Harvey	Georgetown, Tamar estuary	Gunn	*Doxodasya bolbochaete* (Harvey) Falkenberg	Type species of *Doxodasya*
165	*Dasya verticillata*	Harvey	Georgetown, Tamar estuary	Gunn	*Lophothalia verticillata* (Harvey) Kützing	Type species of *Lophothalia*
166	*Polysiphonia versicolor*	Hooker *et* Harvey	Georgetown, Tamar estuary	Gunn	*Herposiphonia versicolor* (Hooker *et* Harvey) Reinbold	
167	*Polysiphonia monilifera*	Hooker *et* Harvey	Georgetown, Tamar estuary	Gunn	*Herposiphonia monilifera* (Hooker *et* Harvey) Falkenberg	
168	*Pollexfenia pedicellata*	Harvey	Georgetown, Tamar estuary	Gunn	*Pollexfenia pedicellata* Harvey	Type species of *Pollexfenia*
169	*Jeannerettia lobata*	Hooker *et* Harvey	Port Arthur, Tasman Peninsula	Jeannerett	*Pollexfenia lobata* (Hooker *et* Harvey) Falkenberg	
170	*Rhodomela australasica*	Montagne	Probably Recherche Bay	Labillardière	*Protokuetzingia australasica* (Montagne) Falkenberg *in* Schmitz *et* Falkenberg	Type species of monotypic genus *Protokuetzingia*
171	*Lenormandia marginata*	Hooker *et* Harvey	Tamar mouth	Gunn	*Lenormandia marginata* Hooker *et* Harvey	
172	*Polyphacum smithiae*	Hooker *et* Harvey	Circular Head	Smith *et* Gunn	*Epiglossum smithiae* (Hooker *et* Harvey) Kützing	Type species of *Epiglossum*
173	*Chylocladia tasmanica*	Harvey	Georgetown, Tamar estuary	Gunn	*Coeloclonium tasmanicum* (Harvey) Womersley	Type species of *Coeloclonium*
174	*Chondria bulbosa*	Harvey	Eastern Tasmania	Gunn	*Chondria bulbosa* Harvey	
175	*Chondria capreolis*	Gordon-Mills *et* Womersley	Tasmania		*Chondria capreolis* Gordon-Mills *et* Womersley	
176	*Laurencia fusifolia*	Hooker *et* Harvey	Sullivans Cove, Hobart	Lyall	*Chondria fusifolia* (Hooker *et* Harvey) Harvey	
177	*Chondriopsis harveyana*	J. Agardh	Georgetown, Tamar estuary	Harvey	*Chondria harveyana* (J. Agardh) De Toni 1903	The longest Tasmanian *Chondria*
178	*Coeloclonium incrassatum*	J. Agardh	Orford, mid-east coast	Meredith	*Chondria incrassate* (J. Agardh) Gordon-Mills *et* Womersley	The widest Tasmanian *Chondria*
179	*Janczewskia tasmanica*	Falkenberg	Tasmania		*Janczewskia tasmanica* Falkenberg	Diminutive parasite
180	*Laurencia tasmanica*	Hooker *et* Harvey *ex* Harvey	Georgetown, Tamar estuary	Gunn	*Laurencia tasmanica* Hooker *et* Harvey *ex* Harvey	
181	*Chondria botryoides*	C. Agardh	Kent Group of Islands, Bass Strait	R. Brown	*Laurencia botryoides* (C. Agardh) R. Brown	

Table 1: (continued)

#	Original name	Author	Type locality	Collector	Current name	Remarks
182	*Chondria pinnatifida var. elata*	C. Agardh	King I., Bass Strait		*Corynecladia elata* (C. Agardh) Cassano, Oliveira et Fujii	
183	*Huonia sandersonii*	G.W. Saunders	Arch Rock, D'Entrecasteaux Channel	G.W. Saunders	*Huonia sandersonii* G.W. Saunders	Type species of monotypic genus
184	*Tytthomenia barretti*	G.W. Saunders	Verona Sands, D'Entrecasteaux Channel	G.W. Saunders	*Tytthomenia barretti* G.W. Saunders	Type species of monotypic genus

Refer to Figure 1 for localities from where the type specimens were collected (Type locality). Details that appear in the table were obtained using AlgaeBase (Guiry and Guiry 2022).

(seagrasses and green algae), II (the browns) and IIIA, B, C and D (the reds) (Womersley 1984, 1987, 1994, 1996, 1998, 2003), and these remain a critically important taxonomic resource. The 'Marine Plants of Tasmania' (Scott 2017) is the first text to focus solely on the diversity of Tasmanian seaweeds.

There is an historical absence of seaweed taxonomists in Tasmania, and so more recent techniques in molecular taxonomy/phylogeny have yet to be as systematically applied to the seaweed flora as they have in other regions. Nevertheless, in taxonomic surveys of southeastern Australia, G.W. Saunders employed DNA-sequencing to accompany morphological features for the establishment of new species, genera, and families (Table 1). Examples include the endemic monotypic genus *Acrothesaurum* (#77), the new endemic species *Mychodea pseudoaciculare* (#74), the resurrection of *M. membranacea* (#72) and *M. terminalis* (#73), the merging of the Tasmanian species *Epymenia halymenioides* (#84) with *Rhodymenia cuneata* (#85) and their transfer to the genus *Halopeltis*. More recently, Weber et al. (2017) discovered *Durvillaea amatheiae* (#23) was previously synonymous with *D. potatorum*, adding to the growing number of species in this genus recorded in New Zealand and Chile (Fraser, C.I. et al. 2020; Fraser, K.M. et al. 2020; Velásquez et al. 2020). An excellent example of the undiscovered diversity of Tasmanian seaweeds is that of Scott et al. (2013), who found *Entwisleia bella* (#79), which represents a previously undescribed genus, family, and order. Even more recent examples include *Huonia sandersonii* (#183) and *Tythomenia barrettii* (#184) (Saunders et al. 2017).

The 750 species of seaweeds in Tasmania is likely a substantial underestimate, and if the flora is carefully assessed combining morpho-taxonomy with molecular methods it is likely that more genera and species will be identified (Scott 2017). For example, systematic surveys in neighbouring New Zealand have revealed a 50% increase in species diversity since the 735 documented in 1985 (Parsons 1985; W.A. Nelson pers. comm.). Specific examples include: the order Bangiales, which includes the commercially important genus *Pyropia*, for which species numbers have increased from 4 to 46 (W.A. Nelson pers. comm.); many new seaweed genera have been described, and since 1983 the number of known invasive seaweeds has increased from 14 to 61 (Nelson et al. 2021). The diversity of coralline algae in Tasmania is likely to increase greatly if molecular taxonomic methods are applied – there are just 37 documented species in Tasmania compared to 122+ in New Zealand (J.C. Sanderson pers. comm.; Twist et al. 2019). The lack of a similar systematic study of the Tasmanian seaweed flora represents a major knowledge gap that is critical to fill if we are to understand how seaweed communities around Tasmania,

and the ecological functioning of coastal ecosystems that they support, will respond to ongoing climate change, and the potential of the flora for natural products and pharmaceuticals.

3.2 Role of culture collections in seaweed taxonomy and applied research

Tasmania is home to the Australian National Algae Culture Collection, (Australian National Algal 2023) (CSIRO, Hobart), which, in line with several other global culture collections such as CCAP in the UK, NIES in Japan and NCMA in the USA, has recently expanded its scope to support the collection of living seaweeds. Historically, seaweeds were preserved as herbarium specimens whereas their smaller counterparts, the microalgae, have been maintained as unialgal strains in serial sub-culture in living culture collections, or dried samples of voucher specimens. At present, of the 41 registered algal collections on the Culture Collections Information or CCINFO (wdcm.org), most hold marine and/or freshwater microalgae and it is not evident what number maintain macroalgae (database search 26 June 2022).

Herbarium specimens, particularly Type specimens, as held at the Tasmanian Herbarium are fundamentally important for taxonomic studies and may even be used as a proxy for studying historical environmental conditions (Miller et al. 2020). The rationale for a macroalgal bioresource is similar to that for microalgae through provisioning living material for eco-physiological and life history studies under controlled conditions, the study of genetic and multi-omics variability within and between species, and for selecting phenotypes that may be best suited for bio-applications ranging from restorative kelp reseeding to multiple bio-products documented in upcoming sections. As not all taxonomic groups of seaweed are amenable to long term collection logistics, the initial focus at ANACC has been on red algae and, through collaborations with the Institute for Marine and Antarctic Studies (IMAS), University of Tasmania, the gametophytes of targeted brown algae such as *Macrocystis pyrifera*. Future research will examine the cryopreservation of desired phenotypes that will alleviate the risks of genetic drift which is liable to occur in serial subculture. An important role of culture collections is not only to acquire and preserve viable living strains (e.g. from the research community) but in the digitization (e.g. provenance, biogeography, image, genetic, trait data) of those strains so that they can be resupplied for further research and industry use. In the case of ANACC, 70% of its 1100 strains (100% of 90 macroalgae) are currently available through the Australian National Algae Supply Service (CSIRO, Hobart, Tasmania).

3.3 Population genetics, contemporary and historical connectivity with mainland Australia

Although Tasmania is currently an island, it has historically been connected to mainland Australia when sea levels dropped during glaciation events including as recently as ~14,000 years ago (Lambeck and Chappell 2001). Contemporary patterns in Tasmanian seaweed population genetics, and relationships with mainland populations, reflect a combination of connectivity during these periods of lower sea levels, along with the dominant oceanography of the region which is characterised by the poleward flowing Zeehan current in western Victoria and western Tasmania and the poleward flowing East Australian Current in eastern regions (Ayre et al. 2009; Fraser, C.I. et al. 2009; Weber et al. 2017; Figure 1). For example, chloroplast and mitochondrial sequences from six dominant seaweed species in Tasmania (*Durvillaea potatorum, Ecklonia radiata, Hormosira banksii, Lessonia corrugata, Macrocystis pyrifera* and *Phyllospora comosa*) showed small phylogeographic variation among populations (Durrant et al. 2015; Fraser, C.I. et al. 2009; Mueller et al. 2018). Species with a greater dispersal capacity, for example *M. pyrifera* and *P. comosa*, have a greater population connectivity than negatively buoyant species (e.g. *H. banksii* and *L. corrugata*).

There is evidence of divergence of haplotypes between eastern and western regions of Tasmania for *Durvillaea potatorum, Ecklonia radiata, Hormosira banksii* and *Lessonia corrugata*. Although there are some unique haplotypes in Tasmanian populations relative to conspecifics from the mainland, eastern Tasmanian haplotypes are found in eastern mainland populations and western Tasmanian haplotypes are found in western mainland populations (Durrant et al. 2015; Fraser, C.I. et al. 2009; Mueller et al. 2018). For *L. corrugata,* which has a limited capacity for dispersal, the availability of intervening habitat (i.e. rocky reef) appears to be a key determinant of population connectivity rather than geographic proximity (Durrant et al. 2015).

Overall, these findings suggest that eastern Tasmania (and the southeast coast of mainland Australia) was a refuge for temperate macroalgae (and other marine organisms, Ayre et al. 2009; Di Battista et al. 2014) during periods of glaciation and that western Tasmania, which experienced intense cooling from subantarctic waters during that time, was subsequently re-invaded in postglacial periods, most likely from southern or western Victoria (Fraser, C.I. et al. 2009; Mueller et al. 2018). More broadly, the limited phylogeographic variation observed in Australian seaweeds, in conjunction with other intra- and interspecific phylogenetic

relationships (e.g. Coleman 2013; Starko et al. 2019), suggests most of these now-dominant species are likely to be relatively recent arrivals to the region (~3 million years ago, MYA). Members of the order Fucales, including *Durvillaea* spp., likely have a longer history as they originated in the Australasian region (Cheshire et al. 1995; Weber et al. 2017). In future work, an emphasis on finer-scale genetic variation and diversity using more variable markers such as microsatellites or single nucleotide polymorphisms (SNPs) would enhance understanding of population-level processes such as gene flow, population connectivity and natural selection (e.g. Coleman et al. 2011; Wood et al. 2021). For example, a recent study using genotype-by-sequencing (GBS) differentiated two genetically distinct *Macrocystis pyrifera* populations, separating into Northern and Southern regions (Iha et al., unpublished). This GBS analysis revealed a greater population diversity and less connectivity between populations than was evident from previous genetic studies. Further, research has focussed on only large brown seaweeds and we have no knowledge of the population genetics of Tasmanian Rhodophyta, the most specious phylum, or Chlorophyta. A greater knowledge of key species from these phyla is critical to the developing Tasmanian seaweed aquaculture industry (see below).

4 Ecology

Tasmania has a strong track record in subtidal benthic ecological research, focussing on understanding the ecology of large brown seaweeds including the factors affecting their distribution, abundance, and role in providing habitat for other species, such as commercially valuable rock lobsters, abalone, and sea urchins (Edgar 1983a, 1984; Edgar and Barrett 1999; Johnson et al. 2005, 2011, 2013; Ling 2008; Ling et al. 2009b, 2010; Sanderson and Thomas 1987; Shelamoff et al. 2022a). Studies that have contributed to the development of ecological theories include those focussed on disturbance dynamics and habitat resilience (e.g. phase shifts), patch dynamics and facilitation, seaweed-herbivore interactions (e.g. urchins), temporal variation/stability and marine-protected areas (Barrett et al. 2009; Edgar and Barrett 1999; Flukes et al. 2014; Johnson et al. 2005, 2011, 2013; Ling et al. 2009a,b, 2015; Ling and Johnson 2012; Perkins et al. 2015, 2020). More recently, ecological research has focused on understanding seaweed responses to climate change, including increasing temperature, marine heat waves, ocean acidification and interactive effects, and the restoration of impacted habitats, particularly *Macrocystis pyrifera* forests

(Britton et al. 2016; Butler et al. 2020; Johnson et al. 2011; Layton et al. 2020b; Ling et al. 2020).

4.1 Distribution of seaweeds along wave-exposure gradients and depth gradients

Examples of the dominant species of Tasmanian seaweeds, and communities, are pictured in Figure 2. The distribution and abundance of the dominant large brown seaweeds within Tasmania are dependent on the availability of rocky substrata, and other key environmental factors, including wave exposure and depth (Edgar 1984; Hill et al. 2010; Sanderson and Thomas 1987). Wave exposure varies enormously around Tasmania: there is typically extremely high exposure on the west and south coasts, moderate exposure on the east coast and low wave exposure on the north coast (Butler et al. 2020). The effect of wave exposure on the distribution of habitat-forming brown seaweeds differs between genera and is partly related to their morphology. On more wave-exposed coasts, *Durvillaea* spp. often dominate intertidal and shallow subtidal habitats while *Phyllospora comosa* and *Ecklonia radiata* are also abundant but occur deeper than *Durvillaea* spp. (Edgar 1984). These species have flat blade morphologies that are more conducive to hydrodynamic streamlining in wave-exposed sites (Hurd 2000). In contrast, *Sargassum* spp. and *Cystophora* spp., which have many lateral branches that would increase drag forces on their small holdfasts, are found in more sheltered shallow subtidal environments, and their occurrence and abundance declines with increasing exposure (Edgar 1984; Hill et al. 2010).

While *Durvillaea* spp. dominate the low intertidal on high energy shores of the east, south and west coasts, *Lessonia corrugata* can be locally abundant in low intertidal habitats on medium energy shores principally in southwestern Tasmania (Barrett et al. 2001; Edgar 1984) and *Hormosira banksii* forms extensive beds on the low wave-energy reefs of the north coast and sheltered embayments on the east coast (Lewis et al. 2021; Mueller et al. 2015). On the north coast, thalli of *Hormosira banksii* are smaller (both shorter fronds and smaller vesicles) which may be a response to the different tidal regime that results in longer exposure to the air (Gemelli et al. 2019; Mueller et al. 2015).

Depth and light availability are also important variables explaining the distribution and abundance of large brown seaweeds that generally require moderate levels of light. On most of the open coasts of Tasmania, *Ecklonia radiata*, *Cystophora* spp., *Phyllospora comosa* and *Sargassum* spp. are

Figure 2: Examples of the diversity of seaweed species in Tasmania. (A) *Hormosira banksii*, (B) *Asparagopsis armata*, (C) *Lessonia corrugata*, (D) *Durvillaea potatorum*, (E) front: *Caulerpa trifaria*; back: *Phyllotrichia verruculosa*, (F) *Macrocystis pyrifera*, (G) *Phyllospora comosa*, (H) *Delisea* sp., (I) assemblage of red seaweeds including *Ballia callitricha*, *Corallina officinalis*, *Delisea plumosa*, *Phymatolithon maisonianum*, *Pterocladiella capillacea*, *Spnderphycus coriaceus*, (J) *Durvillaea* spp. and *Xiphophora gladiata*, (K) reef assemblage including: *Ecklonia radiata*, *Caulerpa trifaria*, *Plocamium cirrhosum*, (L) encrusting red algal assemblage, (M) *Ecklonia radiata*, (N) assemblage of crustose coralline algae, (O) *Sargassum* sp. Photo credits: (A, D, E, F) Joanna Smart, (B) Elysha Kennedy, (C) Michael Guiry (AlgaeBase), (G, K) Matthew Doggett, (N) Elisabeth (Beth) Strain, (I) Christopher Cornwall, (J) Scott Ling, (H and L) Cayne Layton, (M) Jo Lane, (O) Emilliano Cimoli.

the dominant taxa at depths >5 m (Edgar 1984; Sanderson 1990a), although *Durvillaea* spp. can be found down to 20 m depth on the extremely wave-exposed south coast (Edgar 1984). In particular, *E. radiata* dominates reefs with moderate to high wave energy from ~10 to 25 m depth where it forms forests of close to 100% cover (Wernberg et al. 2019). In deeper waters, a decrease in *E. radiata* abundance is strongly related to the reduced availability of light and rock substratum, although forests of ~40–50% cover can still be found at 40 m on the east coast of Tasmania (Marzinelli et al. 2015). Prior to its decline, *M. pyrifera* was also abundant at depths between 10 and 20 m on open coasts (Butler et al. 2020; Johnson et al. 2011) and in many places it has been replaced by *E. radiata* and/or *P. comosa* (Ling and Keane 2018). These patterns are, however, locally variable and further study is underway to examine these trends and associated environmental drivers, including the use of autonomous underwater vehicles (AUV, e.g. Perkins et al. 2020), remotely operated vehicles (ROV, e.g. Sward et al. 2021) and towed video technology which is enhancing understanding of seaweed ecology in Tasmania at greater depths.

4.2 Seasonal patterns of growth, standing stock and demography

Seasonal patterns of growth have been documented for eight species of brown seaweed, but no red or green seaweeds. For *Ecklonia radiata*, maximum blade elongation rates occur in summer (Nov–Dec) and minimum in winter (June–July, Table 2). These rates are higher than those recorded in other regions of Australia (0.03–0.22 cm d^{-1}) but similar to those in southwest New Zealand (0.06–0.45 cm d^{-1}; Wernberg et al. 2019). For juvenile *E. radiata* (initial size 50–150 mm long) growth rates also vary with season, being highest in autumn and lowest in spring and summer (Layton et al. 2019b). In contrast, for *Macrocystis pyrifera,* growth was maximal in spring and minimal in late summer (Sanderson 1990a). For the fucoids, *Phyllospora comosa* has maximal growth rates in summer compared to winter (Sanderson 1990a) and, similarly, percentage cover in the D'Entrecasteaux Channel declines in winter, most likely due to increased wave action removing seaweeds and reduced growth rates, before increasing in summer (White et al. 2021). A seasonal pattern of maximum seaweed length was recorded for *Sargassum fallax* (recorded as *S. bracteolosum*) at Fancy Point, with the longest seaweeds recorded in December-January, and shortest between February and April (Edgar 1983b). No clear seasonal patterns in longest length were recorded for *Phyllotricha verruculosa* (recorded as *Sargassum verruculosum*), *Cystophora retroflexa* and *Caulocystis cephalornithos*, and the small (<14 cm) dictyotalean seaweed *Zonaria turneriana* (Edgar 1983b). The studies of Edgar (1983b) and Sanderson (1990) provide a vital baseline of information that, if repeated at the same sites, may allow the detection of changes in patterns of seasonal growth rates and cycles over the past four decades, during which time surface sea temperatures have increased (Johnson et al. 2011).

A few studies have measured standing stocks of Tasmanian seaweeds, again focussing on large brown seaweeds. The highest known standing stock is 68 kg ww m^{-2} in the low intertidal (0 m) for *Durvillaea potatorum* (probably mixed with *D. amatheiae*) at Eaglehawk Neck, which compares to 20 kg m^{-2} at 2 m depth; the lower biomass at 2 m was due to a high density of small, young seaweeds compared to a lower density of large, mature seaweeds at 0 m (Cheshire and Hallam 1988). Standing stocks at 14 m depth at George III Reef were 36 kg m^{-2} (Sanderson 1990a). These standing stocks are greater than those of *D. antarctica* in New Zealand (10–24 kg ww m^{-2}, South and Hay 1979). The standing stocks of laminarian and other fucalean communities are lower than those of Tasmanian *Durvillaea* spp. at 0.2–8 kg m^{-2} for a mixed community at Fancy Point (Edgar 1983a), 1–8 kg m^{-2} for *E. radiata* beds at Maria Island, George III Reef and Bicheno (Sanderson 1990a) and 2.3 kg m^{-2} for *Phyllospora comosa* at Bicheno (Sanderson 1990a).

The instantaneous or annual production rates of kelps and other canopy forming species in Tasmania is unknown with the exception of the study conducted by Randall et al. (2019), who continuously measured productivity of an *Ecklonia radiata* bed over 11 days in a semi-sheltered bay in eastern Tasmania and found that kelp contributed about half of the total primary production of the macroalgal community on the reef. This finding is in line with work in New Zealand showing that the fucoid canopy of an intertidal community accounted for about half of the total primary production (Tait and Schiel 2018).

The demography of native Tasmanian seaweeds is not well studied except for *Ecklonia radiata* and *Hormosira banksii.* Detailed demographic studies *of E. radiata* in Tasmania revealed some interesting differences from mainland populations, for example, it is larger and more fecund than mainland conspecifics which may be related to more optimal temperatures and nutrients in the cooler Tasmanian waters (Mabin et al. 2013). Reproduction (i.e. sori production and

Table 2: Maximum and minimum growth rates for Tasmanian seaweeds.

Species	Location	Maximum growth rate	Time of maximum growth rate	Minimum growth rate	Time of minimum growth rate	References
Ecklonia radiata (adults)[a]	George III Reef	0.4–0.48	Nov–Dec	0.05–0.1	Jun–Jul	Sanderson (1990)
Ecklonia radiata (juveniles)[a]	Maria Island	0.4 ± 0.03	Autumn	0.21–0.23	Spring and summer	Layton et al. (2019b)
Macrocystis pyrifera[b]	George III Reef	0.6–0.85	Oct–Nov	0.3–0.45	Feb–Mar	Sanderson (1990)
Phyllospora comosa[c]	George III Reef	0.15–0.27	Nov–Jan	0.05–0.07	May–Jun	Sanderson (1990)

Units: [a]lamina elongation rate (cm d^{-1}) measured using the hole-punch method; [b]new blade production in the top 1 m of a frond (blades d^{-1}); [c]main axis elongation (cm d^{-1}).

zoospore release) occurs all year round for *E. radiata* in Tasmania but generally peaks in autumn and winter, and is lowest in summer (Mabin et al. 2013; Sanderson 1990a; Tatsumi et al. 2022). This is different to at least some mainland populations of *E. radiata* (e.g. Western Australia), where the peak in zoospore production/release is earlier (late summer and early autumn) with zoospore production/release outside of that season being negligible (Giraldo-Ospina et al. 2021; Mohring et al. 2014; Wernberg et al. 2019).

The settlement, recruitment, and post-recruitment growth of *Ecklonia radiata* is affected by abiotic changes linked to changes in adult kelp density and patch size (Layton et al. 2019a,b, 2020a; Tatsumi et al. 2021). High densities of adult *E. radiata* provide suitable environments (reduced light, water flow, sediment accumulation and scour) for the settlement and recruitment of microscopic juveniles, whereas the growth of already established older juveniles can be higher in areas where the adult canopy is sparse (Flukes et al. 2014; Layton et al. 2019b; Tatsumi et al. 2021). Thus, altered densities of adult *E. radiata* may facilitate different demographic processes, similar to how variations in *E. radiata* density facilitate associated communities (Flukes et al. 2014; Shelamoff et al. 2019, 2020a,b; Wernberg et al. 2005). The percentage cover of *E. radiata* within Tasmanian macroalgal beds has increased in eastern Tasmanian, particularly in the south and southeast, from 2001–2002 to 2016–2017, which is likely driven by increasing seawater temperatures and concomitant reduction in heavy shading once provided by dense and tall *Macrocystis pyrifera* forest canopy (Ling and Keane 2018). A similar trend was seen within Marine Protected Areas (MPAs) in this region over the period 1992–2002 as part of MPA long-term monitoring (Barrett et al. 2009), again inferred to be in part due to the concurrent decline in *M. pyrifera*. However, Barrett et al. (2009) also demonstrated the remarkable stability of many canopy-forming and understorey species at decadal scales, with the percentage cover of many common species varying by no more than ± 50% of their recorded initial cover over this time period.

A detailed demographic study of a 'dwarf' population of *Hormosira banksii* at Beechford on the north coast of Tasmania showed that although recruitment occurred throughout the year it peaked during summer (Lewis et al. 2021). This higher recruitment in summer is consistent with *H. banksii* in New Zealand (Schiel and Taylor 1999) but different to Victoria where recruitment peaked in April (Bellgrove et al. 2004). Moreover, post-recruitment survivorship was consistently high: up to 80% over 18 months (Lewis et al. 2021). This dwarf morphology of *H. banksii* is relatively slow growing with individuals taking approximately 5 years to grow from recruits to the largest size class of 10 cm (Lewis et al. 2021).

Otherwise, there is limited information on the demography of other large brown seaweeds, including *Macrocystis pyrifera*, *Lessonia corrugata* and *Durvillaea* spp. and of all green and red seaweeds from Tasmania including two species that are the focus of new aquaculture efforts: *Asparagopsis armata,* which is being grown as a feed supplement to mitigate methane production by ruminants, and species in the genus *Caulerpa*, which are being considered for human food. Understanding the fundamentals of annual growth cycles, when and how seaweeds reproduce, and their life cycles, is becoming increasingly important as we tackle responses of seaweeds to climate change (e.g. Leal et al. 2021) and develop a seaweed aquaculture industry (Charrier et al. 2017).

4.3 Subtidal seaweed as habitat-forming ecosystem engineers

Seaweeds of the orders Laminariales and Fucales are ecosystem engineers that provide a complex three-dimensional structure, and directly or indirectly modify resources for themselves and other organisms (Jones et al. 1994). In Tasmania, the structure of *Ecklonia radiata* forests modifies subcanopy irradiance, seawater chemistry, water flow and sedimentation and all of these effects are influenced by the density and/or size of *E. radiata* patches (Britton et al. 2016; Cornwall et al. 2015a; Flukes et al. 2014; Layton et al. 2019a,b; Ling et al. 2020). These modified abiotic factors influence the recruitment, growth and survivorship of microscopic and

macroscopic juvenile *E. radiata* (Layton et al. 2019a,b; Tatsumi et al. 2021), demonstrating a positive intraspecific feedback on demographic functions. Abiotic alterations by *E. radiata* also strongly influence the composition and productivity of associated benthic macroalgal and sessile invertebrate assemblages (Edgar et al. 2004; Shelamoff et al. 2019a,b, 2022b), and the diversity and abundances of other species including mobile macroinvertebrates and fishes (Shelamoff et al. 2020b, 2022a). The living and decaying tissue of *E. radiata* and the attached epiphytes are directly consumed by herbivorous and detritivorous invertebrates such as amphipods, gastropods and sea urchins that are pivotal for secondary productivity and provide food resources for higher trophic levels including species of commercial interest such as southern rock lobster, *Jasus edwardsii* (Palinuridae) (Ling et al. 2009a,b; Shelamoff et al. 2020a). Surprisingly, Shelamoff et al. (2020a) found that epifaunal secondary production in the understorey decreased with patch size but was highest in high-density patches of *E. radiata* and in patches of turf algae in the absence of kelp that had lower epifaunal diversity.

Seaweeds facilitate the settlement and recruitment of invertebrates and can affect species richness. For example, both *Macrocystis pyrifera* and *Ecklonia radiata* appear to provide physical cues and/or release (unidentified) waterborne chemical cues that attract settling southern rock lobster puerulus larvae and provide refuge that improves post-settlement survivorship leading to elevated recruitment (Hinojosa et al. 2015; Shelamoff et al. 2022a). *Ecklonia radiata* also facilitates the recruitment of native oysters (*Ostrea angasi*) and the establishment of other sessile invertebrates through their capacity to suppress competition from algal turfs and modify water flow and particle deposition rates (Layton et al. 2019a,b; Shelamoff et al. 2019a,b). Moreover, increases in *E. radiata* density increase the overall abundance and richness of the fish assemblage, although it does not enhance the recruitment of certain cryptobenthic fish species (Shelamoff et al. 2020b).

More broadly, the structure provided by seaweed is a strong driver of epifaunal invertebrate communities (Ling 2008), with increasing densities of these invertebrates associated with highly branched filamentous seaweeds (i.e. turfs) compared to less branched foliose species (Shelamoff et al. 2020a), although individuals are smaller in size within turf algae (Edgar 1983a; Fraser, C.I. et al. 2021). Large mobile invertebrates (primarily decapods) are more associated with turfing algae on reefs, which supports high epifaunal secondary productivity, than with the macroalgal canopy (Edgar et al. 2004; Shelamoff et al. 2020a, 2022a). Turf- and foliose algal-dominated assemblages in Tasmania support distinctly structured assemblages of epifauna, with the structure of each closely resembling those found elsewhere

in Australia (Edgar 1983a,c; Fraser, C.I. et al. 2020). Increasing richness of epifaunal species is correlated with increasing seaweed species richness (Shelamoff et al. 2020a). Overall, this body of work highlights the critical role of seaweed in facilitating the diversity and productivity of coastal marine ecosystems of Tasmania.

4.4 Invertebrate grazer – seaweed interactions, and trophic cascades

Herbivores have distinct effects on the structure and function of Tasmanian reef ecosystems. At local scales, herbivory can structure reef-scapes and in extreme cases lead to a complete and persistent absence of fleshy/erect macroalgae. This is well-documented on subtidal reefs where the impacts of herbivory are strikingly obvious owing to the formation of barren grounds caused by overgrazing of kelp by sea urchins (Ling 2008; Ling et al. 2010, 2015; Perkins et al. 2015, 2020).

Sea urchin abundance and grazing impacts have increased dramatically in Tasmania in recent decades due to a population explosion of the range-extending diadematid sea urchin *Centrostephanus rodgersii* (Johnson et al. 2005, 2011, 2013; Ling 2008; Ling and Keane 2018; Ling et al. 2009a,b, 2015; Perkins et al. 2020). Since the first detection of an individual urchin on the mainland Tasmanian coast at St. Helens in 1978, the population of *C. rodgersii* in eastern Tasmania has now reached ~20 million (Ling and Keane 2018). From 2001 to 2017, the cover of urchin barrens on eastern Tasmanian reefs caused by *C. rodgersii* increased from ~3% to ~15% and is on target to reach ~50% of eastern Tasmanian reefs in coming decades (Ling and Keane 2018). Observed and expected losses of kelp forests will continue to drastically reduce available habitat and food resources for ~150 kelp-associated taxa (Sanderson 2003), including commercially fished abalone and southern rock lobsters, that are largely absent from urchin barrens (Johnson et al. 2005, 2011, 2013; Ling 2008; Ling and Keane 2018; Strain and Johnson 2009, 2013).

In addition to the increasing grazing effect of *Centrostephanus rodgersii*, the native short-spined sea urchin *Heliocidaris erythrogramma* is also a key herbivore on subtidal Tasmanian reefs (Ling et al. 2010). While *C. rodgersii* overgrazes kelp on wave-exposed eastern Tasmanian reefs (Johnson et al. 2005; Ling et al. 2009a,b), *H. erythrogramma* predominantly overgrazes kelp on moderately sheltered reefs along the north, east and south-east coasts of Tasmania (Ling et al. 2010). Moreover, in contrast to the obligate scraping mode of *C. rodgersii*, the foraging behaviour of *H. erythrogramma* can change from feeding only on drift algae to the more destructive grazing of attached kelp when drift-kelp is absent (Kriegisch et al. 2019).

Relative to historical baselines, and highly visible by comparing fished zones with marine protected areas (MPAs), sea urchin predators have been functionally extirpated across much of the Tasmanian coastline (Barrett et al. 2009; Ling and Johnson 2012; Ling et al. 2009a,b; Pederson and Johnson 2006). Large southern rock lobsters, *Jasus edwardsii* are known predators of both long and short-spined sea urchins, and field experiments show increased predation mortality of urchins in the presence of rebuilt lobster populations relative to fished reefs (Johnson et al. 2013; Ling and Johnson 2012; Ling and Keane 2021; Ling et al. 2009a,b; Pederson and Johnson 2006). Likewise, monitoring of ecological processes within Tasmania's east and southeast coast MPAs has shown that where predators, including lobsters, are protected from fishing, urchin populations are controlled, and reefs remain resilient to barren formation (Barrett et al. 2009; Perkins et al. 2020). While predator abundance, and thus resilience of kelp forests is historically low outside of MPAs, particularly for eastern Tasmania, the "*East Coast Rock Lobster Rebuilding Strategy*" explicitly aims to recover large lobster abundance towards increasing predation on urchins to reduce the risk of barrens formation (https://dpipwe.tas.gov.au/).

Other grazing or browsing species that exert a weaker or smaller-scale influence on algal assemblages include the herring cale (*Olisthops cyanomelas*) which has increased in abundance in Tasmania with warming of Tasmanian coastal waters (Barrett et al. 2014), blacklip abalone (*Haliotis rubra*) (Strain and Johnson 2012) and other species of gastropods (Wernberg et al. 2019). All of these herbivores have specialised feeding mechanisms e.g. herring cale attacking the meristem of kelp rather than the laminae which can be destructive to the kelp. The removal of abalone results in encrusting coralline algae becoming overgrown with sessile invertebrates, filamentous and foliose algae, and the filamentous algae/sediment matrix (Strain and Johnson 2010, 2012). Abalone avoid this overgrown habitat such that heavy fishing of abalone can lead to a transition to a low preference habitat for them (Strain and Johnson 2012). The transition thus appears to represent a form of discontinuous phase shift in benthic community composition (Steneck and Johnson 2014) maintained by positive feedback, and which could have significant negative consequences for the abalone fishery.

4.5 Competition and facilitation among seaweed

Positive and negative interactions among seaweed species are well known (Bennett and Wernberg 2014; Bennett et al. 2015;

Edwards and Connell 2012) but are not well-studied in Tasmanian seaweed communities. Nonetheless, the removal of the *Ecklonia radiata* canopy frees up resources (such as irradiance, which declines by up to ~90% beneath a full *E. radiata* canopy, (Layton et al. 2019b) for competitors that can shift the benthic community toward a foliose algae-dominated state (Flukes et al. 2014). Under a full canopy, the community has a much higher cover of sponges, bryozoans, and encrusting coralline algae. The increase in foliose algae following *E. radiata* canopy loss can in turn negatively impact kelp recruitment, which is lower under a high cover of understorey algae (Tatsumi and Wright 2016). Additionally, the removal of mixed brown algal canopies (primarily fucoids and *E. radiata*), allowed high recruitment of invasive *Undaria pinnatifida*, although the response of *U. pinnatifida* varies with time of year and other levels of disturbance (Edgar et al. 2004; Valentine and Johnson 2003, 2004).

Undaria pinnatifida was first recorded in Tasmania in 1988 (Sanderson and Barrett 1989), and it has established as a winter annual with a seasonal phenology similar to that in other geographic regions that it has invaded (Schaffelke et al. 2005). Experiments to eradicate or control *U. pinnatifida* populations by harvesting sporophytes in the Tinderbox marine reserve showed that the gametophyte phase acts as a 'seed bank' that facilitated the annual re-establishment of the sporophyte generation; after 2.5 years there was no effect of sporophyte removal on the *U. pinnatifida* population (Hewitt et al. 2005). Initial concern that *U. pinnatifida* would outcompete and displace native seaweeds (stemming from observations of extensive macroalgal beds previously dominated by a canopy of *Ecklonia radiata* and fucoids being replaced by mono-specific stands of *U. pinnatifida* in Mercury Passage, e.g. Sanderson 1990b) proved unfounded when experiments demonstrated that *U. pinnatifida* was merely 'tracking' disturbances that removed native species, and that in the absence of disturbance natives would eventually reclaim dominance (Johnson et al. 2004; Reeves et al. 2018; Valentine and Johnson 2003, 2004). Thus, despite high potential for dispersal in *U. pinnatifida* (Sliwa et al. 2006), after more than three decades since its arrival in eastern Tasmania it remains largely a minor component of the canopy of macroalgal beds.

It is more likely that a greater risk to *Ecklonia radiata* and native fucoids maintaining closed-canopy macroalgal beds in Tasmania is the proliferation of filamentous algal turfs and the sediments they accumulate to form a semi-consolidated sediment matrix that severely limits recruitment of large fucoid and laminarian species (Valentine and Johnson 2005a,b). Proliferation of turf algae at the expense of *E. radiata* in Port Phillip Bay in Victoria (Reeves et al. 2018, 2022), and of other canopy-forming species elsewhere in the

world (e.g. Filbee-Dexter and Wernberg 2018; Strain et al. 2014) typically occurs on low wave-exposure reefs subject to poor water quality and other human-instigated stressors, highlighting that attention to water quality in Tasmania should remain a management priority.

4.6 Restoration

One emerging tool in the conservation and management of seaweed-dominated ecosystems is habitat restoration, the science and practice of which is currently undergoing substantial expansion (Eger et al. 2022; Layton et al. 2020b; Morris et al. 2020). Within Australia there have been few attempts to restore kelp forests, however the earliest reported work comes from Tasmania, and outlines attempts to restore areas of disappearing *Macrocystis pyrifera* (Layton et al. 2020b; Sanderson 2003). The projects realised some success, with giant kelp established at one of the >10 sites; however, this too disappeared after some time in keeping with the persistent decline of giant kelp in Tasmania due to climate change and ocean warming (Butler et al. 2020; Johnson et al. 2011; Steneck and Johnson 2014). This illustrates the necessity not only to understand the practical and methodological aspects of kelp forest restoration, but also to address and understand the drivers of habitat decline (Abelson et al. 2020). Work is currently underway in Tasmania that has identified and planted giant kelp genotypes that display increased tolerance of warm water as the foundation of ongoing restoration efforts (Layton and Johnson 2021).

Additional research from Tasmania has increased understanding of the factors likely affecting the successful restoration of kelp forests. Valentine and Johnson (2005) illustrated that, even after the removal of grazing urchins, heavy inoculation with *Ecklonia radiata* kelp spores was unable to promote kelp reestablishment – presumably due to recruitment inhibition by the turf algae and sediments that had proliferated in the absence of the kelp (also see Layton et al. 2019b). Conversely, if healthy kelp forests are close to denuded areas (e.g. urchin barrens), the removal of urchins can facilitate rapid natural recovery of kelp and other macroalgae (Ling 2008) – however >90% of urchin biomass has to be removed from a given area in order to promote natural macroalgal recovery (reviewed by Ling et al. 2015; Marzloff et al. 2016). Layton et al. (2019b, 2021) demonstrated a method for the successful transplantation of >1000 adult *E. radiata* on artificial reefs in Tasmania. Following abundant natural recruitment from the transplanted kelp, some of those reefs eventually supported self-sustaining areas of *E. radiata*, but crucially, this only occurred where there were adequate adult *E. radiata* to

facilitate juvenile conspecifics via modification of the physical environment.

5 Physiology

Seaweed physiology is a more recent (~2010) focus for Tasmania. It has been studied largely in the context of responses and acclimatory mechanisms to environmental drivers including ocean global change (ocean acidification and warming) and local anthropogenic drivers such as nitrogen enrichment, including the mitigation of nitrogen waste from salmon and mussel farms using integrated multi-trophic aquaculture (Smart et al. 2022).

5.1 Dissolved inorganic carbon uptake mechanisms

The inorganic carbon physiology of some Tasmanian seaweed communities is globally unique. Cornwall et al. (2015b) revealed that, based on carbon stable isotope signatures and pH-drift experiments, up to 90% of populations at Tinderbox and Ninepin Point do not operate a carbon-dioxide concentration mechanism (CCM), i.e. they rely on dissolved CO_2 and cannot take up bicarbonate (termed non-CCM seaweeds). This finding contrasts sharply with other regions studied – Southern New Zealand, the Great Barrier Reef and a volcanic vent in Italy – where only ~5% are non-CCM (Cornwall et al. 2017; Diaz-Pulido et al. 2016; Hepburn et al. 2011). In Tasmania, almost all non-CCM species are red seaweeds, and these communities provide a unique opportunity to understand the underpinning physiological mechanisms of inorganic carbon uptake as, internationally, previous work has focussed on green and brown seaweeds. Further, the photosynthetic rates of non-CCM seaweeds are unlikely to be saturated at present-day pCO_2 levels and this has implications for their response to ocean acidification (see below). As carbon and nitrogen metabolisms are tightly linked, non-CCM seaweeds are also predicted to have unique features of their nitrogen physiology, which is yet to be studied in detail but warrants attention (Paine et al. 2021b).

5.2 Photosynthesis and respiration

Net photosynthetic and respiration rates have been measured for a range of species, in the laboratory, focussing on red seaweeds due to their interesting carbon physiologies (Cornwall et al. 2015b). Rates are within the ranges reported for other species worldwide, and there are no clear

Table 3: Net photosynthesis and respiration rates measured in the laboratory for seaweeds with and without a carbon dioxide concentrating mechanism (CCM and non-CCM, respectively) under a variety of light and temperature conditions, and ambient conditions of pH and seawater dissolved inorganic carbon.

Phylum	Species	Net photosynthesis (μmol O_2 gww^{-1} h^{-1})	Respiration (μmol O_2 gww^{-1} h^{-1})	Temperature (°C)	Light (μmoles m^{-2} s^{-1})	Carbon uptake strategy	References
Rhodophyta	Lomentaria australis	4.34		12.5	25–30	CCM	Van der Loos (2019)
	Craspedocarpus ramentaceus	3.12		12.5	25–30	Non-CCM	Van der Loos (2019)
	Callophyllis lambertii	5.91	0.76	14	80	Non-CCM	Briton et al. (2019)
	Plocamium dilatatum	11.3	2.21	14	80	Non-CCM	Briton et al. (2019)
	Plocamium dilatatum	7.7		15.5	50	Non-CCM	Schmid et al. (in preparation)
	Hemineura frondosa	4.18		12	50	Non-CCM	Cornwall and Hurd (2019)
	Plocamium angustum	4.07		12	50	Non-CCM	Cornwall and Hurd (2019)
	Rhodymenia sp.	3.35		12	50	Non-CCM	Cornwall and Hurd (2019)
	Grateloupia subpectinata	8.8		15.5	50	Unknown	Schmid et al. (in preparation)
	Hymenena affinis	13.3		15.5	50	CCM	Schmid et al. (in preparation)
	Phacelocarpus peperocarpos	6.9		15.5	50	CCM	Schmid et al. (in preparation)
	CCA assemblages	0.092[a]		15	10	Unknown	Britton et al. (2021)
Ochrophyta	Ecklonia radiata	0.32[a]		14	28	CCM	Britton et al. (2016)
	Phyllospora comosa	6.57	6.07	15	50	CCM	Britton et al. (2020a)
	Macrocystis pyrifera	14.06		17	125	CCM	Fernandez et al. (2020)
	Carpoglossum confluens	4.1		15.5	50	CCM	Schmid et al. (in preparation)
	Cystophora torulosa	3.1		15.5	50	CCM	Schmid et al. (in preparation)
	Sargassum fallax	10.8		15.5	50	CCM	Schmid et al. (in preparation)
	Xiphophora gladiata	3.6		15.5	50	CCM	Schmid et al. (in preparation)

[a]μmol O_2 cm^{-2} h^{-1}. CCA, crustose coralline algae.

differences between seaweeds with and without CCMs (Table 3). However, there are no published studies on the effects of light (photosynthesis-irradiance curves) or dissolved inorganic carbon (photosynthesis-DIC curves) on photosynthetic rates and this is a substantial omission in our understanding of the photosynthetic physiology of Tasmanian seaweeds.

5.3 Nitrogen physiology and C:N ratios

Typical of temperate regions worldwide, the two forms of inorganic nitrogen available for uptake by Tasmanian seaweeds are nitrate (NO_3^-) and ammonium (NH_4^+), and concentrations vary spatially and temporally with season and anthropogenic influences. There has not been a systematic study of seasonal patterns of NO_3^- and NH_4^+ in Tasmanian waters, however concentrations of NO_3^- on the east coast are <3 µM year-round (Smart et al. 2022; Thompson et al. 2009), although a point measurement at Bruny Island in winter 2021 was ~6 µM (E.R. Paine pers comm). These concentrations of total inorganic nitrogen are much lower than in other temperate regions, for example winter NO_3^- concentrations of ~10 µM in the north Atlantic and ~20 µM in the north Pacific (Hurd et al. 2014), indicating that Tasmanian waters are comparatively oligotrophic. The inorganic nitrogen uptake rates of only a few species have been studied. For ammonium, *Macrocystis pyrifera*, *Lessonia corrugata*, and *Ecklonia radiata* uptake rates are saturable with a maximum uptake rate (V_{max}) of 200, 45.8 and 45 µmol NH_4^+ gDW^{-1} h^{-1} and half-saturation constants (K_s) of 361.3, 104.2 and 121 µM, respectively (Smart et al. 2022). *Phyllospora comosa* (order Fucales) showed evidence of both passive and active uptake mechanisms (biphasic uptake) for spring and autumn but not summer (i.e. two of three study seasons); this is only the third time globally that bi-phasic uptake has been reported for a brown seaweed – all of which were members of the Order Fucales (Smart et al. 2022).

The effect of light on uptake and assimilation of nitrate and ammonium for the non-CCM red seaweed *Hemineura frondosa* found that saturating irradiance (150 µmol photons $m^{-2} s^{-1}$) resulted in increased uptake rates of ammonium and nitrate compared to limiting (30 µmol photons m^{-2} s^{-1}) irradiance. This finding was attributed to an increased utilization of stored tissue nitrogen under low light, rather than the allocation of energy to the assimilation of new nitrate via nitrate reductase – the activity of which did not change with irradiance – which is an energetically costly process (Paine et al. 2021b).

The ratio of tissue carbon: nitrogen can be used as an indicator of whether seaweed growth is nitrogen limited and also of the nutritional content of a seaweed, because higher nitrogen content is related to a higher protein content (Hurd et al. 2014). A 'rule of thumb' is that seaweeds with a C:N <15–20 are nitrogen sufficient, and those >20–25 are nitrogen-limited for growth (Hurd et al. 2014). The C:N ratios of red and green Tasmanian seaweeds are within the ranges of species studied elsewhere (Sheppard et al. unpublished data). However, the Tasmanian seaweeds *Durvillaea* spp., *Phyllospora comosa*, *Lessonia corrugata* and *Ecklonia radiata* have some of the highest C:N ratios globally, with values for *E. radiata* of up to 100, compared to the global mean of 27.2 (Sheppard et al. unpublished data). C:N ratios in juvenile *P. comosa* (Flukes et al. 2015) and *Macrocystis pyrifera* (Mabin et al. 2019a) from Fortescue Bay in SE Tasmania were ~15 which is likely due to the much lower structural carbon content of juveniles compared to adults. C:N ratios varied with depth, season and year for adult *E. radiata* (~13–21), and with season and year for *P. comosa* (range ~21–32) with complex interactions among these factors. *Macrocystis pyrifera* showed large seasonal fluctuations in C:N ratios from means of ~10 in winter to ~45 in summer (Flukes 2015). Overall, the comparatively high C:N ratios of Tasmanian brown seaweeds indicate that they either have nitrogen-limited growth or a low nitrogen requirement for growth: the ability to grow productively in relatively low ambient inorganic nitrogen concentrations is likely an adaptation to relatively oligotrophic waters. Future work to elucidate the physiological and biochemical mechanisms of such adaptations by comparing *M. pyrifera*, which has a wide biogeographic distribution, from Tasmania with other locations (Chile, Canada, New Zealand, USA) will be important in assessing population responses to the ongoing global decline in nitrate concentrations due to climate change (Pörtner et al. 2014).

5.4 Water motion

Water motion is a key driver of seaweed primary production through its influence on seaweed morphology and the thickness of velocity and diffusion boundary layers that affect rates of photosynthesis, nutrient uptake, and growth (Hurd 2000, 2015). Field studies comparing seawater flows above and within Tasmanian seaweed beds (Ninepin Point and Tinderbox) revealed that velocity and turbulence are reduced by 90% irrespective of background flow regimes, due to dampening by the seaweeds (Kregting et al. 2021). Velocities within the beds were 3 cm s^{-1} and this work adds to the small number of studies that report substantial flow attenuation by natural seaweed beds (see Table 1 in Kregting et al. 2011, 2021). Reductions of mainstream flows of ~55%

beneath *Ecklonia radiata* canopies have also been observed at various depths in Tasmania (Layton et al. 2019b). In flume experiments at water velocities of 6 cm s^{-1}, communities of understorey algae and small kelp were each found to be capable of reducing flows by 30 and 60%, respectively (Layton et al. 2019a). Diffusion boundary layer (DBL) thickness at the surface of *E. radiata* blades in flows of 0.5 and 8 cm s^{-1} was 0.5 and 0.1 cm, respectively, but when the blade surface was covered by the bryozoan *Membranipora membranacea*, the DBL thickness was between 80 and 200% thicker than for bare blades (Noisette and Hurd 2018). Thick DBLs allow the seawater chemistry at the surface of seaweeds to be biologically modified and may act as a refuge for calcifying organisms such as *M. membranacea* from the ongoing reduction in seawater pH due to ocean acidification (Hurd 2015; Layton et al. 2019b; Noisette and Hurd 2018; Noisette et al. 2022).

Recent studies are revealing that Tasmanian brown seaweeds may have unique nitrogen metabolisms that allow them to grow in seawater that has persistently low nitrogen concentrations compared to well-studied temperate regions of the northern hemisphere (Hurd et al. 2014). Communities of red seaweeds are uniquely dominated by non-CCM species to the extent that CCM-red seaweeds can be difficult to locate for experimental work along the south-east coast (D. Britton pers comm). Tasmania's rich and diverse flora provides the ideal system to study physiological mechanisms by which seaweeds metabolise carbon and nitrogen and allow better understanding of how these unique systems will acclimate and adapt to climate change. Further to this, an underpinning physiological knowledge is needed to domesticate seaweeds for aquaculture, and to explore potential bioactive compounds.

6 Anthropogenic impacts

6.1 Ecological changes in diversity and range shifts that can be directly linked to ocean global change

Ocean warming along Tasmania's east coast is 3–4 times the global average due to the strengthening of the East Australian Current, making Tasmania a 'natural laboratory' for climate change research (Johnson et al. 2011). As discussed above (*Invertebrate grazer – seaweed interactions and trophic cascades*), this has led to the range-expansion of the sea urchin *Centrostephanus rodgersii* into eastern Tasmania and, subsequently, significant declines in kelp and seaweed assemblages (Johnson et al. 2005, 2011; Ling 2008; Ling and Keane

2018; Ling et al. 2009a,b; Perkins et al. 2015). Since the 1950s, eastern Tasmania has also suffered ~ 95% declines in giant kelp (*Macrocystis pyrifera*) forest surface canopy cover, which is attributed to the increasing influence of the warm, nutrient-poor waters of the EAC in Tasmania (Butler et al. 2020; Johnson et al. 2011; Steneck and Johnson 2014), with overgrazing by sea urchins likely to have exacerbated the problem (also see Ling and Keane 2018). Consequently, in 2012 *M. pyrifera* forests of southeast Australia became the first marine community listed as Endangered under the Australian Federal Government Environment Protection and Biodiversity Conservation Act (Evans et al. 2017). Where those losses have occurred, *M. pyrifera* has been largely replaced by *Ecklonia radiata*, which is more thermally tolerant, or urchin barrens (Johnson et al. 2011; Ling and Keane 2018).

In addition to *Centrostephanus rodgersii*, numerous other marine species are moving south with the EAC into Tasmania's waters. In fact, Tasmania has more records of range shifting species than any other marine region in Australia, and >80 new marine species have been recorded in Tasmania in recent decades (Gervais et al. 2021). While the vast majority of investigations of range expansions have focussed on fishes and other animals, range shifts are also likely to have occurred for seaweed (Wernberg et al. 2011). Ultimately, with the ongoing threat of climate change, declines of key habitat-forming species such as the kelps and an increasing number of novel species, Tasmania's marine ecosystems are currently experiencing unprecedented change.

6.2 Future projections of changes in seaweed assemblages based on laboratory manipulative studies

To help understand ecological shifts that are ongoing in Tasmania, a range of manipulative experiments have been conducted assessing how seaweeds will respond to ocean global change. Studies have primarily examined the effect of ocean acidification in isolation (Britton et al. 2016, 2019; Cornwall and Hurd 2019; van der Loos et al. 2019) and warming in conjunction with nutrient limitation (Fernández et al. 2020; Flukes. et al. 2015; Mabin et al. 2013; Schmid et al. 2020). However, the combined drivers of warming and acidification (Britton et al. 2020a; 2021), warming and light (Paine et al. 2021a), and warming, light and nutrient limitation (Mabin et al. 2019a) have also been investigated.

The effects of ocean acidification on the responses of fleshy (i.e. non-calcifying) seaweeds is thought to depend on their inorganic carbon uptake strategies (Hepburn et al. 2011). Given the large proportion of non-CCM seaweeds in

Tasmania (Cornwall et al. 2015b), this island presents a unique opportunity to study how the response of seaweeds to ocean acidification is mediated by their inorganic carbon uptake mechanisms. The response of both non-CCM and CCM species to elevated CO_2 have been tested with varying responses. Non-CCM species tested (*Plocamium dilatatum*, *Callophyllis lambertii* and *Craspedocarpus ramentaceus*) in medium-term (1–2 weeks) laboratory growth experiments did not display elevated growth rates, however net photosynthesis increased in *C. lambertii* (Britton et al. 2019; van der Loos et al. 2019). Short-term (hours) exposure to elevated CO_2 increased dissolved inorganic carbon uptake in three species (*Plocamium angustum, Heminuera frondosa* and *Rhodymenia* sp.), however this translated into an increase in photosynthesis only for *P. angustum* (Cornwall and Hurd 2019). Species with a CCM appear likely to down-regulate the energetically costly CCM to rely more on diffusive CO_2 as an inorganic carbon uptake strategy (Britton et al. 2016, 2020a; van der Loos et al. 2019). However, it is unclear whether this will lead to a widespread benefit for CCM species because only the red seaweed *Lomentaria australis* showed an increase in growth rates following CCM down-regulation (van der Loos et al. 2019). No increases in growth were detected for the kelp *Ecklonia radiata* (Britton et al. 2016) or the fucoid *Phyllospora comosa* (Britton et al. 2020a), despite evidence of CCM down-regulation. In the only study testing responses of calcified seaweeds, mixed CCA assemblages were highly sensitive to the combined effects of warming and ocean acidification, with negative effects detected in conditions projected to occur by 2030 (Britton et al. 2021).

The effects of warming have been predominately negative for the species tested so far, with temperatures at and above 22 °C negatively affecting growth in *Ecklonia radiata* gametophytes and microscopic sporophytes (Mabin et al. 2013, 2019b), *Phyllospora comosa* juveniles (Flukes et al. 2015) and *Macrocystis pyrifera* juveniles (Mabin et al. 2019a). Temperature also affects germination of *M. pyrifera* gametophytes and differences between the northern and southern Tasmanian populations are evident (Iha et al., unpublished), with a germination temperature of 14–15 °C for northern strains and 13–14 °C for southern strains, while temperatures above 19 °C were fatal. The number of days until germination also varied between northern and southern populations, with southern population gametophytes germinating after 11 days and northern population after 15–19 days. However, thermal performance is enhanced with nitrogen sufficiency in *M. pyrifera* (Fernández et al. 2020; Schmid et al. 2020) and elevated CO_2 concentrations in *P. comosa* (Britton et al. 2020a). The remodelling of cell membrane fatty acids is an important mechanism of acclimation to high temperature, nutrient limitation and ocean acidification (Britton et al. 2020a; Schmid et al. 2020). Gametophytes of the endemic kelp *Lessonia corrugata* appear to be highly sensitive to elevated temperatures with a thermal optimum of 17 °C detected regardless of light levels, and strongly negative responses above this temperature (Paine et al. 2021a).

6.3 Local anthropogenic stressors

As urban density is highest in coastal regions, local anthropogenic stressors can impact seaweeds, manifesting in a variety of ecosystem responses (e.g. Strain et al. 2014, 2020). These stressors include the addition of excess nutrients, heavy metals and sedimentation from increased urbanisation, land uses in the catchment such as agriculture, and coastal industries including finfish aquaculture. In Tasmania, the majority of research in this area has focused on assessing the effects of excess nutrients from salmon aquaculture (Fowles et al. 2018a; Oh et al. 2015; White et al. 2022), heavy metals and sedimentation via storm water drains and shipping activities (Fowles et al. 2018a; Ling et al. 2018).

The addition of nutrients and heavy metals into coastal systems can impact seaweed directly through uptake but also through the interaction with excess sediment (Strain et al. 2015), decreased light availability (Kavanaugh et al. 2009), and other stressors all of which can indirectly impact seaweed communities and their trophic interactions (White et al. 2018). The response of Tasmanian seaweed communities to excess nutrients is comparable to that described by Pearson and Rosenberg (1978) such that, when systems are enriched, longer-lived and more stable species are progressively replaced with faster growing ephemeral species (Fowles et al. 2018a; Oh et al. 2015; White et al. 2022). In Tasmania, this manifests in the decline of brown seaweeds such as *Ecklonia radiata,* Dictyopteris *muelleri, Zonaria* spp. and foliose red seaweeds (Fowles et al. 2018a,b) and the proliferation of green seaweeds including *Ulva, Cladophora,* and *Chaetomorpha billardierii*, the red seaweed *Asparagopsis armata*, and a variety of turfing, epiphytic and filamentous seaweeds (Fowles et al. 2018a; Oh et al. 2015). These fast-growing species can reduce the availability of light for other species for space, and the combined effects of nutrient enrichment and sedimentation can lead to greater shifts in the overall community dynamics with larger kelps being replaced by smaller turf-forming seaweeds (Ling et al. 2018; Oh et al. 2015; Schiel and Gunn 2019; Strain et al. 2014). Increased cover of the matrix created by filamentous turfs and accumulated sediment represents a discontinuous phase shift in community

dynamics since the sediment matrix greatly inhibits or prevents recruitment of large canopy-forming species (Filbee-Dexter and Wernberg 2018; Reeves et al. 2018, 2022; Strain et al. 2014; Valentine and Johnson 2005a,b).

In the Tasman Peninsula region of Tasmania, local environmental impacts on seaweed appear to be strongly influenced by wave exposure (White et al. 2022). In more exposed locations, nutrients and heavy metals are more dispersed compared to sheltered locations (Fowles et al. 2018a; Oh et al. 2015). As wave exposure is also a fundamental driver of seaweed community composition (Edgar 1984; Hill et al. 2010), understanding the relationship between exposure and nutrient enrichment is key to evaluating the vulnerability or resilience of seaweed communities in any given location.

6.4 Seaweeds as bioindicators and biomonitors of nutrient and metal pollution

Seaweeds have also successfully been used as bioindicators for nutrient and heavy metal pollution in Tasmania. For example, changes in the responses of different seaweed functional groups (e.g. canopy-forming algae, enrichment indicator species and encrusting seaweeds) have been used to provide insights into the potential environmental effects of nutrient addition from salmon farming in south-east Tasmania, at both local (Fowles et al. 2018a; Oh et al. 2015; White et al. 2022) and regional (White et al. 2021) spatial scales.

Stable isotopes are tools used to track sources of nutrient enrichment. Where there are excess nutrients in the water column, green and red seaweeds will preferentially assimilate the lighter nitrogen isotope, with prolonged exposure changing the ratio of nitrogen in seaweed tissues (Howarth et al. 2019; Viana and Bode 2013). For example, in the Derwent estuary, changes in the isotopic signature of nitrogen in *Ulva* spp. revealed that the two major sources of nitrogen in the estuary are sewage and natural marine activities (van Os 2020). Further, *Ulva australis* is a useful bioindicator of heavy metal pollution including arsenic, cadmium, copper, lead, selenium, and zinc (Farias et al. 2017a,b, 2018, 2019). *Ulva australis* accumulated zinc in relatively high concentrations, with spatial variation in tissue concentrations of zinc within the estuary reflecting relative concentrations in seawater (Farias et al. 2018, 2019). Bioindicator and biomonitor research in Tasmania has highlighted a key role of seaweeds in the monitoring and assessment of impacts of various anthropogenic stressors.

7 Applications and industries

7.1 Bioactive compounds and natural products

Seaweeds are a rich source of natural products and 1000s of compounds with biological activity have been identified (Holdt and Kraan 2011; Ntie-Kang and Svozil 2020). This is particularly the case for red seaweeds which contain compounds currently used in a range of applications including cosmetics, pharmaceuticals, human food and health, and as supplements in agriculture (Aziz et al. 2020). For example, the red algal genus *Laurencia* has over 1000 secondary metabolites described (Davis and Vasanthi 2011). However, with very few exceptions, we know little about the natural products of Tasmanian seaweeds.

7.2 Fucoidan

Since the early 2000s, Tasmania has established a successful commercial fucoidan extraction industry, Marinova Pty Ltd, initially developed from harvesting the introduced kelp *Undaria pinnatifida* (Sanderson 1990b; Valentine and Johnson 2004) but more recently based on imported *U. pinnatifida* and other species including *Ascophyllum nodosum* from Canada. Fucoidans are sulfated, complex, fucose-rich polymers found in brown seaweeds and echinoderms (Fitton 2011; Fitton et al. 2015). Their function in brown seaweeds is to protect against pathogens, with the highest concentrations associated with the reproductive parts of the algae. Commercially, fucoidans have been used as an ingredient in food supplements for at least two decades, where they support human health in a complementary setting and are also used as topical cosmetic ingredients, but they are not currently used in any therapeutic applications classified as "pharmaceutical" (Citkowska et al. 2019; Fitton et al. 2015). Fucoidans have also been studied for their potential use as anticoagulants, anti-inflammatory, and anticancer agents *in vivo*. They are known as viral entry blocking agents and are effective against a wide range of coated viruses and some bacteria and have well-documented effects on cancer cell cycle arrest, enzyme inhibition, thrombolytic activity, and immune modulation (Gueven et al. 2020; Park et al. 2022; Zayed et al. 2022).

Fucoidans have structures that are species-specific, with properties that vary in composition, depending on the source biomass used. The polysaccharide backbone is typically composed of fucose monomers, but can also have significant contributions from galactose, xylose, arabinose, and

Table 4: Yields of different bioactive components from fucoidan extracts of four native Tasmanian seaweeds (order Fucales).

	% Yield	% Polyphenol	% Carbohydrate	% Fucose	% Galactose	% Glucose	% Xylose	% Mannose	% Other	Peak MW (kDa)
Cystophora polycystidea	5.88	15.3	55.0	31.0	17.6	33.5	7.8			171
Sargassum sp.	4.00	28.0	26.0	35.0	21.2	21.0	11.2	10.6		73
Cystophora retorta	9.13	43.7	22.7	39.6	27.2	15.4	11.8	5.2	0.8	79
Cystophora moniliformis	7.63	16.2	56.8	37.0	14.5	34.5	5.5	3.8	4.7	264

MW, molecular weight. Previously unpublished data, methods below. *Methods for the analysis of fucoidans from a range of Tasmanian brown seaweeds:* The yield, polyphenol and carbohydrate content were assessed, after which the saccharide composition, and MW profile of each extract was determined. The carbohydrate profile was obtained using a gas chromatography (GC)-based method for the accurate determination of individual monosaccharide ratios in a sample. This method relies on the preparation of acetylated alditol derivatives of the hydrolyzed samples (Morvai-Vitányi et al. 1993) The uronic acid content was determined by spectrophotometric analysis of the hydrolyzed compound in the presence of 3-phenylphenol, against glucuronic acid standards, based on a previously described method (Filisetti-Cozzi and Carpita 1991). Sulfate content was analyzed spectrophotometrically using a $BaSO_4$ precipitation method ($BaCl_2$ in gelatin), based on existing work (Dodgson 1961). Cations, including Na, K, Ca, and Mg, were determined by standard flame atomic absorption spectroscopy. Molecular weight profiles were determined by gel permeation chromatography, with the aid of a size-exclusion column and are reported relative to dextran standards. The polyphenolic components can be determined spectrophotometrically using the Folin-Ciocalteau reagent (Jiménez-Escrig et al. 2001; Zhang et al. 2006).

rhamnose. Worldwide, fucoidans are extracted from *Fucus vesiculosus, Ascophyllum nodosum, Ecklonia* spp., *U. pinnatifida, Cladosiphon* spp., *Laminaria japonica, Macrocystis pyrifera, and Kjellmaniella crassifolia* with manufacturers of bulk fucoidan operating in Japan, Russia, China, South Korea, Vietnam, Taiwan, and Australia. Although commercial fucoidan extraction from Tasmanian macroalgae has focussed on the introduced *U. pinnatifida,* other species have also been examined and here we report new information on the presence of fucoidan in native Tasmanian seaweeds within the family Sargassaceae (*Cystophora polycystidea, Cystrophora retorta, Cystophora moniliformis* and a *Sargassum* sp.; Table 4). Each of these Tasmanian species yielded a water-soluble co-extract rich in both fucoidan and polyphenol – the latter expressed as polyphloroglucinol equivalents. Interestingly, the fucoidan fractions included relatively high galactose contents, contrasting with the high abundance of fucose in many fucoidans extracted from other species within the order Fucales, such as *Fucus vesiculosus.* This high galactose content is not without precedent, however, with similar fucose:galactose ratios observed in extracts from the order Laminariales such as *Ecklonia radiata* and *Lessonia* sp. (Fitton 2011; Zayed et al. 2022).

7.3 Fatty acids

Seaweeds have gained increasing attention as a source of fatty acids, especially long chain polyunsaturated fatty acids for applications in functional foods and dietary supplements (van Ginneken et al. 2011). A 2018 screening of 61 Tasmanian seaweeds species indicated a promising resource for omega-3 fatty acids (Schmid et al. 2018). The survey comprised 11 Chlorophyta, 17 Phaeophyceae (Ochrophyta), and 33 Rhodophyta and showed that total fatty acid (TFA) concentrations varied considerably (between 0.6 and 7.8% of dry weight) between species. On average the Phaeophyceae exhibited the highest concentrations followed by Chlorophyta and Rhodophyta (Schmid et al. 2018). Results of the phylum-specific fatty acid profiles were in line with other studies around the world (Galloway et al. 2012; Kumari et al. 2013; Schmid et al. 2014). The fatty acid profile of most species was characterised by high proportions of polyunsaturated fatty acids (PUFA), and a low ratio of n-6/n-3 PUFA, which is beneficial when considering seaweeds for foods (Simopoulos 2002). An investigation of seasonal patterns in fatty acid composition at various Tasmanian locations (Bicheno, Coal Point, Mouldy Hole) indicate that they vary substantially with season and site, indicating that multiple environmental drivers influence fatty acid composition (Britton et al. 2020b).

7.4 Liquid fertilizers

Tasmania has two established companies that produce liquid fertilizers, Seasol™ established in 1974 (Arioli et al. 2015), and Natrasol™ and, for both, the raw material is from local beach-cast *Durvillaea* spp. and imported *Ascophyllum nodosum.* Seaweeds contain a range of compounds including

macro- and microelements (N, P, K, etc.), amino acids, vitamins, polysaccharides, and plant hormones (including cytokinins, auxins, abscisic acid) that have enormous benefits for agricultural and horticultural production, including enhanced crop yield, improved plant development like flowering and leaf development and fruit set, as well as enriching the soil microbiology and water holding capacity. Applications of seaweed extracts can enhance the tolerance of crops to a wide range of abiotic and biotic stresses such as enhanced ability to tolerate climatic stresses, plant disease, and improved resistance to insect and fungal attack such as mould and mildew (Arioli et al. 2015; Righini et al. 2018; Roberts et al. 2015).

7.5 Seaweed aquaculture including IMTA

The Australian seaweed industry, including Tasmania, is small but expanding rapidly. It has a current estimated value of AU$3 million, with the main source of seaweeds being wild harvest but, with the development of new aquaculture species, it is predicted to grow substantially in the upcoming decades (Kelly 2020). Much of this growth is predicted to be centred around the southern temperate regions, as demonstrated by the 5248 ha of marine farming leases allocated for seaweed aquaculture and other species in Tasmania (Kelly 2020). In Tasmania, there are three seaweed-related industries: (i) alginates, (ii) fertilisers and feeds for agriculture, and (iii) fucoidan bioactive compounds (see above, Lee et al. 2012). The alginate and fertiliser industries are primarily driven by the collection of beach-cast bull kelp (*Durvillaea* spp.) since the 1970s by Kelp Industries Pty Ltd. on King Island, Tasmania (Supplementary Table S1). Other Tasmanian based enterprises that collect bull kelp, albeit in smaller amounts, are TasKelp Ltd (King Island) and Kelpomix Ltd. (Granville Harbour). Overall, bull kelp from King Island supplies ~5% of the world's production of alginates, providing the island with an income of about AU $2.5 million. In 2017, the Tasmanian state government introduced a formal management plan under the *Living Marine Resources Management Acts (1995)* for the collection of beach-cast native marine plants and the harvest of some introduced pest species, including wakame (*Undaria pinnatifida*) for commercial purposes. Kai Ho Ocean Treasure harvests *U. pinnatifida* which is dried and sold as wakame. Market testing by Kai Ho of local seaweed species harvested under permit in 2016–2018 indicated strong interest for products from *Lessonia corrugata, Macrocystis pyrifera, Ulva* spp., *Chaetomorpha coliformis, Codium fragile* and the introduced *Grateloupia turuturu* as foods (J.C. Sanderson pers. comm.).

There is considerable interest in farming seaweeds in Tasmania, building on early work that identified various native species (47 reds, 31 greens, 18 browns) as suitable for the edible market, and trial cultivations of *Macrocystis pyrifera* and red seaweeds (e.g. *Gracilaria* spp. and *Gelidium* spp.) in the late 1980s and early 1990s – which focussed on the supply of feed for abalone (Scott and Sanderson 1994). There is currently no formal legislation on the source location of seedstock with respect to distance to the farm site nor regulations regarding at-sea farming of selectively bred high performing strains in Tasmania. At the time of writing, however, commercial and research permits are provided on a case-by-case basis. A permit application typically includes a description of the target species, an environmental impact assessment and monitoring plan, and some consideration of biosecurity and provenance of seedstock as well as the scale of the farming operations.

Ongoing research and development projects aim to initiate and expand seaweed cultivation in Tasmanian waters (Table S1). These include the development of kelp (*Ecklonia radiata, Lessonia corrugata* and *Macrocystis pyrifera*) aquaculture as part of an Integrated Multi-Trophic Aquaculture (IMTA) with salmon. Of these species, *M. pyrifera* has the highest ammonium uptake rates at both low and high concentrations, making it the preferred species (Smart et al. 2022). Optimal nursery conditions for reproduction and growth of juvenile sporophytes are: *E. radiata* = 15 °C and 30 μmol photons m^{-2} s^{-1}, *L. corrugata* = 12 °C and 60 μmol photons m^{-2} s^{-1}, and *M. pyrifera* = 12 °C and 30 or 60 μmol photons m^{-2} s^{-1} (Visch et al., unpublished). *Lessonia corrugata* gametophytes had a very narrow range of temperature over which gametophytes grew optimally at 15.7–17.9 °C (Paine et al. 2021a). The first trials of near-shore cultivation of *M. pyrifera* in south-eastern Tasmania indicate that, to optimise yield and quality of the cultured biomass, the kelp deployed in April (autumn) should be harvested in July-August (mid to late winter) (Biancacci et al. 2022a). The nutritional composition and heavy metal profile *M. pyrifera* and *L. corrugata* cultured in proximity to salmon and mussel farms indicate that they are suitable for human and animal consumption, except for the iodine content which was above the maximum tolerable level in dried seaweed established by Food Standards Australia New Zealand (Biancacci et al. 2022b). A similar result was found for wild-harvested *M. pyrifera* proximal and distal to salmon farms (Biancacci et al. 2022c). Modelling studies suggest that commercial scale aquaculture of *M. pyrifera* alongside salmon farms can significantly reduce nitrogen concentrations and chlorophyll levels (from phytoplankton) in adjacent waters, indicating the potential for nitrogen mitigation by the kelp (Hadley et al. 2018).

Another focus is the cultivation of *Asparagopsis armata*, which is native to Tasmania, as a livestock feed supplement to reduce methane emissions via enteric fermentation in ruminants. Methane emissions from ruminants contribute 9.2% of Australia's total Greenhouse Gas emissions (~14% globally) and small amounts of *Asparagopsis* containing the bioactive compound bromoform, fed to ruminants, reduce methane production by between 80 and 98% (Kinley et al. 2020; Roque et al. 2021; Stefenoni et al. 2021). Although there have been concerns raised about the potential toxicity of bromoforms via absorption by livestock and humans and potential ozone depletion due to mass cultivation of *Asparagopsis*, these risks appear very low (Glasson et al. 2022; Jia et al. 2022). Large-scale cultivation of *Asparagopsis* is suggested as a priority for the emerging Australian seaweed aquaculture industry (Kelly 2020) and in 2019 Sea Forest Ltd established a marine farm at Triabunna on the east coast to grow *Asparagopsis* as a feed supplement for livestock. Initial work in Tasmania has focussed on both on-land and ocean-based farming where the latter occurs via regrowth of gametophytes utilising the naturally occurring 'barbs' on thalli that hook onto ropes (Wright et al. 2022).

8 Summary

Tasmania has a diverse seaweed flora with 750 known species that is critically understudied with respect to fundamental information on taxonomy, developmental biology, demography, ecology and physiology for the vast majority of species. The best studied seaweeds are the important ecosystem engineers of the order Laminariales *Ecklonia radiata* and *Macrocystis pyrifera*, but Tasmania has a low diversity of 'true' kelps with just four species, and it is crucial to understand the roles of other large browns including the highly specious order Fucales. There is almost no knowledge about red seaweeds which appear to have globally unique carbon and nitrogen physiologies, and we lack basic information on life histories and seasonality. We recommend a renewed research focus on under-studied but ecologically dominant species, and the use of molecular phylogeny coupled with taxonomic research to assess the diversity of the seaweed flora, particularly the phylum Rhodophyta including coralline algae and order Fucales, if we are to better understand the functioning of Tasmanian seaweed communities, their responses to climate change, and to support management and industry development and Traditional practices and communities.

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Bionotes

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