Botany
An International Journal
for Plant Biology

Research Article

New and interesting seaweed records from the Hakai area of the central coast of British Columbia: Phaeophyceae

Sandra C. Lindstrom[a,b], **Matthew A. Lemay**[a,b], **Carly Janusson**[b], **Samuel Starko**[a,b], **Katharine R. Hind**[a,b], **and Patrick T. Martone**[a,b]

[a]Department of Botany and Biodiversity Research Centre, #3156–6270 University Blvd., University of British Columbia, Vancouver, BC V6T 1Z4, Canada; [b]Hakai Institute, Heriot Bay, Quadra Island, BC V0P 1H0, Canada

Corresponding author: **Sandra C. Lindstrom** (email: Sandra.Lindstrom@botany.ubc.ca)

Abstract

After 13 years of intensive sampling of seaweeds in the Hakai area of the central coast of British Columbia, we report on our collection of 67 of the approximately 100 brown algal species expected in the area based on known distributions. Most of these 67 species are distributed broadly in the northeast Pacific region. They were identified morphologically using primary and secondary literature and by sequencing the COI (cytochrome c oxidase subunit 1) gene in most instances. *Laminaria yezoensis* is recorded near its southern distribution limit, and *Dictyoneurum reticulatum* is recorded at its northern distribution limit. Although drift specimens of *Postelsia palmaeformis* have washed ashore, the species has not been found growing on Calvert Island but rather on the mainland just to the southeast. A number of species are reported for the first time in the northeast Pacific: we identified *Hecatonema terminale*, based on efforts to sequence several host species of red algae, an undescribed species of Acinetosporaceae previously identified erroneously as *Hincksia granulosa* that still requires a name, and undescribed species of *Pylaiella* and *Ectocarpus*. We describe as new to science *Protohalopteris petersonii* and *Petrospongium munckiae* and note a number of other species that require work before they can be identified to species, including a *Ralfsia*-like crust in the Chordariaceae. Distinctive haplotypes were found in at least four species, contributing to the uniqueness of this area.

Key words: biogeography, British Columbia central coast, brown algae, Hakai, Phaeophyceae, taxonomy

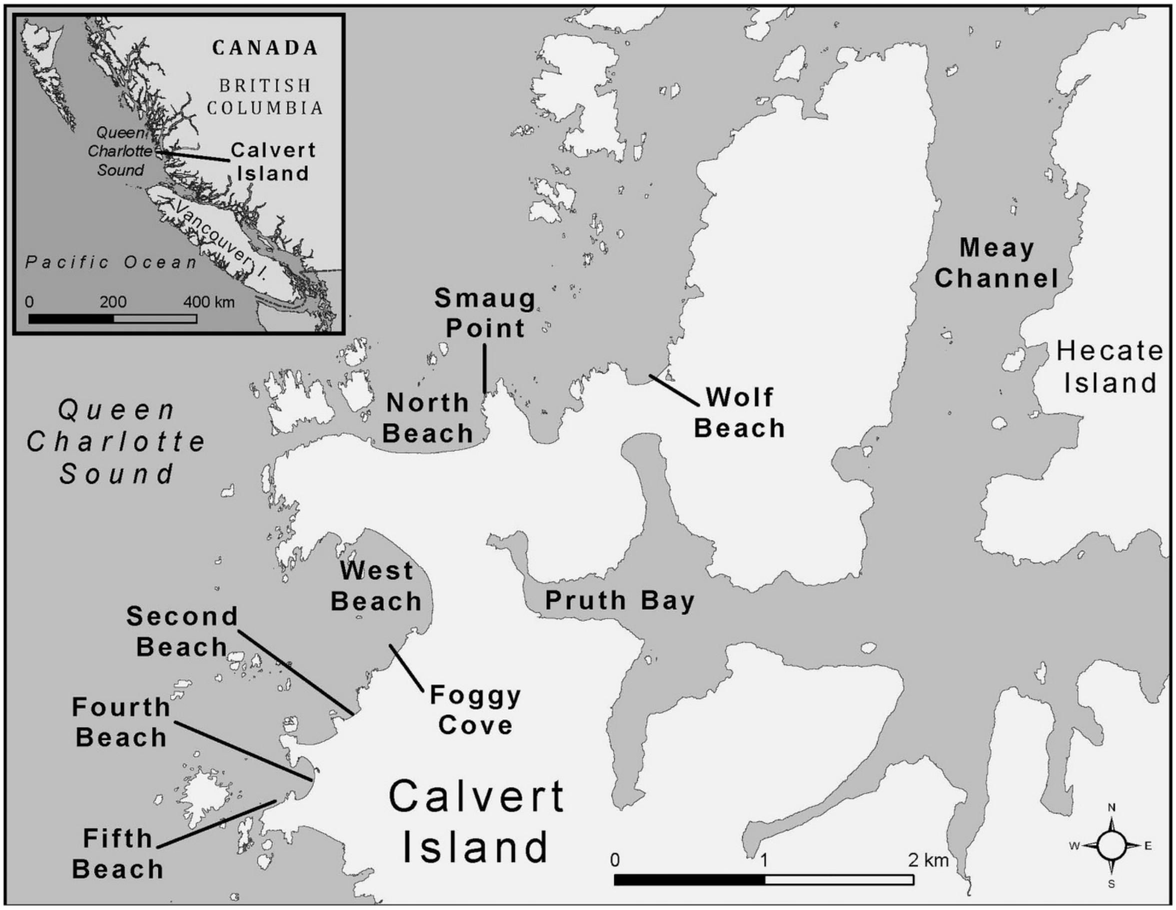
Introduction

Brown algae (Class Phaeophyceae, Phylum Heterokontophyta), one of the three major groups of seaweeds, are a significant part of the benthic marine environment. Kelps (order Laminariales) and other large, habitat-forming species like members of the Desmarestiales and Fucales are especially important foundational species in nearshore ecosystems (Steneck et al. 2002; Teagle et al. 2017). Many of these species have economic value as food or sources of phycocolloids (Critchley and Ohno 1998), and they have recently been recognized as potential natural climate solutions because of their capacity for carbon dioxide removal, storage, and export (Hurd et al. 2024; McHenry et al. 2024). Although smaller species of Phaeophyceae generally have lesser value economically and ecologically, some still play a significant role in these arenas (e.g., the chordarialean genera *Cladosiphon* and *Nemacystus* as human food (Critchley and Ohno 1998) and endophytic browns (including alternate phases in heteromorphic life histories) as significant food for mesoherbivores (Amsler et al. 2009; Aumack et al. 2010)). Because of the importance of brown algae as key habitat-forming organisms and integral members of the food web, it is critical that we understand their diversity and biogeographic ranges, especially given ongoing impacts of global change (Filbee-Dexter and Wernberg 2018; Wernberg et al. 2024).

No comprehensive taxonomic study of brown algae in British Columbia has been published, but more than 100 species of brown algae have been documented in the province in the most recent comprehensive list (Gabrielson and Lindstrom 2018). Early work, summarized in Scagel et al. (1989), included studies of kelps and other brown algal species by many of Scagel's students and post-docs. Since then, most taxonomic studies on BC seaweeds have used DNA sequencing to decipher species' identities and evolutionary relationships (with a smattering of life history and ecological studies). These studies have refined species boundaries and names and added several new species to the BC flora (Saunders and McDevit 2014; McDevit and Saunders 2017; Parente and Saunders 2019).

This paper represents the second in a series on the seaweed flora of the Hakai area of the central coast of British Columbia based on research carried out at the Hakai Institute's field station on Calvert Island. The name Hakai comes from the Heiltsuk language and means "wide passage". It refers to the wide pass between Calvert and Hecate Islands to the south and Stirling and Nalau Islands to the north and is a world-renowned fishing destination. This name was also bestowed

Fig. 1. Location of Calvert Island along the central coast of British Columbia (inset) and local collecting sites. This map was created using ArcGIS Desktop 10.8.2. Shoreline data adapted by the Hakai Institute in 2021 sourced from OpenStreetMap contributors. Retrieved from https://planet.openstreetmap.org, 2021. Border data sourced Natural Earth, retrieved from www.naturalearthdata.com, 2021. Map created by Keith Holmes, Hakai Institute.



on the surrounding Hakai Lúxvbális Conservancy, established on 23 May 2008 and encompassing the area where our studies were conducted. This region is the traditional territory of the Wuikinuxv and Heiltsuk First Nations. Our first paper (Lindstrom et al. 2021) covered the green seaweeds (Chlorophyta), and subsequent papers will cover the much more diverse red algal flora (Rhodophyta). As noted in Lindstrom et al. (2021), our study sites are primarily on Calvert Island and vicinity (Fig. 1). Since our earlier paper, the area has continued to experience significant heat waves (Whalen et al. 2023). Thus, this paper represents a snapshot of the flora during more than a decade of change from 2011 to 2024.

The central coast of BC represents a transitional area between the temperate flora of California and the more boreal flora of Alaska. Saunders (2014) noted the similarities of the subtidal flora of Haida Gwaii to California, which he attributed at least in part to long distance kelp rafting. However, another possible explanation for species diversity in the area is post-glacial recolonization (Lindstrom et al. 1997). Recent heat waves provide an additional dimension to the diversity discussion, as species ranges have started to shift at large and small spatial scales (Whalen et al. 2023; Starko et al. 2024*a*, 2024*b*).

Much work remains to be done on Phaeophyceaen algae in British Columbia. Determining the correct name to apply to an individual species may require additional work beyond just keying it out. If a species was originally described from BC or nearby areas, then it is reasonable to assume that the name is correctly applied. However, if a species was originally described from further afield, such as northern Europe or Japan, then more careful comparisons are required. Below, we reference studies that compare DNA sequences to show that some species are the same as those from more distant regions, whereas other species are distinct despite their morphological similarities, as has been observed with other cryptic species in the region (Lindstrom et al. 2011; Hind et al. 2015; Wade et al. 2023).

The present study offers one of the most comprehensive investigations of the brown algal flora of British Columbia, focusing on an area that has been inadequately sampled or studied until now. We follow the taxonomy of Gabrielson and Lindstrom (2018) unless noted otherwise, and this report serves to update that publication. We also update some names in Barcode of Life Data (BOLD) and GenBank. A number of papers have already highlighted some of the new species and records of red and green algae from this area

(Hind et al. 2015, 2016; Lindstrom et al. 2015, 2021; Lindstrom 2018). In addition to reporting new records, we also discuss species and species complexes that require further work.

Methods and materials

Intertidal seaweed collections have been made annually every summer since 2011 (except for 2020) on the northwest corner of Calvert Island and vicinity (Fig. 1), usually in late May to mid June (collections in 2011 were in mid August and those in 2012 in early July). Subtidal collections were made in 2013, 2017, 2018, 2019, 2022, and 2023, and winter visits were made in mid February 2014 and late March 2018. Voucher specimens are deposited in the phycological herbarium of the Beaty Biodiversity Museum, University of British Columbia (UBC), and molecular sequences have been deposited in GenBank. Identifications were made using morphology, following the keys of Gabrielson and Lindstrom (2018) and original literature as needed, as well as molecular data.

The majority of samples were submitted to the Canadian Centre for DNA Barcoding (CCDB) for DNA extraction, amplification and sequencing of the barcode region of the mitochondrial cytochrome oxidase 1. DNA extractions were carried out using the protocol described by McDevit and Saunders (2009). Amplification used the primers GazF2-GazR2 (Lane et al. 2007) or GHalF-GazR1 (Saunders 2005, 2008) to amplify and sequence the 5′ end of the mitochondrial COI gene. Some additional samples were processed at the Hakai Institute Genomics Lab using the Qiagen DNEasy Plant Kit for DNA extractions, amplified using the same primers as above, and sequenced at the Genome Quebec sequencing facility. Samples processed in the Martone Lab at UBC were extracted following McDevit and Saunders (2009), amplified as above, and also sequenced at the Genome Quebec sequencing facility. All sequences were compared to accessions in NCBI and in the BOLD system (Ratnasingham and Hebert 2007) as part of the process of determining species identity. Puillandre et al. (2012), in developing their Automatic Barcode Gap Discovery method, found the level of divergence between species of metazoa to lie between 1 and 3%, numbers similar to those found for *Ralfsia*, Scytosiphonaceae and other brown algal COI sequences (McDevit and Saunders 2009, 2017; Saunders and McDevit 2013; Parente and Saunders 2019). We used these numbers as guidelines; actual species delimitations need to be complemented with other evidence in an integrative taxonomic approach.

For a few specimens, DNA amplification targeted the ribulose-1,5-bisphosphate carboxylase/oxygenase large subunit (rbcL) using primers rbcL3F: 5′-GGC ACC GGA GAA TCT ATA TG-3′, and rbcL616R: 5′-GTT GTG AGT TAA TAT TTT CAT CAT C-3′ (Peters and Ramírez 2001). PCR reactions were comprised of 12.5 μL of 2X Master Mix Taq (FroggaBio), 0.6 μL of each 10 μmol L^{-1} primer, 3.75 μL of BSA (New England Biolabs) at 10 mg mL^{-1}, 6.05 μL of nuclease-free water, and 1.5 μL of DNA template at ∼5–10 ng μL^{-1} for a final volume of 25 μL. PCR conditions included polymerase activation at 94 °C for 4 min, followed by 38 cycles of denaturation, amplification, and elongation at 94 °C for 1 min, 50 °C for 30 s, and 72 °C for 1 min, respectively, followed by a final elongation step at 72 °C for 7 min. These amplifications were done at the Hakai Institute Genomics Lab, and products were sequenced at the Genome Quebec facility.

For the present study, maximum likelihood phylogenetic analyses were performed using MEGA12: Molecular Evolutionary Genetics Analysis version 12 (Kumar et al. 2024) with 500 bootstrap replicates, GTR model, gamma distribution for invariant sites, and five threads. Hakai specimens are identified by an asterisk in all trees.

Results

Class Phaeophyceae

We sequenced 55 species of Phaeophyceae (Table 1—we follow the taxonomic order in Gabrielson and Lindstrom 2018, as elaborated in Table S1). In addition, we identified morphologically an additional 12 species, for which we were unable to obtain DNA sequences. All told, these records represent slightly more than 50% of the species of brown algae recorded for British Columbia (Gabrielson and Lindstrom 2018; Table S1). Sequences for *Dictyota binghamiae* J. Agardh (order Dictyotales, family Dictyotaceae) and *Phaeostrophion irregulare* Setchell & N.L. Gardner (order Sphacelariales, family Phaeostrophiaceae) were identical to published sequences from other areas of British Columbia. Discussions of the other species we sequenced follow.

Order Sphacelariales
Family Stypocaulaceae

Material from a single specimen in this family (PTM512, Table 1), which was field identified as *Sphacelaria rigidula* Kützing, was sequenced by Starko et al. (2021). Although there were difficulties in assembling its mitochondrial genome (MZ156064) into a full circle due to a complex assembly graph and possible contamination (Starko et al. 2021), there were no such problems with the chloroplast genome (MZ156028). A maximum likelihood (ML) phylogeny of *rbc*L and *psb*C genes shows that this species is most closely related to *Protohalopteris radicans* (Dillwyn) Draisma, Prud'homme & H. Kawai in the family Stypocaulaceae (Fig. 2) but is evolutionarily distinct. We describe this species as new to science.

Protohalopteris petersonii sp. nov. S.C. Lindstrom, Starko & Martone (Fig. 3)

Thalli to 20 mm tall (Fig. 3*a*) and 50–60 μm diam., forming dense carpets (Fig. 3*b*) or scattered tufts (Fig. S1) on intertidal rock, often in areas scoured by sand and sometimes near beach run-off. Thalli dark (olive) brown. Abundant thalli arising from small basal discs of radiating, branched, coalescent filaments with apical growth (Figs 3*c* and 3*d*). Uprights sparingly branched to one or two orders from hypacroblastic branching. Pericysts present (these are evident as dark inclusions in Figs 3*e*–3*i*). Surface peripheral cells subdivided by 1–3 transverse walls (Fig. 3*f*). Rhizoids rare (Figs 3*f* and 3g). Presumptive reproductive branches abundant on a few uprights (Figs 3*h* and 3*i*) but mostly absent (it is unclear whether these produce unangia or plurangia since no actual reproductive

Table 1. Sample information and collection data for sequenced specimens.

Species	Sample ID	Collection date	Location	Habitat	UBC accession	COI accession
Dictyota binghamiae	PTM432	22 May 2013	Wolf Beach	Subtidal 8 m on boulder	A089753	PV694765
	PTM459	24 May 2013	West Beach	Subtidal 6 m on boulder	A090383	PV694766
	SCL 17060	26 July 2017	Foggy Cove	Subtidal 5.5 m (*Nereocystis* bed)	A094327	PV694767
	SCL 17201	1 August 2017	North Beach	Subtidal on cobble (*Nereocystis* bed) at <23′	A094438	PV694768
	PTM2008	10 June 2022	Fifer Bay	Subtidal 3–5 m	A101829	PV694769
Phaeostrophion irregulare	SCL 17484	5 June 2019	North Beach, W end	Low intertidal boulder	A100736	PV694770
Protohalopteris petersonii	PTM512	27 May 2013	North Beach bench	High intertidal near freshwater	A089833	MZ156064; MZ156041 (plastid complete genome)
Desmarestia aculeata	PTM496	25 May 2013	North Beach bench	Subtidal 6–8 m	A089817	PV694771
	PTM580	28 May 2013	Between Fifth & Sixth Beaches	Subtidal 3.5 m on boulder	A089901	PV694772
	PTM1581	26 July 2017	Foggy Cove	Subtidal 3 m	A093219	PV694773
	SCL 16997	24 July 2017	North Beach, W end	Low intertidal rock near sand	A094269	PV694774
Acinetosporaceae (not *Hincksia granulosa*)	SCL 17132	30 July 2017	Rattenbury Island	Sloping soft sediment down to ~40’ below ELLW, on worm tube		PV694775
Hincksia sandriana	PTM2010	10 June 2022	Fifer Bay	Subtidal 4 m	A101823	PV694776
Pylaiella 1	SCL 17371	17 June 2018	Pruth lagoon	High intertidal, mixed with dwarf Fucus	A096336	PV694778
	SCL 17841	20 June 2022	Pruth lagoon	Intertidal	A101806	PV694779
Pylaiella 2	SCL 17373	17 June 2018	Pruth lagoon	Mid intertidal mud or in stream	A096338	PV694780
	PTM1727	13 June 2018	Fifth Beach site	High intertidal	A096913	PV694781
	PTM2003b	10 June 2022	Convoy Pass	Subtidal, 2–5 m	A101816	PV694782
Acrothrix gracilis	SCL 17230	1 August 2017	Head of Pruth Bay	Under dock, subtidal ~2 m	A094448	PV694783
Coilodesme bulligera	PTM545	27 May 2013	Meay Islet	Subtidal 3.5 m	A089866	PV694784
Dictyosiphon sinicola	SCL 17043	26 July 2017	Pruth islet site	Lying loose in a shallow eelgrass bed	A094310	PV694786
	SCL 17426	28 June 2018	Pruth Bay	NA	A096370	PV694787
Elachista sp.	SCL 16944	22 July 2017	Little Wolf Beach	Mid intertidal, on Fucus distichus	A094234	PV694788
Hecatonema terminale	SCL 16937	22 July 2017	Little Wolf Beach	Low intertidal, in/on *Smithora naiadum*	A094228	PV694789
	SCL 17025	25 July 2017	Fifth Beach exposed	Very high intertidal pool, in/on *Neorhdomela oregona*	A094295	PV694790
	PTM1731	13 June 2018	Fifth Beach	In/on *Bossiella*	A096917	PV694791
Leathesia marina	PTM505	27 May 2013	“West Beach Bench”	Lower mid intertidal	A089826	PV694792
	SCL 15321	27 May 2013	North Beach, E end	Lower mid intertidal boulder	A090291	PV694793
Microspongium globosum	SCL 17825	18 June 2022	Foggy Cove	Low intertidal, endophytic in *Dilsea*		PV694794
Myriocladia lovenii	PTM2003a	10 June 2022	Convoy Pass	Subtidal 3.5 m	A101815	PV694795
	PTM2004	10 June 2022	Convoy Pass	Subtidal 3.5 m	A101817	PV694796
	SCL 17745	10 June 2022	Corvette Island	Subtidal 2–5 m	A101800	PV694797
Punctaria expansa	SCL 17364	16 June 2018	Head of Pruth Bay	On dock just below water level or floating	A096331	PV694798
	SCL 17394	23 June 2018	Choked Pass	Unreported but probably in an eelgrass bed	A096352	PV694799

Table 1. (*continued*).

Species	Sample ID	Collection date	Location	Habitat	UBC accession	COI accession
Punctaria tenuissima	SCL 16807	27 May 2017	Meay Channel site	Low intertidal (low, mid, high transects)	A094179	PV694800
	SCL 17456	3 June 2019	Meay Channel site	Low intertidal (mid transect)	A100717	PV694801
"Ralfsioid"	MAL 202	21 March 2015	Foggy Cove	"Rocky intertidal shore"	A101419	MK959574
	MAL 205	19 March 2015	Foggy Cove	"Rocky intertidal shore"	A101420	MK959560
	MAL 281	19 March 2015	Foggy Cove	"Rocky intertidal shore"	A101423	MK959546
	MAL 539	21 March 2015	Foggy Cove	"Rocky intertidal shore"	A101439	MK959539
	SCL 17446	3 June 2019	Meay Channel site	Low intertidal cobble (between mid & high transects)		PV694802
Saundersella simplex	SCL 16838	29 May 2017	Little Wolf Beach	Low intertidal, on *Analipus japonicus*	A094204	PV694803
Soranthera ulvoidea	PTM1760	11 June 2018	Foggy Cove	Drift		PV694804
Ectocarpus "6"	PTM513	27 May 2013	North Beach	Low intertidal, epiphytic on *Hedophyllum sessile*	A089834	PV694808
Ectocarpus 2	SCL 17279	22 March 2018	Little Wolf Beach	Mid intertidal, epiphytic on old Halosaccion		PV694807
Ectocarpus "1"	SCL 17408	26 June 2018	Head of Pruth Bay	On dock, epiphytic on *Scytosiphon*		PV694806
Petrospongium munckiae	PTM1558	30 May 2017	Fifth Beach exposed	Mid intertidal bedrock, near *Endocladia*, in channel	A093594	PV694809
Colpomenia peregrina	MAL 142	22 March 2015	Foggy Cove	"Rocky intertidal shore"		MK959529
	SCL 17052	26 July 2017	Foggy Cove	Subtidal 5.5 m in *Nereocystis* bed	A094319	PV694811
Dactylosiphon bullosus	MAL 490	22 March 2015	Foggy Cove	"Rocky intertidal shore"	A101430	PV694812
	PTM1550	26 May 2017	North Beach, E end	Low intertidal boulder	A093592	PV694813
	PTM1578	May 2017	North Beach site	Low intertidal bedrock	A101809	PV694814
Melanosiphon intestinalis	SCL 16849	30 May 2017	Foggy Cove	Low intertidal boulder	A094213	PV694815
Petalonia sp.	PTM1574	May 2017	North Beach	Low intertidal bedrock		PV694817
Scytosiphon lomentaria	PTM577	28 May 2013	Fourth Beach	Low intertidal rock in sand	A089898	PV694820
	SCL 17487	5 June 2019	North Beach, W end	Low intertidal boulder	A100739	PV694822
	PTM1715	9 June 2016	Foggy Cove	Low intertidal	A093597	PV694821
Fucus distichus	MAL 35	19 March 2015	Foggy Cove	"Rocky intertidal shore"	A101425	MK959542
	MAL 44	20 March 2015	Foggy Cove	"Rocky intertidal shore"	A101428	PV694823
	MAL 79	18 March 2015	Foggy Cove	"Rocky intertidal shore"	A101448	PV694824
	MAL 119	18 March 2015	Foggy Cove	High intertidal sediment		MK959558
	MAL 226	21 March 2015	Foggy Cove	"Rocky intertidal shore"	A101421	PV694825
	MAL 500	18 March 2015	Foggy Cove	"Rocky intertidal shore"	A101433	PV694826
	MAL 517	19 March 2015	Foggy Cove	"Rocky intertidal shore"	A101435	PV694827
	MAL 536	20 March 2015	Foggy Cove	"Rocky intertidal shore"	A101438	PV694828
	MAL 543	21 March 2015	Foggy Cove	"Rocky intertidal shore"	A101440	PV694829

Table 1. (*continued*).

Species	Sample ID	Collection date	Location	Habitat	UBC accession	COI accession
	MAL 558	20 March 2015	Foggy Cove	“Rocky intertidal shore”	A101442	PV694830
	SCL 17838	20 June 2022	Pruth lagoon	High intertidal sediment	A101805	PV694831
Fucus spiralis	MAL 60	20 March 2015	Foggy Cove	“Rocky intertidal shore”	A101446	PV694832
	MAL 514	20 March 2015	Foggy Cove	“Rocky intertidal shore”	A101434	PV694833
Sargassum muticum	SCL 17042	26 July 2017	Meay Channel site	Low intertidal cobble	A094309	PV694835
	SCL 17444	3 June 2019	Meay Channel site	Drift	A100710	PV694836
Stephanocystis geminata	PTM1653	31 July 2017	Kelpie Point	Subtidal 23 m	A093290	PV694837
Agarum clathratum	SCL 17066	26 July 2017	East end Kwakshua Channel	Subtidal	A094333	PV694839
Costaria costata	MAL 496	19 March 2015	Foggy Cove	Intertidal rock	A101432	MK959530
Dictyoneurum reticulatum	SCL 17045	26 July 2017	Foggy Cove	Subtidal	A094312	PV694840
	SCL 17046	26 July 2017	Foggy Cove	Subtidal	A094313	PV694841
Neoagarum fimbriatum	PTM534	27 May 2013	Meay Islet	Subtidal 3.5 m	A089855	PV694842
	SCL 16365	8 June 2016	Meay Channel site	Low intertidal		PV694843
Alaria marginata	MAL 65	20 March 2015	Foggy Cove	“Rocky intertidal shore”	A101447	PV694844
	MAL 494	19 March 2015	Foggy Cove	“Rocky intertidal shore”	A101431	MK959557
	MAL 527	20 March 2015	Foggy Cove	“Rocky intertidal shore”	A101436	PV694845
	MAL 564	19 March 2015	Foggy Cove	“Rocky intertidal shore”	A101444	PV694846
	SCL 17981	30 May 2023	Outside Draney Narrows	Subtidal 2–6 m, high current area	A101807	PV694847
Lessoniopsis littoralis	PTM574	28 May 2013	Fifth Beach exposed	Low intertidal bedrock	A089895	PV694848
Pleurophycus gardneri	SCL 16960	23 July 2017	Smaug Point	Low intertidal bedrock		PV694849
Pterygophora californica	SCL 16998	24 July 2017	North Beach W end	Low intertidal rock near sand	A094270	PV694850
	SCL 17184	1 August 2017	Triquet Island	Subtidal, in *Macrocystis* bed	A094425	PV694851
Cymathaere triplicata	SCL 17996	4 June 2023	North Beach	Drift	A101808	PV694852
Hedophyllum nigripes	SCL 17056	26 July 2017	Foggy Cove	Subtidal kelp bed	A094323	PV694853
	SCL 17196	1 August 2017	Triquet Island	In Macrocystis bed	A094434	PV694854
	SCL 17793	15 June 2022	Meay Channel	Low intertidal cobble	A101802	PV694855
	MAL 532	21 March 2015	Foggy Cove	“Rocky intertidal shore”	A101437	MK959550
	MAL 546	19 March 2015	Foggy Cove	“Rocky intertidal shore”	A101441	MK959570
Hedophyllum sessile	SCL 17832	19 June 2022	North Beach	Low intertidal bedrock	A101804	PV694856
Laminaria ephemera	PTM971	12 June 2014	West Beach	Drift		PV694857
Laminaria setchellii	MAL 426	19 March 2015	Foggy Cove	“Rocky intertidal shore”	A101426	MK959536
Laminaria yezoensis	MAL 444	21 March 2015	Foggy Cove	Intertidal rock	A101429	MK959576
Macrocystis tenuifolia	SCL 16924	22 July 2017	Little Wolf Beach	Low intertidal boulder	A094217	PV694858
Nereocystis luetkeana	SCL 15324	27 May 2013	North Beach, E end	Very low intertidal boulder	A090296	PV694859
	SCL 16954	23 July 2017	Smaug Point chasm	Low intertidal bedrock	A094241	PV694860
	SCL 17483	5 June 2019	North Beach, E end	Low intertidal boulder	A100735	PV694861

structures were seen, or whether these are merely young vegetative branches). Hairs, propagules, and acroblastic branching not seen.

TYPE SPECIMEN: PTM512 (UBC A089833), intertidal rock near beach runoff, North Beach, 27 May 2013, Leg. P.T. Martone (Fig. 3*a*).

ETYMOLOGY: The specific epithet honours Eric Peterson, whose generous support facilitated work on this and other seaweeds on the central coast of British Columbia.

Draisma et al. (2010) differentiated *Protohalopteris* (based on its type and only species, *P. radicans*) from other Stypocaulaceae in having a radial pattern of cell division in transverse section (versus periclinal in other genera), no differentiation into a medulla and cortex, and zoidangia not formed in axils. Our light microscope examination of *P. petersonii* showed that these characters also hold true for this species. Moreover, *Protohalopteris* shows a combination of acroblastic branching, which it has in common with other Stypocaulaceae but not other Sphacelariales, and hypacroblastic branching, which it shares with *Sphacelorbus*. Also, like other Stypocaulaceae, phaeophycean hairs, when present, occur in clusters. The description of the monotypic *Protohalopteris* in AlgaeBase, contributed by Prud'homme van Reine, largely applies to the new species, with the following differences: hairs not observed (in groups in *P. radicans*), only hypacroblastic branching seen (some laterals arising by acroheteroblastic or by dichotoblastic branching in *P. radicans*), and presumptive reproductive filaments many cells long and branched (versus sessile or with unicellular stalks (unangia) or on 1–4 celled stalks (plurangia) in *P. radicans*). This is the first record of the family Stypocaulaceae in the region (Gabrielson and Lindstrom 2018).

Although other species of Sphacelariales have been reported from British Columbia (Scagel et al. 1989; Gabrielson and Lindstrom 2018), no species of *Protohalopteris* has been recorded. However, two unpublished COI sequences of *P. petersonii* in BOLD (accessed 24 January 2024), one from the Bamfield area and the other from the Prince Rupert area of British Columbia, suggest that this species is broadly distributed in the region albeit probably under different names.

Order Desmarestiales
Family Desmarestiaceae

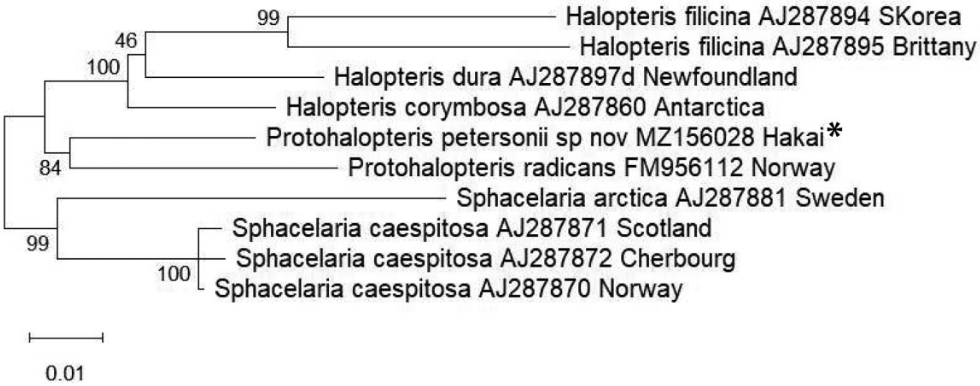
Although we collected specimens we identified as *Desmarestia aculeata* (Linnaeus) J.V. Lamouroux, *Desmarestia herbacea* (Turner) J.V. Lamouroux, *Desmarestia ligulata* (Stackhouse) J.V. Lamouroux, and *Desmarestia viridis*, we obtained sequences only for *D. aculeata*, perhaps due to interference from the HCl vacuoles in the other species. As noted previously (Peters et al. 1997), *D. aculeata* appears to be separated into two different clades, with the Pacific one more closely allied with *Desmarestia latifrons* (Ruprecht) Kützing from southern Oregon to southern California than with the Atlantic one (based on ITS1 and ITS2 sequences from the nuclear rRNA cistron—data not shown). An ML analysis of COI sequences (Fig. S2), including those from the Hakai area, also puts North Pacific sequences on a separate branch from European *D. aculeata*.

Table 1. (*concluded*).

Species	Sample ID	Collection date	Location	Habitat	UBC accession	COI accession
Saccharina latissima	PTM1690	5 August 2017	Outer Sandspit	Attached to cobble	A093319	PV694862
Egregia menziesii	PTM506	27 May 2013	"West Beach Bench"	Low intertidal	A089827	PV694864
	MAL 43	20 March 2015	Foggy Cove	Intertidal rock	A101427	MK959534
Eisenia arborea	PTM2017	11 June 2022	Jeffery Pinnacle	Subtidal, 9 m	A101826	PV694865
	PTM2022	11 June 2022	Jeffery Pinnacle	Subtidal, 9 m	A101821	PV694866
Analipus japonicus	PTM502	27 May 2013	North Beach	Low intertidal bedrock	A089823	PV694867
	MAL 300	22 March 2015	Foggy Cove	"Rocky intertidal shore"	A101424	MK959545
	MAL 562	22 March 2015	Foggy Cove	"Rocky intertidal shore"	A101443	PV694868
	MAL 569	22 March 2015	Foggy Cove	"Rocky intertidal shore"	A101445	MK959548
Ralfsia unimaculata	SCL 17049	26 July 2017	Foggy Cove	Subtidal 5.5 m in *Nereocystis* bed	A094316	PV694870

Note: Voucher specimens for most are deposited in the UBC Beaty Biodiversity Museum and can be searched for there (https://collections.beatymuseum.ubc.ca/) by collector number (Sample ID) or UBC Accession number. GenBank numbers are provided for COI accessions. Species that are new records for the area are highlighted in bold.

Fig. 2. Maximum likelihood (ML) phylogeny of species of Stypocaulaceae based on published concatenated *rbc*L and *psb*C sequences.



However, in this analysis, Canadian Arctic specimens were identical to European *D. aculeata*, whereas other northwest Atlantic specimens (from Newfoundland, New Brunswick, and Nova Scotia) were more closely related to Pacific specimens albeit on a separate branch. Complete plastid genomes have been sequenced for both Atlantic (NC_085300.1 (https://www.ncbi.nlm.nih.gov/nucleotide/NC_085300.1?report=genbank&log$=nucltop&blast_rank=2&RID=B7E8HFPF016)) and Pacific (MZ156041.1 (https://www.ncbi.nlm.nih.gov/nucleotide/MZ156041.1?report=genbank&log$=nucltop&blast_rank=1&RID=B7E8HFPF016)) *D. aculeata*; they are 99.26% identical (GenBank, 7 August 2024). These results raise the possibility that a different name should be applied to Pacific and NW Atlantic *D. aculeata* (the type locality of the species is between England and France—Silva et al. 1996). Another name does exist for Pacific *D. aculeata*: *Desmarestia intermedia* Postels & Ruprecht; this species is recognized by the Russians (Perestenko and Zakhodnova 2007; Klochkova et al. 2009), although not by other North Pacific phycologists, and no sequences are available for this species. Further work is required on this and the other large and ecologically important *Desmarestia* species.

Order Ectocarpales
Family Acinetosporaceae

We obtained COI sequences for eight Acinetosporaceae specimens (Table 1; Fig. 4), which included two *Pylaiella* species, *Hincksia sandriana* (Zanardini) P.C. Silva, and one undetermined species. The undetermined species (SCL17132) was initially identified as *Hincksia granulosa* (Smith) P.C. Silva based on morphology. It had a COI sequence identical to two South American specimens: an unpublished Falkland Is. sequence provided by Akira Peters, and a Chilean sequence (LN828736), also identified as *H. granulosa* (Mystikou et al. 2016), which had a number of erroneous inserts (Fig. 4). None of these sequences was closely related to true *Hincksia granulosa* (Fig. 4, LM995250), which was the most abundant species encountered by Peters et al. (2015) in their mainly European study of microscopic brown algae. These specimens were 99.18%–99.26% similar to Japanese specimens identified as *Hincksia fuscata* (Zanardini) P.C. Silva; however, since the type locality of this species is Italy, it is unclear whether this species name is applied appropriately. Both the Chilean and BC specimens occurred subtidally on a soft bottom, the Chilean specimen at 13 m beneath an aquaculture installation, and the BC specimen at ∼12 m on a worm tube. Both specimens were distinguished by thalli reaching several cm in length and possessing frequent subopposite branches. Plurangia on the Chilean material were numerous, ovoid, irregular on main and side branches, sessile or on few-celled stalks (Mystikou et al. 2016), characters suggesting *H. granulosa*. The significant genetic distinction of these Chilean and BC specimens from true *H. granulosa* (<85% similar) suggests that these specimens represent a distinct species if not a separate genus. Other BC specimens identified as *Hincksia granulosa* were collected at Stanley Park, Vancouver (UBC A063334), Calvert Island (UBC A090488), and Triple Island, northern BC (UBC A020672); the identities of these specimens have not been verified by sequencing, and they require re-examination before the presence of *H. granulosa* in BC can be confirmed. In contrast, the occurrence of *H. sandriana* is confirmed on the coast, with sequenced specimens from Bamfield and the Hakai area, BC, as well as Sitka, Alaska, to the north; this species occurs in a strongly supported clade with the type of the genus *Hincksia hincksiae* (Harvey) P.C. Silva (Fig. 4).

Genus *Pylaiella*

Two species of *Pylaiella*, both initially identified as *Pylaiella littoralis* (Linnaeus) Kjellman, were found on Calvert Island (Fig. 4), but they differed by at least 5% from true *P. littoralis* (type locality: Europe “in Europae marinis rupibus”—in European marine waterways). (The identity of true *P. littoralis* is uncertain because two sympatric species identified by that name have been found along the Brittany coast (Geoffroy et al. 2015)). One of our species is the same as what has been called *Pylaiella washingtoniensis* C.C. Jao in BOLD and GenBank, but we have not been able to ascertain why these specimens were identified by this name. The name *P. washingtoniensis*

Fig. 3. *Protohalopteris petersonii*. (*a*) Holotype. PTM512, intertidal rock near beach seepage, North Beach, 27 May 2013. Scale bar = 1 cm. (*b*) Typical habit in clumps on low intertidal rock near sand, West Beach, 10 June 2024, SCL 18272. Scale bar = 2 cm. (*c*) Basal crust of coalescent filaments with apical growth. Scale bar = 60 µm. (*d* and *e*) Abundant, sparingly branched uprights arising from basal crust. Scale bar = 200 µm (*d*), 60 µm (*e*). (*f*) Rhizoid arising from basal cell of branch. Pericysts evident in main axis. Scale bar = 60 µm. (*g*) Elongate rhizoidal filament. Scale bar = 60 µm. (*h* and *i*) Abundantly branched, possibly reproductive filaments arising from main axis and lateral branches. Scale bar = 100 µm (*h*), 60 µm (*i*).

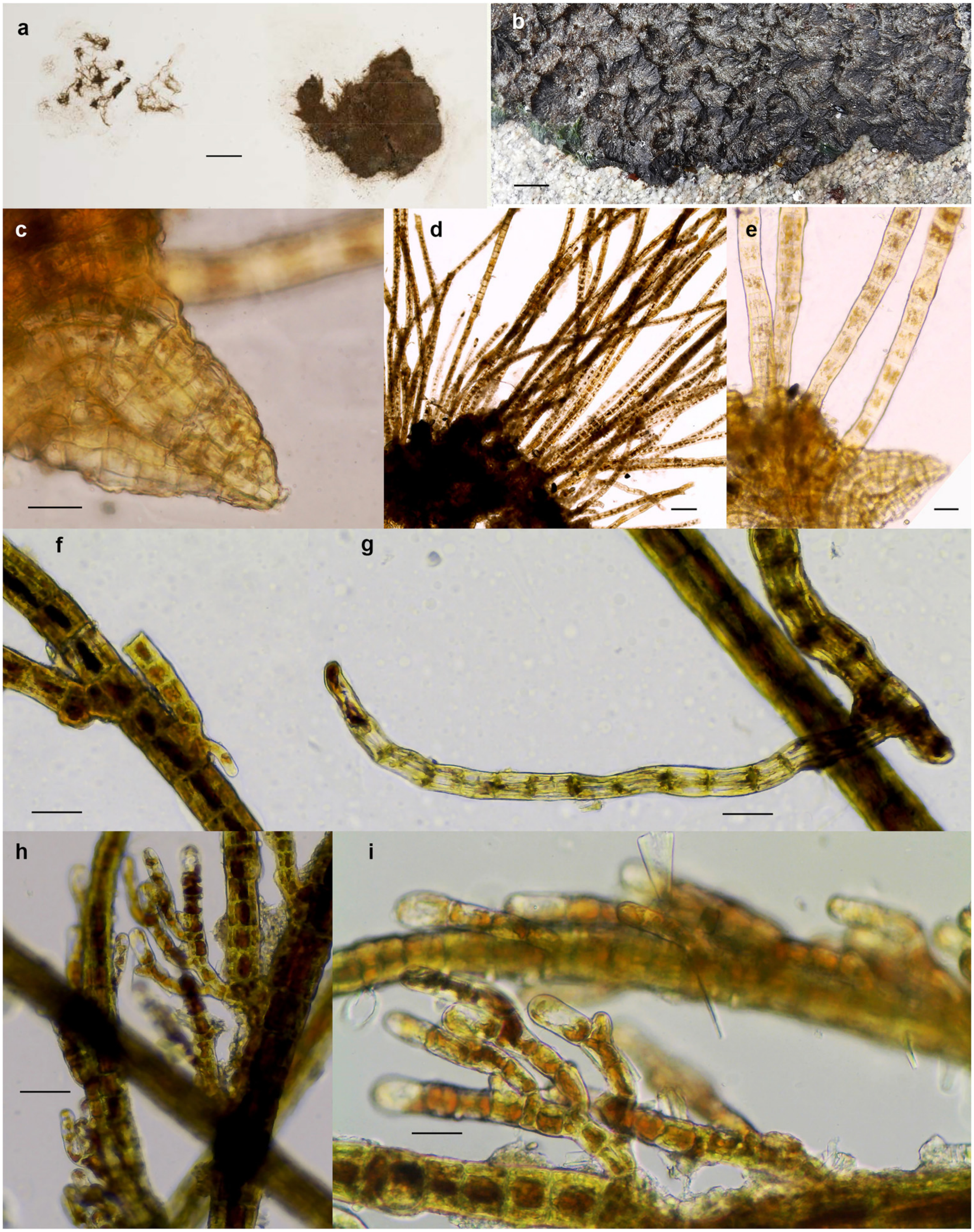
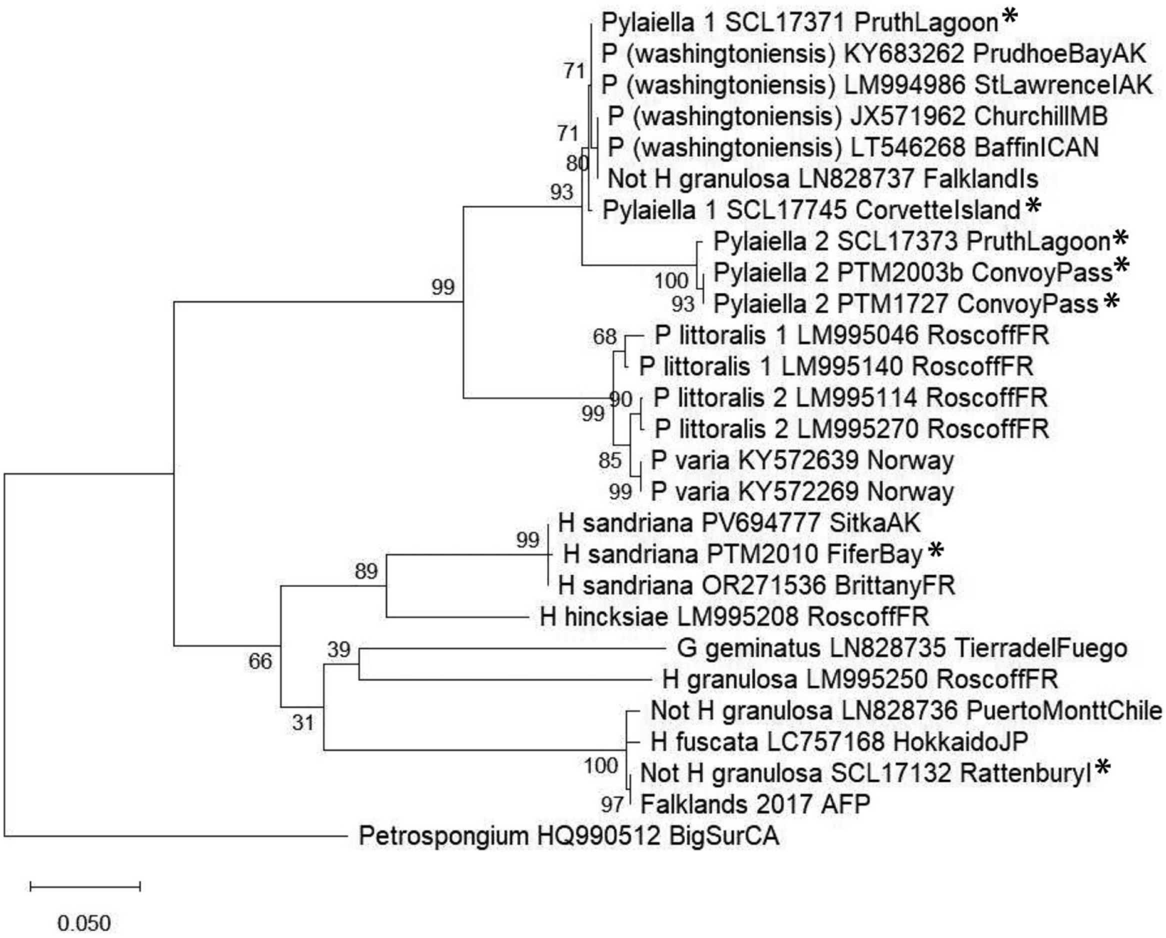


Fig. 4. Maximum likelihood (ML) phylogeny of Acinetosporaceae COI sequences from the Hakai area and elsewhere.



was applied to a species of *Pylaiella* from the Churchill area on Hudson Bay (Saunders and McDevit 2013) and was subsequently used by Peters et al. (2015) and Küpper et al. (2016). In comparing our two species, we find that both equally fit the description of *P. washingtoniensis* (SCL 17373, Fig. 5*a*; SCL 17371, Fig. 5*b*). *Pylaiella washingtoniensis* was originally described as up to 20 cm long, with long dichotomous lower branches and short, lateral upper branches and with numerous rhizoidal filaments; it grew on a concrete wall at high water mark in the ship canal between Lake Washington and Puget Sound (Jao 1937). SCL 17371, our specimen that groups with *P. "washingtoniensis"*, is short (~1 cm tall) with only sparse lateral branches (Figs. 5*c* and 5*d*), whereas SCL 17373 is at least 10 cm in length with opposite branching as well as short laterals—like true *P. littoralis* (Figs. 5*e* and 5*f*). (It is possible that the twisted axes in Fig. 5*e* could be misinterpreted as rhizoidal filaments). Specimens with the same sequence as SCL 17371 are widely distributed from British Columbia through the Canadian Arctic; the other species is thus far known only from the Prince Rupert, Masset Inlet, and Hakai areas of BC. For now, we identify both species as *Pylaiella* sp.

Family Chordariaceae

We sequenced 13 species in this family (Table 1; Fig. 6).

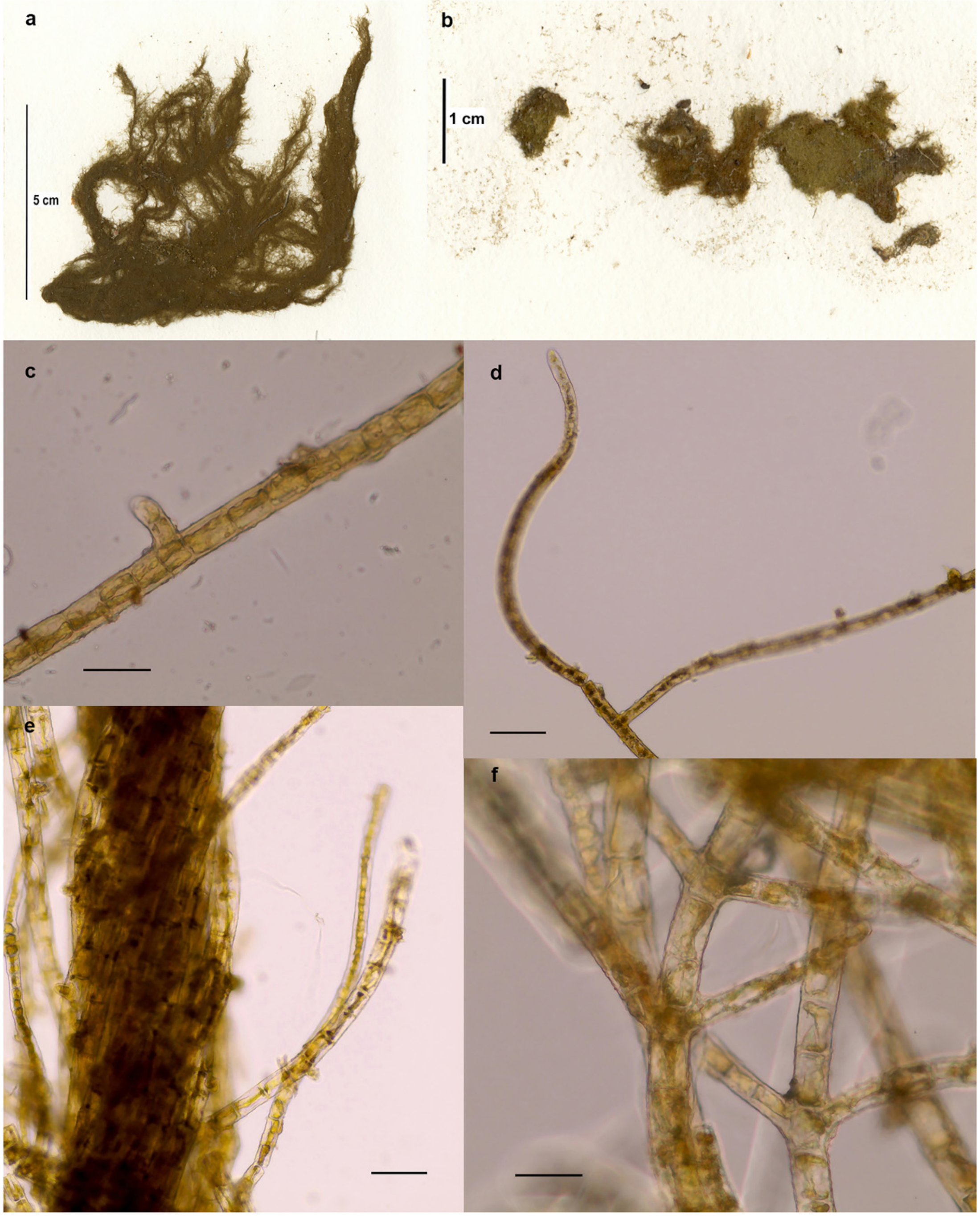
Genus *Acrothrix*

A subtidal specimen of *Acrothrix gracilis* Kylin (Fig. 7*a*), collected below the Pruth Bay dock in ~2 m, was confirmed by a COI sequence. This species was first recorded in the NE Pacific from Haida Gwaii by Bob Hooper (UBC A053709) and later from southern Sea Otter Sound, Southeast Alaska (Wynne 1987). It has since been collected elsewhere in Alaska (UBC A089220) and BC (BOLD, unpublished) as well as in the northwest Atlantic. Although material from the type locality (Bohuslän, Sweden) has not been sequenced, material from Norway was 99.85% identical to our material (Bringloe et al. 2019), the single nucleotide difference being a possible misread near the 5′ end of our sequence.

Genus *Coilodesme*

The COI sequences of *Coilodesme bulligera* Strömfelt from the Hakai area and Alaska differed from each other by a single bp (0.2%) but from a Quebec specimen by 1.43% (Fig. 6; no sequences were available from elsewhere–the type locality is Iceland), so it remains unclear whether the Pacific populations should be recognized as a distinct species. Figure 6 indicates that although sequences of *Coilodesme californica* (Ruprecht) Kjellman group with *C. bulligera*, the type species of the genus, there is little support for this

Fig. 5. *Pylaiella* spp. (*a* and *e*–*f*) SCL 17373. (*b*–*d*) SCL 17371. (*c*) Branch initiation. Scale bar = 50 μm. (*d*) Mature lateral branch and branch tip. Scale bar = 100 μm. (*e*) Entwined filaments with occasional lateral branches. Scale bar = 100 μm. (*f*) Opposite branching among free filaments. Scale bar = 50 μm.



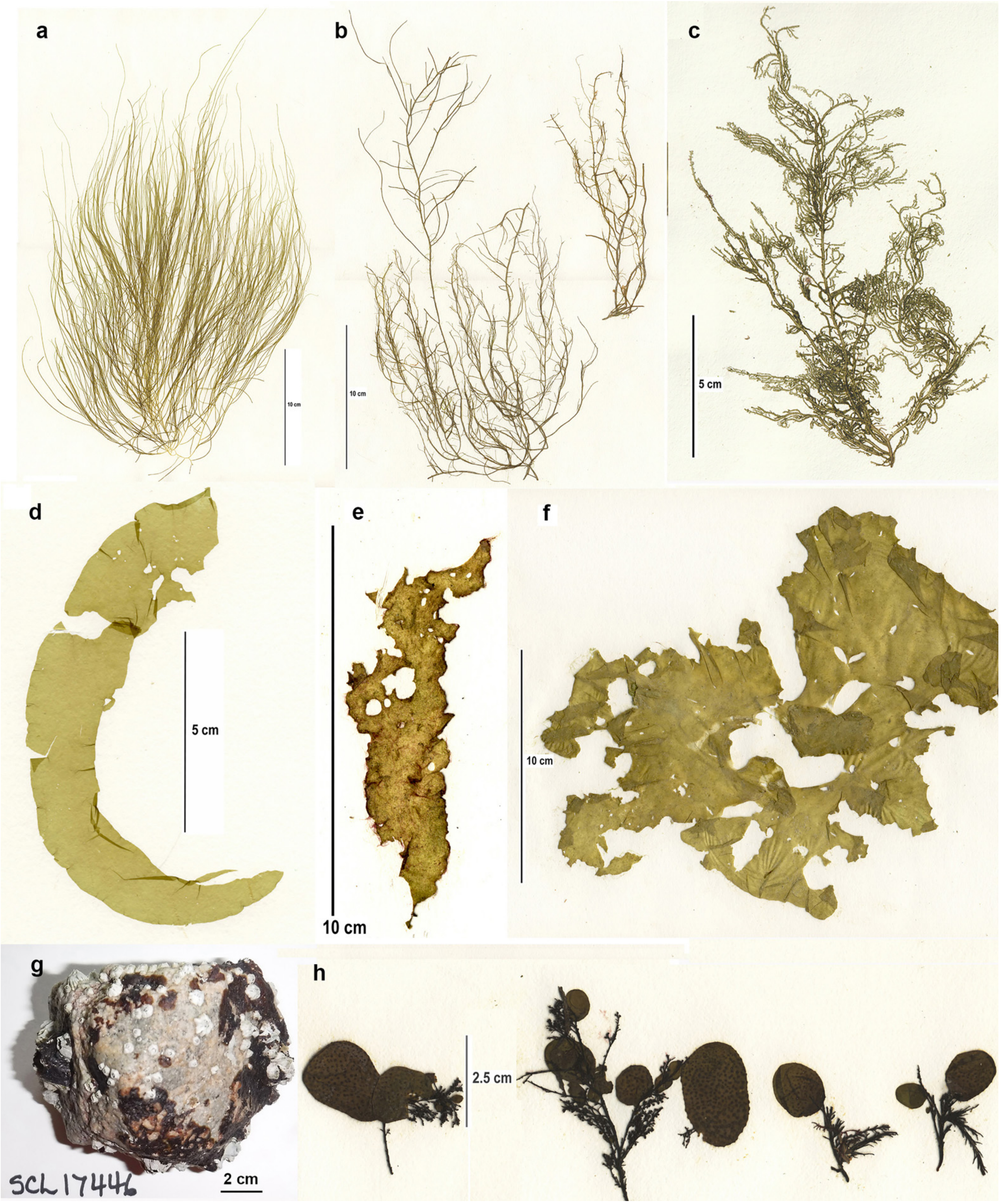
relationship (bootstrap value is only 56%). The sequences of *C. californica* are very similar to western Pacific *C. japonica* (data not shown); *C. californica* has priority. We have yet to obtain a sequence of *C. californica* from the Hakai area.

Genus *Dictyosiphon*

A single species of *Dictyosiphon* occurs in wave-protected areas at Hakai (Fig. 7*b*). We first observed it in 2014 and identified it as *Dictyosiphon sinicola* N.L. Gardner because it fit Gardner's (1940) description: "Fronds relatively soft and flaccid, 20–30 cm. high, up to 3 mm. diam., hollow in the older parts, moderately and irregularly alternately branched, larger branches of the main axes often widely divaricate…, all giving rise to short, scattered, attenuated ramuli of the third to fifth order, these terminating in a single series of cells; cortical cells arranged somewhat in longitudinal rows, rectangular, 10–16 μ diam.; medullary cells think-walled, 60–80 μ diam., variable in length but several diameters long." Like Gardner's, our specimens were collected "on rock and muddy

Fig. 6. Maximum likelihood (ML) phylogeny of Chordariaceae COI sequences from the Hakai area and elsewhere.

Fig. 7. Habits of species of Chordariaceae found at Hakai (collection data found in Table 1). (*a*) *Acrothrix gracilis* (SCL 17230). (*b*) *Dictyosiphon sinicola* (SCL 17043). (*c*) *Myriocladia lovenii* (SCL 17745). (*d*) *Punctaria expansa* (SCL 17394). (*e*) *Punctaria tenuifolia* (SCL 16807). (*f*) *Punctaria tenuifolia* (SCL 17456). (*g*) “Ralfsioid” on cobble (SCL 17446). (*h*) *Soranthera ulvoidea* (SCL 14981).



bottoms in quiet waters". Gardner collected the type from a small bay at the southern end of San Juan Island, Washington, and made a second collection in Clayoquot Sound, Vancouver Island, BC. Subsequently, Tom Mumford collected the species in Washington State in 1980 (as determined by Mike Wynne: Gabrielson et al. 2012). Our collections represented only the second report of this species since 1940 until the recent publication by Kawai et al. (2021). Specimens with COI sequences identical to ours have been reported from Churchill, Manitoba (Saunders and McDevit 2013), and from additional sites in British Columbia (BOLD, unpublished). These sequences, together with the extensive data in Kawai et al. (2021) and other sequences in GenBank, indicate that this species is widely distributed in northern waters, from Washington State through British Columbia and Alaska to Kamchatka and through the Bering Strait into the western Arctic as far north as Baffin Island and as far south to Nova Scotia in the western Atlantic. It is clearly distinct from *Dictyosiphon foeniculaceus* (Hudson) Greville, the species with which it had previously been confused; their COI sequences are only 95%–96% similar.

Genus *Elachista*

Although the quality of our COI sequence of *Elachista* was rather poor, it fit with sequences from other BC sites (Fig. 6). These sequences were divergent from North Atlantic specimens of *Elachista fucicola* (Velley) Areschoug (type locality: UK) from New Brunswick, Norway, and France: only 97.26% or less identical. This suggests the NE Pacific species should be recognized by another name. Whether our species should be identified as *Elachista lubrica* Ruprecht from the NW Pacific (type locality: Cape Nichta, Okhotsk Sea) remains to be determined. For now, we use *Elachista* sp. for collections from the Hakai area.

Genus *Hecatonema*

Hecatonema terminale (Kützing) Kylin, an inconspicuous filamentous epiphyte, was identified from COI sequences from three different red algae: the high tidepool *Neorhodomela oregona* (Doty) Masuda, the low intertidal surfgrass epiphyte *Smithora naiadum* (C.L. Anderson) Hollenberg, and an undetermined species of *Bossiella*. The sequence from *Smithora* was 99% identical to *Hecatonema maculans* (Collins) Sauvageau, a species considered synonymous with *H. terminale* (Fletcher 2024), from a variety of mostly European locales (Peters et al. 2015) and a single collection from China (Du and Xue, unpublished). Among species isolated by Peters et al. (2015), *H. maculans* was the second most abundant following *Hincksia granulosa*, and it occurred in a strongly supported cluster basal to the remaining members of the Chordariaceae and including *Myrionema balticum* (Reinke) Foslie and *Ascocyclus orbicularis* (J. Agardh) Kjellman among other, undescribed species. One of the Peters et al. (2015) specimens was isolated from *Palmaria palmata* (Linnaeus) F. Weber & D. Mohr from Maine, USA; the type of *H. maculans* is a specimen from Maine growing on *Palmaria palmata*. *Hecatonema terminale* (as *H. maculans*) has not been reported previously from the northeast Pacific although there are unpublished sequences from Bamfield and Haida Gwaii, BC, in BOLD. Despite obtaining sequences from three distinct specimens, we did not observe the epiphytic *Hecatonema* species when we examined host specimens microscopically.

Genus *Leathesia*

Compared to COI sequences in GenBank, our sequences of *Leathesia marina* (Lyngbye) Decaisne ranged from being identical to specimens from China and Japan to being only 99.05% identical to specimens from France and Norway.

Genus *Microspongium*

Our COI sequence of *Microspongium globosum* Reinke came from an epiphyte of *Dilsea californica* (J. Agardh) Kuntze and was identical to a Pachena Beach, BC, sequence but differed by 2 bp from a Kamchatka sequence in GenBank (Fig. 6). The two GenBank sequences were from epiphytes of *Alaria*. This species was reported previously from BC as *Myrionema globosum* f. *affine* Setchell & N.L. Gardner (Gabrielson and Lindstrom 2018). The type of the species is from Europe (Kiel Bight); a *rbc*L sequence from Europe (AF207805) was identical to a partial sequence from Kamchatka (MT766300), supporting the identification of our specimen as this species.

Genus *Myriocladia*

Specimens of *Myriocladia lovenii* J. Agardh (Fig. 7*c*) were collected in the shallow subtidal at two sites east of Fitz Hugh Sound (Corvette Islands and Convoy Passage). COI sequences were identical to a specimen from near Bonne Bay, Newfoundland (BOLD, unpublished); the species is also known from northern Europe (type locality: in sinu Codano; Bahusiae, in the Skagerrak region of Sweden), but no European material has been sequenced. Our specimens represent the second record of the species in the northeast Pacific; it was previously recorded by Wynne (1987) from two sites near Sitka Sound, Alaska.

Genus *Punctaria*

We obtained COI sequences for two species of *Punctaria* from specimens collected in the protected waters of Pruth Bay and Meay Channel. We identify one species as *Punctaria expansa* Setchell & N.L. Gardner. This is one of at least two names of NE Pacific species available for consideration, namely *P. expansa* and *Punctaria occidentalis* Setchell & N.L. Gardner. Both were described by Setchell and Gardner (1924), the former from Penn's Cove, Whidbey Island, Washington, and the latter from Monterey, California. Both were described as having gametangia scattered on both surfaces of the frond and protruding beyond the surface by about one-half their length, as do our specimens. As the name implies, *P. expansa* is a broadly expanded blade of four cell layers, very fragile, whereas *P. occidentalis* is a moderately rigid, linear–lanceolate, oblanceolate or broadly ellipsoidal blade of 2–7 cell layers and usually tapering to a short stipe ∼5 mm long. Our material (Fig. 7*d*) falls between the descriptions of the two species. Like *P. expansa*, the blades of our samples have four cell layers. However, young specimens, from which we obtained sequences, were linear–lanceolate with short stipes, like *P. occidentalis*. The habitat of most of our specimens better coincides with that of *P. expansa* (a small quiet cove) than with the open coast of Monterey, California. Although Kawai and Hanyuda (2021) used the name *P. occidentalis* for a specimen from Hokkaido, Japan, which was genetically identical to ours (Fig. 6), they provided no justification for using that name, and therefore we do not follow them but rather apply the name *P. expansa* pending further work. Sequencing of type material of both *P. expansa* and *P. occidentalis* would help confirm our identification.

Our second species was identified as *Punctaria tenuissima* (C. Agardh) Greville (type locality: Kattegat, between Sweden and Denmark; Figs. 7*e* and 7*f*, this study) based on COI sequencing. We follow Parente et al. (2010) and earlier authors who felt that *P. tenuissima* should be considered a synonym of *Punctaria latifolia* Greville (type locality: Sidmouth, England—across the English Channel from Roscoff, France: our material had an identical sequence to a specimen from Roscoff). *Punctaria tenuissima* has priority over *P. latifolia*, so we use that name. Fletcher (2024) considered *P. latifolia* and *P. tenuissima* to be distinct species.

In addition to the sequenced specimens, we collected specimens (SCL 17044, 17393) that had crenulate margins as described for *Punctaria lobata* (D.A. Saunders) Setchell & N.L. Gardner and *Punctaria chartacea* Setchell & N.L. Gardner from Alaska. Like these species, our material was epiphytic on *Zostera marina*. We were unable to sequence these specimens. We tentatively identify them as *Punctaria lobata* (Table S1).

Genus *Ralfsia*

"Ralfsioid": A *Ralfsia*-like crust was identified from material collected both at Foggy Cove and in Meay Channel, where it occurred on boulder, cobble, and clam shell (Fig. 7*g*). COI sequences have also been reported from California: a sequence from Jade Cove was 100% identical to our material, whereas one from Pigeon Pt was only 98.94% identical (Fig. 6). None of these sequences was close to any other Chordariaceae, although the specimens clustered with *Elachista* with low bootstrap support in our ML analysis. It is possible that this species is one of several species of "*Ralfsia*" described from California for which no sequence data are available (Setchell and Gardner 1924; Smith 1944; Hollenberg 1969). Until these California species have been studied sufficiently (e.g., sequencing of type material), we refrain from describing this species as new, but it is clear that a new genus is required for this distinctive lineage, which is a member of the Chordariaceae (order Ectocarpales) and not the Ralfsiaceae (order Ralfsiales).

Genus *Saundersella*

The COI sequence of the Hakai specimen of *Saundersella simplex* (D.A. Saunders) Kylin was essentially identical to sequences from elsewhere in BC (Bamfield area and Haida Gwaii), the only region where the species has been sequenced. A single bp difference may be due to the poor quality of the Hakai sequence.

Genus *Soranthera*

The COI of the single *Soranthera ulvoidea* Postels & Ruprecht specimen sequenced (PTM1760) was only 97% similar to the majority of specimens identified as this species from the BC coast (type locality: Sitka, Alaska; Fig. 7*h* is a specimen from the same site as PTM1760). Based on divergence rates for COI in other brown algae, this suggests that our specimen represents a distinct species. Whether the Hakai specimen or the other BC genotype represents the same species as the type material has yet to be determined.

Family Ectocarpaceae
Genus *Ectocarpus*

We obtained COI sequences for three species of *Ectocarpus* Lyngbye, and we show the relationships of our *Ectocarpus* species to closely related species in Fig. 8, using LM995013 as the outgroup, following Peters et al. (2015). All three species fall within the *Ectocarpus siliculosus* (Dillwyn) Lyngbye complex, a widely distributed and speciose complex of genetically distinct and mostly reproductively isolated species that have yet to be thoroughly studied and described (Peters et al. 2010*a*, 2010*b*, Montecinos et al. 2017). PTM513, which was epiphytic on *Hedophyllum sessile* (C. Agardh) Setchell, appears to be the same species as a Chilean specimen, which was epiphytic on *Lessonia* (GenBank LM995010); this species is identified as *Ectocarpus* 6 in Montecinos et al. (2017), where a number of other Chilean isolates and one Oregon isolate are also included. GenBank also includes two California records of this species. Montecinos et al. (2017) recorded Chilean specimens of this species from mid intertidal pools to the subtidal zone but noted it was most abundant in the low intertidal.

SCL 17279, which was epiphytic on *Halosaccion* (S.G. Gmelin) Ruprecht, is most closely related to FP885846 and KU134013 from Peru and Chile, respectively (Fig. 8), but still only 97.38% similar and likely represents a distinct species. The third species of *Ectocarpus* (SCL 17408) was epiphytic on *Scytosiphon* growing on the dock at the Hakai Institute on 26 June 2018. Like other opportunistic species growing on man-made structures, this species appears to be widely distributed, having been collected in Chile (KT983223), Oregon (KT983251), and New Zealand (LM995018). Montecinos et al. (2017) called this species *Ectocarpus* 1. This species has been crossed with other species (*E. siliculosus* and *Ectocarpus* 7), producing sporophytes that were viable but incapable of meiosis (summarized in Montecinos et al. 2017).

There are a number of northeast Pacific species of *Ectocarpus* to which some of our specimens could be assigned. These include *Ectocarpus acutus* Setchell & N.L. Gardner, *Ectocarpus commensalis* Setchell & N.L. Gardner, *Ectocarpus corticulatus* D.A. Saunders, *Ectocarpus dimorphus* P.C. Silva, *Ectocarpus flagelliferus* Setchell & N.L. Gardner, *Ectocarpus fructuosus* Setchell & N.L. Gardner, *Ectocarpus parvus* (D.A. Saunders) Hollenberg, and *Ectocarpus taoniae* Setchell & N.L. Gardner, or European species such as *Ectocarpus pygmaeus* Areschoug. Studies of *Ectocarpus* species from type material or their type localities are warranted.

Family Petrospongiaceae

We obtained both COI and *rbc*L sequences for a species of *Petrospongium* from the mid intertidal zone of an exposed site near Fifth Beach (PTM1558). The COI sequence was 97.86% similar to a specimen from Central California (PTM1718, GenBank Accession PV694810), but the *rbc*L sequences were

Fig. 8. Maximum likelihood (ML) phylogeny of Ectocarpaceae COI sequences from the Hakai area and elsewhere.

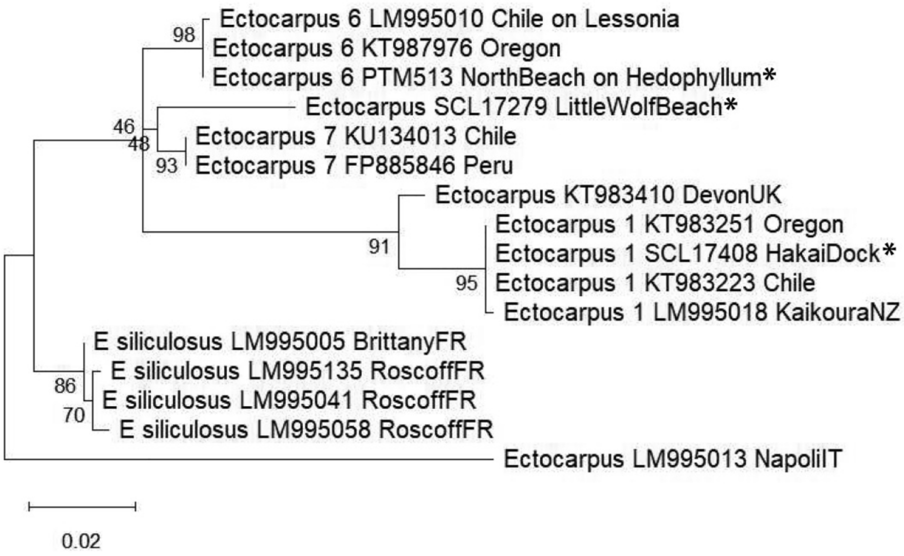
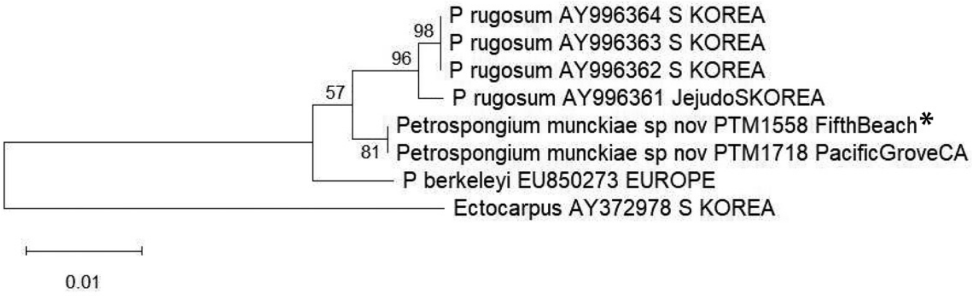


Fig. 9. Maximum likelihood (ML) phylogeny of *Petrospongium rbc*L sequences from the Hakai area and elsewhere.



identical (GenBank Accessions PV694871 and PV694872). Although the NE Pacific species of *Petrospongium* had been identified as *Petrospongium rugosum* (Okamura) Setchell & N.L. Gardner, a Japanese species (Gabrielson and Lindstrom 2018), comparison of *rbc*L sequences with Korean *Petrospongium* (Fig. 9) indicate that the NE Pacific species is sufficiently distinct from the Western Pacific species to warrant description. We therefore provide a new name for the Hakai species. Further work is required to determine whether the California species is the same or requires its own epithet.

Petrospongium munckiae Martone & S.C. Lindstrom (Fig. 10)

Thallus medium to dark brown, pulvinate, circular when young, becoming convoluted and irregular in outline when older (Fig. 10*a*). Pigmented cortical filaments of 7–8 cells, branched to several orders; cells 5–8 μm diam. and 12–14 μm long (Figs 10*b*). Less pigmented inner cortical cells larger, elongate, 18–22 μm diam. and 25–40 μm long. Unpigmented medullary cells even more elongate, sparsely branched (Fig. 10*c*). Hairs sparse, single, or in small clusters. Reproductive structures not seen. Occurring on lower mid intertidal bedrock exposed to waves.

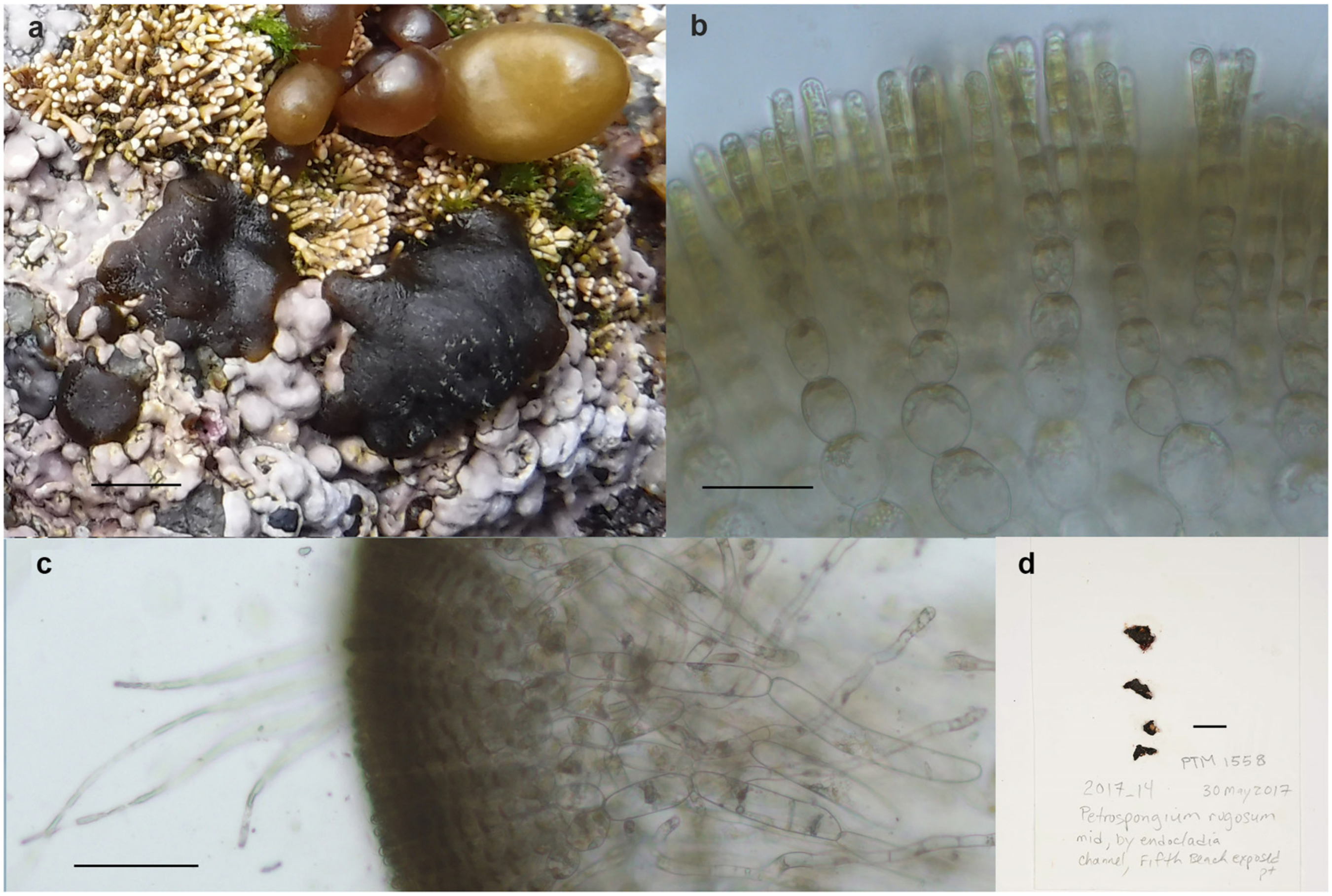
TYPE SPECIMEN: PTM1558 (Fig. 10*d*), mid intertidal bedrock near *Endocladia*, Fifth Beach exposed site (51°38.351′N 128°09.378′W), 30 May 2017 (UBC A093594).

ETYMOLOGY: This species honours Christina Munck, whose ongoing support made possible the work on this and other seaweeds of the central coast of British Columbia.

Family Scytosiphonaceae

An ML phylogeny of COI sequences of Scytosiphonaceae from the Hakai area together with specimens from other regions appears in Fig. 11. We use the same outgroup as Santiañez et al. (2018), viz., the Cock et al. (2010) mitochondrial sequence of "*Ectocarpus siliculosus*" (see Peters et al. 2010*a* regarding the origin of this strain). *Dactylosiphon bullosus* (D.A. Saunders) Santiañez, K.M. Lee, S.M. Boo & Kogame specimens were identical or nearly identical to other specimens from BC as well as ones from Hokkaido, Japan, and Santa Cruz, California (the type locality is Pacific Grove, CA). As

Fig. 10. *Petrospongium munckiae*. (*a*) Habit of species in the field at the type locality. Scale bar = 2 cm. (*b*) Branched cortical filaments. Scale bar = 30 μm. (*c*) Branched medullary and cortical filaments with a small cluster of hairs. Scale bar = 100 μm. (*d*) Holotype. PTM1558, mid intertidal bedrock, near *Endocladia*, in channel, Fifth Beach exposed site, 30 May 2017 (UBC A093594). Scale bar = 1 cm.



Santiañez et al. (2018) have shown, based on mitochondrial cytochrome oxidase 3 (cox 3) gene sequences, this species is more closely related to *Scytosiphon* than to other species of *Colpomenia*, the genus in which it had been placed. All sequences of *Melanosiphon intestinalis* (D.A. Saunders) M.J. Wynne in GenBank from both the northeast Pacific and northwest Atlantic were at least 99% similar to the specimen (SCL 16849) from the Hakai area. Since the type locality is in the North Pacific (Popof I., Shumagin Is., AK), there should be little doubt that this name applies to our specimens.

Genus *Colpomenia*

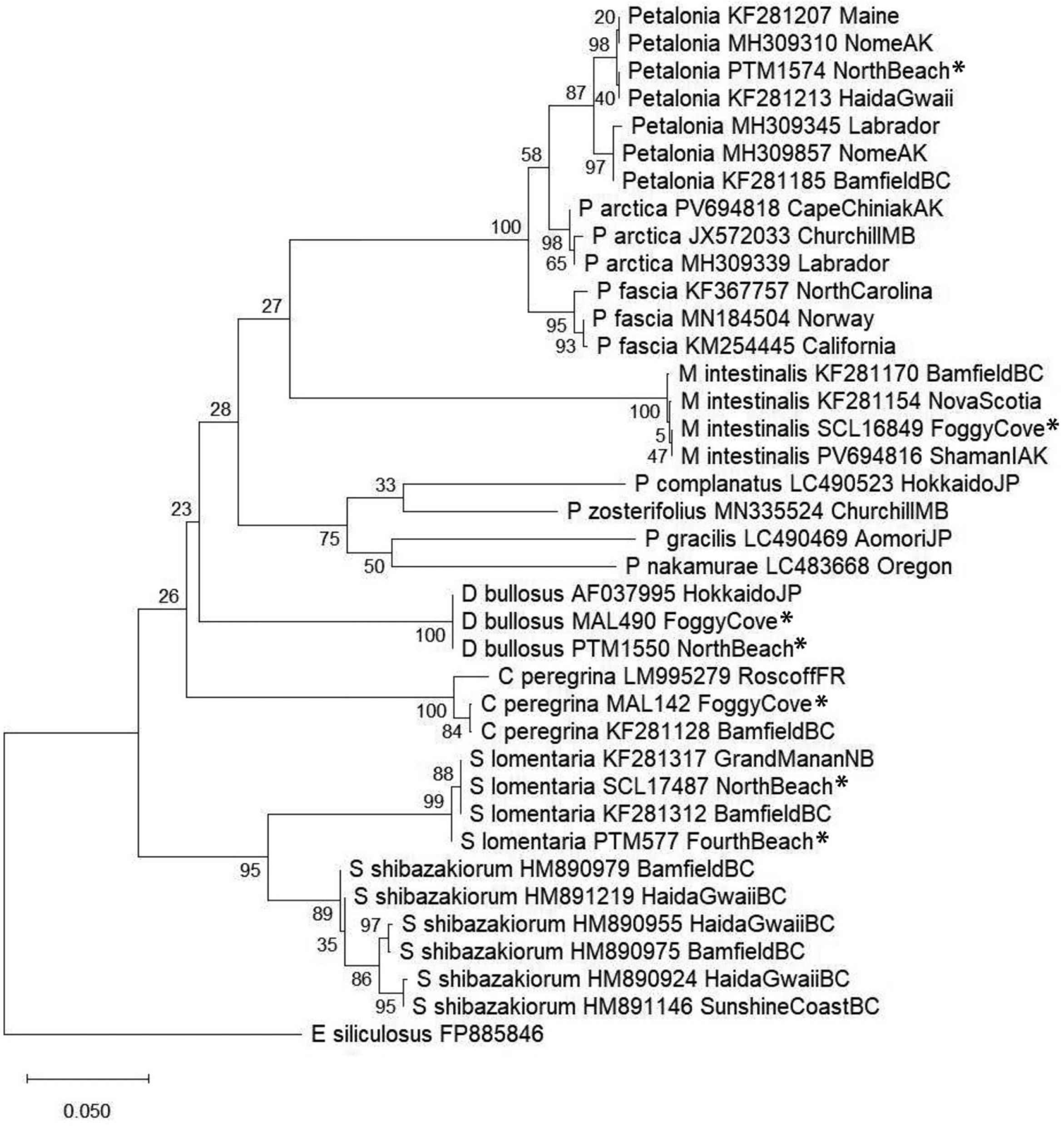
The COI sequences of BC specimens of *Colpomenia peregrina*, including those from Hakai, were only 98.1% similar to a sequence of this species from Roscoff, France (type locality: Morbihan, France—Dy et al. 2023), but an unpublished *rbc*L sequence of a Saunders specimen from Bamfield, BC, was 100% identical to an *rbc*L sequence of *C. peregrina* from Roscoff. Incongruencies between mitochondrial and other genetic markers have been observed in other Scytosiphonaceae: Kogame et al. (2015) and McDevit and Saunders (2017) found mitochondrial introgression or incomplete lineage sorting in *Scytosiphon*, the former due to nuclear and plastid DNA being inherited from both parents (Kato et al. 2006), whereas mitochondrial DNA is inherited from only a single parent (Kimura et al. 2010).

Genus *Petalonia*

The COI sequence of *Petalonia* from the Hakai area falls within one of the two groups that do not include what appears to be true *Petalonia fascia* (O.F. Müller) Kuntze, which has a type locality of Kristiansand, Norway (Fig. 11). A sequenced specimen from Stora Kalsoy, Norway, as well as other *Petalonia fascia* from Europe (and elsewhere: Australia, China, Korea, California, and North Carolina) was only 95% similar to our *Petalonia*. This suggests that another name is needed for our Hakai specimen. The Hakai species occurs together with other northeast Pacific specimens in a strongly supported clade that also includes northwest Atlantic specimens. This clade is sister to another strongly supported clade with a similar geographic distribution but without representation in the Hakai area.

During our studies we also sequenced the COI of specimens of a distinctive *Petalonia* from Alaska (e.g., SCL 16500, Gen-

Fig. 11. Maximum likelihood (ML) phylogeny of Scytosiphonaceae COI sequences from the Hakai area and elsewhere.



Bank Accession PV694818; SCL 17576, GenBank PV694819). The sequences of these specimens were 99.66%–98.38% identical to those of *Petalonia arctica* G.W. Saunders & C.W. Schneider, based on specimens from Churchill, Manitoba, and Labrador and thought to be "largely confined to the Canadian Arctic" (Saunders 2024). Our specimens are from Cape Chiniak and Cold Bay, Alaska, where they occurred on low intertidal rock near sand; these specimens extend the distribution of this species into the cold temperate waters of the North Pacific.

Genus *Scytosiphon*

The identity of true *Scytosiphon lomentaria* (Lyngbye) Link (type localities: Faeroe Islands and Denmark) was clarified by McDevit and Saunders (2017), who showed that the species has constrictions, phaeophycean hairs, and lacks ascocysts (unicellular paraphyses) in contrast to previous concepts of the species, in which ascocysts were said to be present. Their results were confirmed by Hoshino et al. (2021). The COI sequences of our specimens were identical to or differed by a single bp from McDevit and Saunders' concept of *S. lomentaria*, which has also been sequenced from China, Japan, Pacific and Atlantic Canada, New England, USA, and France. We did not find *Scytosiphon shibazakiorum* Hoshino & Kogame, which was recently reported to be widely distributed in BC and has a distribution including Far East Russia, northern Japan, British Columbia, Manitoba, eastern Canada, Maine, and Iceland (Hoshino et al. 2021).

Order Fucales

We obtained COI sequences for all four species of Fucales occurring in the Hakai area. *Fucus distichus*, the dominant intertidal fucoid, had a sequence identical to specimens ranging from Coos Bay, Oregon to Nome, Alaska, and was 99.85% identical to specimens from Manitoba, New Brunswick, Nova Scotia, and Norway. *Fucus spiralis*, which occurs just above *F. distichus* in the mid to high intertidal zone, was identical to specimens from California, southern BC, and Norway, and 99.85% similar to specimens from northern BC, New Brunswick, Maine, and Norway. *Sargassum muticum*, which is so far restricted to more protected waters in the Hakai area, was 100% identical to almost all *S. muticum* in GenBank, including specimens from Venice Lagoon, China, and southern BC (this species shows almost no genetic diversity outside its native range—Le Cam et al. 2020). We obtained a sequence for *Stephanocystis geminata* (C. Agardh) Draisma, Ballesteros, F. Rousseau & T. Thibaut from a subtidal population at Kelpie Point, although we never observed the species growing on Calvert Island itself.

Order Laminariales

We obtained COI sequences for all 20 species of kelp we observed in the Hakai area (a selection of images of some of these species can be seen in Fig. S3). Kelps are arguably the most studied species of seaweeds due to their ecological importance as well as their commercial use (Critchley and Ohno 1998; Starko et al. 2019), so abundant public sequences exist for comparison. All but two of the Hakai kelps had identical sequences to specimens from other sites in BC, most notably Haida Gwaii (*Alaria marginata* Postels & Ruprecht, *Costaria costata* (C. Agardh) D.A. Saunders, *Cymathaere triplicata* Postels & Ruprecht) and beyond for other species. Sequences of *Hedophyllum sessile* (C. Agardh) Setchell from southwest Vancouver Island (FJ409206 et al.) were identical to each other but differed at two fixed bp from northwest Vancouver Island specimens and three bp from Haida Gwaii specimens (FJ 409205 et al.); our *H. sessile* sequence was identical to the Haida Gwaii specimens at all but one nucleotide site, which was unique to the Hakai material. *Laminaria setchellii* P.C. Silva from the Hakai area also differed from all other published sequences of this species at a single nucleotide site. We identified our *Dictyoneurum* as *Dictyoneurum reticulatum* (D.A. Saunders) P.C. Silva following Kawai et al. (2017) based on sequence data and morphology.

In 2012–2013, we collected *Laminaria yezoensis* Miyabe from wave-exposed intertidal boulders at Foggy Cove (Fig. S3g). This cold temperate species occurs from northern Japan and Kamchatka, Russia, through Alaska to British Columbia, where it reaches its southern limit in Queen Charlotte Strait. Our Calvert Island collections are near this southeastern distributional limit. After marine heat waves swept through the region in the 2010s, increasing ocean temperatures and altering intertidal seaweed communities (Whalen et al. 2023), this species has disappeared from the intertidal zone.

We provide a new collection record for *Eisenia arborea* Areschoug along the BC coast. Previously, the species had been reported from Haida Gwaii and the west coast of Vancouver Island (Scagel et al. 1989). Bringloe et al. (2021) and Watson et al. (2021) provided more recent records and updated the sites where this strictly subtidal species is known to occur in BC. We confirmed the Watson et al. (2021) site of Jeffery Pinnacle and added Donald Island in the Hakai area. Our COI sequences were identical to specimens from the Bamfield area along southwest Vancouver Island but were only 99.85% identical to specimens from Haida Gwaii due to a single bp difference.

We follow Lindstrom (2023) in using the name *M. tenuifolia* for the local species of *Macrocystis*. Gonzalez et al. (2023) showed that the names we had previously used for the BC species with a rhizomatous holdfast, first *Macrocystis integrifolia* and later subsumed in *Macrocystis pyrifera*, clearly belong to species with distinct genotypes from the southern hemisphere, and these are divergent from our northern hemisphere species. Since both *M. integrifolia* and *M. pyrifera* have southern hemisphere types, it is clear that a species name with a northern hemisphere type is required. Of the names available, only *Macrocystis tenuifolia* Postels & Ruprecht (1840), with a type locality of “in sinu Norfolk (now Sitka Sound, Alaska) ad littoral Americae boreali-occidentalis” was available and appropriate. This name applies to specimens with both rhizomatous and conical holdfasts from Washington to Alaska (following the analyses of J. Bemmels & G. Owens, unpublished: Bemmels, pers. comm. 25 April 2025); appropriate names for the species of *Macrocystis* in California have yet to be determined.

Postelsia palmaeformis Ruprecht has not been found growing on Calvert Island, but it was found in the drift on West Beach in 2016 (Jenn Burt, pers. comm., 11 July 2016; Fig. S4) and attached on the mainland just south of Calvert Island at the southern end of Fitz Hugh Sound near Cranstown Point (51.37°N 127.78°W, Zach Montieth, pers. comm. 11 July 2023). Previously, it was recorded as far north as Hope Island, at the southern end of Queen Charlotte Sound (Scagel et al. 1989). Yola Metti (pers. comm., 27 November 2007) found it just south of Cape Caution at ~51°08’21″N 127°43’50″W in the late 1990s—all of which indicates that the species range is expanding northward. The COI sequence of the Cranstown Point specimen was 99.70%–99.85% identical to specimens from the Bamfield area (these differences may be due to misreads of the respective sequences) and 99.39% identical to a sequence from Point Lobos, California (just south of the Monterey Peninsula).

Order Ralfsiales

We obtained COI sequences for *Analipus japonicus* from several Hakai sites: the sequences from Foggy Cove were identical to a sequence from the Bamfield area and to the complete mitochondrial genome in GenBank (MZ156065), for which the provenance was not revealed. These sequences were distinct from other *A. japonicus* sequences in GenBank and BOLD for at least 3 bp positions, including a sequence from North Beach, which also had a unique nucleotide. Otherwise, the North Beach sequence was identical to other sequences from the Bamfield area, Haida Gwaii (which also had a single unique nucleotide) and Alaska (sequences from a third group of Bamfield specimens were identical to those of specimens from California). It may be of interest that in their study of *A. japonicus* on the Pacific coast of North America, Nelson and DeWreede (1989) found unilocular sporangia (indicating the occurrence of sexual reproduction) only on plants from central California, near the species southern limit, among specimens examined from across its range.

The single *Ralfsia* specimen sequenced from Hakai was identified as *Ralfsia unimaculata* Parente & G.W. Saunders. This species is thus far known only from British Columbia (Parente and Saunders 2019), primarily from Haida Gwaii, but there are a few records from southern BC (Bamfield and Sechelt). We have tentatively identified other specimens from the area as *Ralfsia fungiformis* (Gunnerus) Setchell & N.L. Gardner based on morphology but have yet to obtain sequences from these.

Species still requiring sequences for verification in the flora

In addition to species already mentioned, we did not obtain sequences for the following species, which were identified morphologically; these require molecular confirmation: *Haplogloia andersonii* (Farlow) Levring, *Hecatonema streblonematoides* (Setchell & N.L. Gardner) S. Loiseaux, *Myrionema strangulans* Greville, *Streblonema transfixum* Setchell & N.L. Gardner, *Compsonema intricatum* Setchell & N.L. Gardner, and *Compsonema serpens* Setchell & N.L. Gardner. Santiañez and Kogame (2017) have summarized evidence that *Compsonema*-like species represent the alternate, sporophytic phase of *Planosiphon* spp., which are thus far known only from the North Atlantic and northern Japan (McDevit and Saunders 2017; Santiañez and Kogame 2017). *Hecatonema* and *Streblonema* spp. may also represent alternate phases in the life histories of other brown algae (Fletcher 2024 summarizes examples of these).

Missing species

There are species we expected to find in the Hakai area that have yet to be found. These are species that have been collected both to the north and south of Hakai (Scagel et al. 1989; McDevit and Saunders 2017). Although primarily small if not microscopic, these species have distinctive morphologies. Included among these are *Battersia norrisii* (Hollenberg) P.W. Gabrielson, S.C. Lindstrom & O'Kelly, *Microzonia abyssicola* (Setchell & N.L. Gardner) Camacho & Fredericq, *Leptonematella fasciculata* (Reinke) P.C. Silva, *Hapterophycus canaliculatus* Setchell & N.L. Gardner, *Ralfsia robertii* Parente & G.W. Saunders, *Ralfsia tenebris* Parente & G.W. Saunders, *Scytosiphon promiscuus* McDevit & G.W. Saunders, and *Scytosiphon shibazakiorum*. These species are perennials or, if annuals, they have been found in BC in spring or early summer (within the window when our collections were made), making their absence particularly noteworthy.

Several species have been recorded as reaching their northern limit just south of Calvert Island. *Laminaria sinclairii* and *Pelvetiopsis limitata* have been recorded as far north as Hope Island, at the southern end of Queen Charlotte Sound (Scagel et al. 1989); they have not yet been found on Calvert Island.

Discussion

Even after 13 years of intensive collecting and surveying shores for marine algae, we continue to discover species not seen previously on the central coast of British Columbia. Of the 67 species we have identified to date (of which we sequenced 55), *Hincksia terminale* and the undescribed species of Acinetosporaceae are reported for the first time from the North Pacific, and we provide additional records of *Pylaiella* and *Ectocarpus* spp. for the region. Specimens of another *Ectocarpus* and a *Ralfsia*-like species in the Chordariaceae are unique, not having been reported previously, and need further work. *Protohalopteris petersonii* and *Petrospongium munckiae* are described as new to science. More than 30 species that occur to the north and south have yet to be collected in the Hakai area. Many of these species are subtidal and small, but we still expect to find them in the area with continuing efforts.

There are a number of reasons we may not have found these species. Although our visits have been during "summer" months, they have varied from late May (in 2013, 2017, 2021, and 2023) to mid August (in 2011). During this interval, the area was impacted by highly variable interannual weather in general and temperature in particular, most notably a marine heatwave in 2014–2016 known as the Blob (Cavole et al. 2016 (https://www.earthdata.nasa.gov/learn/sensing-our-planet/blob); Di Lorenzo and Mantua 2016; Tseng et al. 2017), followed by another marine heatwave in 2019 (Chen et al. 2021) and to a lesser extent the heat dome of 2021 (White et al. 2023). These marine heatwaves are thought to have significantly impacted the diversity and distribution of macroalgal species (Whalen et al. 2023), as has been documented in other locations (Wernberg et al. 2016; Wernberg and Filbee-Dexter 2019). This highlights the importance of baseline surveys and long-term datasets in identifying when and where species ranges shift.

Moreover, while we started with sampling moderately exposed sites in 2011, we only added protected sites in 2014. Also, until Bio-blitz efforts in 2017–2019, which added diverse subtidal habitats, we had only sampled the subtidal during our visit in 2013. During every trip, we have added species not seen previously, and there are a significant number of species we expect to find that we have yet to record. Indeed, at present we have only recorded 67 of the 100 or so species of brown algae currently recognized to occur in British Columbia (Gabrielson and Lindstrom 2018), suggesting that our list of species recorded for this area will continue to grow.

Our understanding of brown algae in this area would benefit substantially from culture studies. Culturing material would provide clean isolates for DNA sequencing and morphological examination (e.g., Peters et al. 2015; Kawai and Hanyuda 2021; Kawai et al. 2021). As noted above, we obtained DNA sequences for species we never saw (viz., *Hecatonema terminale*). In another instance, when we examined the herbarium voucher of the undetermined Acinetosporaceae, it was a species of *Ectocarpus*, not Acinetosporaceae, suggesting a mixed collection. Also, the failure to locate many of the brown algae that should occur in this area suggests that, as has been found in Antarctic waters, these species may be grazed down by herbivores and can only be observed in grazer-free cultures (Peters 2003; Amsler et al. 2009, 2012).

From a biogeographic perspective, the brown algal flora of the Hakai area on the central coast of British Columbia clearly fits within the region (Table S2): 42% of species are restricted to the northeast Pacific, with most of these distributions ranging from Alaska to California or even Baja California, Mexico; 54% of these are kelps. This diversity is consistent with the hypothesis that the northeast Pacific was an important area for the origin of complex kelps (Starko et al. 2019; Kiel et al. 2024). The remaining species are distributed nearly equally among various biogeographic patterns: North Pacific (i.e., Asia through Alaska and British Columbia to Washington, Oregon, California, or even Baja California)—13%; Trans Arctic (i.e., North Pacific through the Arctic to the North Atlantic)—13%; Pacific–Atlantic disjuncts (i.e., North Pacific and North Atlantic but absent from the Arctic)—15%; and Widely Distributed (having unclear geographic affinities and including introduced species)—2%. Four percent of the species are "endemics" (these species had no closely related sequences in GenBank): *Protohalopteris petersonii* and *Pylaiella* 2 are known only from British Columbia, and *Ectocarpus* 2 is thus far known only from the Hakai area. These species are likely more widely distributed, but lack of collecting and sequencing along other parts of the coast may account for lack of records from elsewhere. It is interesting that some species appear to be widely distributed, with identical sequences for specimens from British Columbia and France, e.g., such as *Hincksia sandriana* and *Punctaria tenuissima*, which may represent recent introductions. In other cases, such as *Leathesia marina* and *Colpomenia peregrina*, differences between these two areas suggest the possibility of incipient speciation. A closer examination of these biogeographic patterns may be warranted.

The occurrence of specimens from the Hakai area with unique haplotypes adds to the speculation that this area may have been a refugium during Pleistocene glaciations on the Northeast Pacific coast (Lindstrom et al. 2021). Among brown seaweeds, unique haplotypes were observed for specimens of *Analipus japonicus*, *Hedophyllum sessile*, *Laminaria setchellii*, and *Scytosiphon lomentaria*. Several private haplotypes were also found among green algal specimens from Hakai (Lindstrom et al. 2021). This line of enquiry continues.

This study represents an important benchmark or baseline on species diversity for future studies to reference as species distributions change through ocean warming, invasions, or disasters (e.g., oil spills). As oceans warm, species ranges are expected to move poleward (Sunday et al. 2015; Bell et al. 2024). Here we extend the northern distribution limit of *Dictyoneurum reticulatum* from southern Vancouver Island (Scagel et al. 1989) to the Hakai area and the northern distributional limit of *Postelsia palmaeformis* from Hope Island, BC (Scagel et al. 1989) to Cranstown Point, approximately 50 km north, at the southern entrance to Fitz Hugh Sound. The search for *P. palmaeformis* on Calvert Island is ongoing. We have also documented the decline of *Laminaria yezoensis* on Calvert Island and the possible recession of its southern distributional limit. We have noted the occurrence of the invasive species *Sargassum muticum* in the Hakai area, as well as changes in its abundance at several sites (Whalen et al. 2023) but have not found the invasive kelp *Undaria pinnatifida* (Harvey) Suringar, which has yet to be reported from British Columbia

Working together, many First Nations, the Province of British Columbia, and the Government of Canada recently developed a plan for a Marine Protected Area network in the Northern Shelf Bioregion, which extends north from Vancouver Island (Quadra Island/Bute Inlet) to the Canada–Alaska border (https://mpanetwork.ca/). The plan envisions an ecologically comprehensive, resilient, and representative network of MPAs that protects the biological diversity and health of this area of the coast, while continuing to support community, cultural, and economic values for present and future generations (MPA Network BC Northern Shelf Initiative 2023). This effort was recently updated by Beaty et al. (2024). Our study adds to these efforts.

Acknowledgements

We thank Hakai Institute, Tula Foundation, particularly Eric Peterson and Christina Munck, for inviting us to Calvert Island and hosting us there. We are grateful to the Heiltsuk Nation and the Wuikinuxv Nation for their stewardship of their land and water and for their commitment to biodiversity on Calvert Island. We also thank the students and others who helped us with these collections, notably Laura Anderson, Kyra Janot, Emma Jourdain, Lauran Liggan, Elliot Porcher, Rachael Wade, and the divers who collected seaweeds for us: Neha Acharya-Patel, Aaron Galloway, Kyle Hall, Andy Lamb, Derek van Mannen, Zach Monteith, Angeleen Olsen, Gustav Paulay, Ondine Pontier, Tanya Prinzing, Gillian Sadlier-Brown, Brenton Twist, and Matt Whalen. We thank Cassandra Jensen for benchwork in the Martone Lab. We are grateful to the Tula Foundation for providing funds for sequencing and other laboratory expenses and to Gillian Sadlier-Brown for coordinating sequencing at CCDB. We thank Keith Holmes and the Hakai Geospatial team for constructing the map in Fig. 1. This work benefited immensely from the availability of a number of online databases, notably AlgaeBase (https://algaebase.org), GenBank (https://www.ncbi.nlm.nih.gov/genbank/), and the Index Nominum Algarum (https://ucjeps.berkeley.edu/INA.html).

Article information

History dates

Received: 9 January 2025
Accepted: 24 June 2025
Version of record online: 14 October 2025

Notes

This paper is part of a collection entitled "UN Decade of Ocean Science for Sustainable Development".

Copyright

Data availability

Accession numbers for herbarium vouchers in the Beaty Biodiversity Museum (https://collections.beatymuseum.ubc.ca/) and for GenBank sequences (https://www.ncbi.nlm.nih.gov/genbank/) are listed in Table 1.

Author information

Author ORCIDs

Sandra C. Lindstrom https://orcid.org/0000-0001-5838-8595

Author notes

Present address for Matthew A. Lemay is Hakai Institute, 1002 Wharf Street, Victoria, BC.

Present address for Samuel Starko is UWA Oceans Institute & School of Biological Sciences, University of Western Australia, 54 Fairway, Crawley, Western Australia, Australia 6009.

Present address for Katharine R. Hind is Department of Biology, University of New Brunswick, Fredericton, NB.

Author contribution

Conceptualization: SCL, PTM
Data curation: SCL, MAL, CJ, PTM
Formal analysis: SCL, CJ
Funding acquisition: CJ, PTM
Investigation: MAL, CJ, SS, KRH, PTM
Methodology: SCL, MAL
Resources: MAL, PTM
Writing – original draft: SCL
Writing – review & editing: SCL, MAL, SS, KRH, PTM

Competing interests

The authors declare there are no competing interests.

Funding Information

Natural Sciences and Engineering Research Council of Canada, (Grant / Award Number: 'RGPIN 2014-06288; 2049-06240 to Patrick Martone').

Supplementary material

Supplementary data are available with the article at https://doi.org/10.1139/cjb-2025-0003.

References

Amsler, C.D., Amsler, M.O., McClintock, J.B., and Baker, B.J. 2009. Filamentous algal endophytes in macrophytic Antarctic algae: prevalence in hosts and palatability to mesoherbivores. Phycologia, **48**: 324–334. doi:10.2216/08-79.1.

Amsler, C.D., McClintock, J.B., and Baker, B.J. 2012. Amphipods exclude filamentous algae from the western Antarctic Peninsula: experimental evidence. Polar Biol. **35**: 171–177. doi:10.1007/s00300-011-1049-3.

Aumack, C.F., Amsler, C.D., McClintock, J.B., and Baker, B.J. 2010. Chemically mediated resistance to mesoherbivory in finely branched macroalgae along the western Antarctic Peninsula. Eur. J. Phycol. **45**: 19–26. doi:10.1080/09670260903171668.

Beaty, F., Brown, K.H.T., Braun, J., Diggon, S., Hartley, E., Heidt, A., and Worsley, K. 2024. From design to implementation: lessons from planning the first marine protected area network in Canada. Mar. Policy, **170**: 106360. doi:10.1016/j.marpol.2024.106360.

Bell, L.E., Westphal, L., O'Brien, E., Toy, J.A., Damron, H., and Kroeker, K.J. 2024. Season influences interspecific responses of canopy-forming kelps to future warming and acidification at high latitutde. Ecosphere, **15**: e4745, 16pp. doi:10.1002/ecs2.4745.

Bringloe, T.T., Brooks, C., Bruce, M., and Saunders, G.W. 2021. Revisiting a DNA barcode survey of Haida Gwaii kelp; the quest for *Eisenia arborea* (Arthrothamnaceae, Laminariales). Botany, **99**: 289–292. doi:10.1139/cjb-2020-0160.

Bringloe, T.T., Sjøtun, K., and Saunders, G.W. 2019. A DNA barcode survey of marine macroalgae from Bergen (Norway). Mar. Biol. Res. **15**: 580–589. doi:10.1080/17451000.2019.1699659.

Cock, J.M., Sterck, L., Rouzé, P., Scornet, D., et al. 2010. The *Ectocarpus* genome and the independent evolution of multicellularity in brown algae. Nature, **465**: 617–621. doi:10.1038/nature09016. PMID: 20520714.

Cavole, L.M., Demko, A.M., Diner, R.E., Giddings, A., Koester, I., Pagniello, C.M.L.S., and Franks, P.J.S. 2016. Biological impacts of the 2013–2015 warm-water anomaly in the Northeast Pacific: winners, losers, and the future. Oceanography, **29**: 273–285. doi:10.5670/oceanog.2016.32.

Chen, Z., Shi, J., Liu, Q., Chen, H., and Li, C. 2021. A persistent and intense marine heatwave in the Northeast Pacific during 2019–2020. Geophys. Res. Lett. **48**: e2021GL093239. doi:10.1029/2021GL093239.

Critchley, A.T., and Ohno, M. (*Editors*). 1998. Seaweed Resources of the World. Japan International Cooperation Agency, Yokosuka, Japan. xviii + 431 + xii pp.

Di Lorenzo, E., and Mantua, N. 2016. Multi-year persistence of the 2014/15 North Pacific marine heatwave. Nat. Clim. Change, **6**: 1042–1048. doi:10.1038/NCLIMATE3082.

Draisma, S.G.A., Prud'homme van Reine, W.F., and Kawai, H. 2010. A revised classification of the Sphacelariales (Phaeophyceae) inferred from a *psb*C and *rbc*L based phylogeny. Eur. J. Phycol. **45**: 308–326. doi:10.1080/09670262.2010.490959.

Dy, M.J.C., Hoshino, M., Abe, T., Yotsukura, N., Klochkova, N., Lee, K.M., and Kogame, K. 2023. *Colpomenia borea* sp. nov (Scytosiphonaceae, Phaeophyceae) from Japan and Far East Russia. Phycol. Res. **71**: 81–89. doi:10.1111/pre.12510.

Filbee-Dexter, K., and Wernberg, T. 2018. Rise of turfs: a new battlefront for globally declining kelp forests. Bioscience, **68**: 64–76. doi:10.1093/biosci/bix147.

Fletcher, R.L. 2024. Brown seaweeds (Phaeophyceae) of Britain and Ireland. Pelagic Publishing, London. pp. x + 806.

Gabrielson, P.W., and Lindstrom, S.C. 2018. Keys to the seaweeds and seagrasses of Southeast Alaska, British Columbia, Washington, and Oregon. Phycological Contribution No. 9. PhycoID, Hillsborough, North Carolina. pp. iv + 190.

Gabrielson, P.W., Lindstrom, S.C., and O'Kelly, C.J. 2012. Keys to the seaweeds and seagrasses of Southeast Alaska, British Columbia, Washington, and Oregon. Phycological Contribution No. 8. PhycoID, Hillsborough, North Carolina. pp. iv + 192.

Gardner, N.L. 1940. New species of melanophyceae from the Pacific coast of North America. Univ. Calif. Publ. Bot. **19**: 267–286.

Geoffroy, A., Mauger, S., De Jode, A., Le Gall, L., and Destombe, C. 2015. Molecular evidence for the coexistence of two sibling species in *Pylaiella littoralis* (Ectocarpales, Phaeophyceae) along the Brittany coast. J. Phycol. **51**: 480–489. doi:10.1111/jpy.12291. PMID: 26986664.

Gonzalez, S. T., Alberto, F., and Molano, G. 2023. Whole-genome sequencing distinguishes the two most common giant kelp ecomorphs. Evolution, **2023**: 1–16. doi:10.1093/evolut/qpad045.

Hind, K.R., Miller, K.A., Young, M., Jensen, C., Gabrielson, P. W., and Martone, P.T. 2015. Resolving cryptic species of *Bossiella* (Corallinales, Rhodophyta) using contemporary and historical DNA. Am. J. Bot. **102**: 1912–1930. doi:10.3732/ajb.1500308. PMID: 26542846.

Hind, K.R., Gabrielson, P.W., Jensen, C.P., and Martone, P.T. 2016. *Crusticorallina*, gen. nov., a nongeniculate genus in the subfamily Corallinoideae (Corallinales, Rhodophyta). J. Phycol. **52**: 929–941. doi:10.1111/jpy.12449. PMID: 27434825.

Hollenberg, G J. 1969. An account of the ralfsiaceae (Phaeophyta) of California. J. Phycol. **5**: 290–301. doi:10.1111/j.1529-8817.1969.tb02617.x. PMID: 27096446.

Hoshino, M., Tanaka, A., Kamiya, M., Uwai, S., Hiraoka, M., and Kogame, K. 2021. Systematics, distribution, and sexual compatability of six *Scytosiphon* species (Scytosiphonaceae, Phaeophyceae) from Japan and the description of four new species. J. Phycol. **57**: 416–434. doi:10.1111/jpy.13089. PMID: 33098679.

Hurd, C.L., Gattuso, J.-P., and Boyd, P.W. 2024. Air-sea carbon dioxide equilibrium: will it be possible to use seaweeds for carbon removal offsets? J. Phycol. **60**: 4–14. doi:10.1111/jpy.13405. PMID: 37943584.

Jao, C.-C. 1937. New marine algae from Washington. *In* Papers of the Michigan Academy of Sciences, Arts and Letters 22. pp. 99–116.

Kato, Y., Kogame, K., Nagasato, C., and Motomura, T. 2006. Inheritance of mitochondrial and chloroplast genomes in the isogamous brown alga *Scytosiphon lomentaria* (Phaeophyceae). Phycol. Res. **54**: 65–71. doi:10.1111/j.1440-1835.2006.00409.x.

Kawai, H., and Hanyuda, T. 2021. Discovery of a novel brown algal genus and species *Setoutiphycus delamareoides* (Phaeophyceae, Ectocarpales) from the Seto Inland Sea, Sci. Rep. **11**: 13901. doi:10.1038/s41598-021-93320-7. PMID: 34230612.

Kawai, H., Hanyuda, T., Gao, X., Terauchi, M., Miyata, M., Lindstrom, S.C., and Miller, K.A. 2017. Taxonomic revision of the agaraceae with a description of *Neoagarum* gen. nov. and reinstatement of *Thalassiophyllum*. J. Phycol. **53**: 261–270. doi:10.1111/jpy.12511. PMID: 28078742.

Kawai, H., Hanyuda, T., Cheng, Q., Miller, K.A., and Peters, A.F. 2021. Taxonomic revision of *Dictyosiphon* (Ectocarpales s.l., Phaeophyceae) from the north-western Pacific, with descriptions of *D. asiaticus* sp. nov. and *D. sparsus* sp. nov. Eur. J. Phycol. **57**: 251–263. doi:10.1080/09670262.2021.1959653.

Kiel, S., Goedert, J.L., Huynh, T.L., Krings, M., Parkinson, D., Romero, R., and Looy, C.V. 2024. Early Oligocene kelp holdfasts and stepwise evolution of the kelp ecosystem in the North Pacific. Proc. Natl. Acad. Sci. USAProc. Natl. Acad. Sci. **121**(4): e2317054121. doi:10.1073/pnas.2317054121.

Kimura, K., Nagasato, C., Kogame, K., and Motomura, T. 2010. Disappearance of male mitochondrial DNA after the four-cell stage in sporophytes of the isogamous brown alga *Scytosiphon lomentaria* (Scytosiphonaceae, Phaeophyceae). J. Phycol. **46**: 143–152. doi:10.1111/j.1529-8817.2009.00779.x.

Klochkova, N.G., Korolyova, T.N., and Kusidi, A.E. 2009. Marine Algae of Kamchatka and Surrounding Areas. Vol. 1. p. 218 [In Russian].

Kogame, K., Rindi, F., Peters, A.F., and Guiry, M.D. 2015. Genetic diversity and mitochondrial introgression in *Scytosiphon lomentaria* (Ectocarpales, Phaeophyceae) in the north-eastern Atlantic Ocean. Phycologia, **54**: 367–374. doi:10.2216/15-016.1.

Kumar, S., Stecher, G., Suleski, M., Sanderford, M., Sharma, S., and Tamura, K. 2024. MEGA12: Molecular Evolutionary Genetics Analysis version 12 for adaptive and green computing. Mol. Biol. Evol. **41**: 1–9. doi:10.1093/molbev/msae263.

Küpper, F.C., Peters, A.F., Shewring, D.M., Sayer, M.D., Mystikou, A., Brown, H., and Wilce, R.T. 2016. Arctic marine phytobenthos of northern Baffin Island. J. Phycol. **52**: 532–549. doi:10.1111/jpy.12417. PMID: 27037790.

Lane, C E., Lindstrom, S.C., and Saunders, G.W. 2007. A molecular assessment of northeast Pacific *Alaria* species (Laminariales, Phaeophyceae) with reference to the utility of DNA barcoding. Mol. Phylogenet. Evol. **44**: 634–648. doi:10.1016/j.ympev.2007.03.016. PMID: 17544704.

Le Cam, S., Daguin-Thiébaut, C., Bouchemousse, S., Engelen, A.H., Mieszkowska, N., and Viard, F. 2020. A genome-wide investigation of the worldwide invader *Sargassum muticum* shows high success albeit (almost) no genetic diversity. Evol. Appl. **13**: 500–514. doi:10.1111/eva.12837.

Lindstrom, S.C. 2018. An undescribed species of putative Japanese *Pyropia* first appeared on the central coast of British Columbia, Canada, in 2015. Mar. Pollut. Bull. **132**: 70–73. doi:10.1016/j.marpolbul.2017.07.016. PMID: 28735967.

Lindstrom, S.C. 2023. A reinstated species name for north-eastern Pacific *Macrocystis* (Laminariaceae, Phaeophyceae). Notul. Algar. **290**: 2.

Lindstrom, S.C., Olsen, J.L., and Stam, W.T. 1997. Post-glacial recolonization and the biogeography of *Palmaria mollis* (Rhodophyta) along the northeast Pacific coast. Can. J. Bot. **75**: 1887–1896. doi:10.1139/b97-900.

Lindstrom, S.C., Hughey, J.R., and Martone, P.T. 2011. New, resurrected and redefined species of *Mastocarpus* (Phyllophoraceae, Rhodophyta) from the northeast Pacific. Phycologia, **50**: 661–683. doi:10.2216/10-38.1.

Lindstrom, S.C., Hughey, J.R., and Aguilar-Rosas, L.E. 2015. Four new species of *Pyropia* (Bangiales, Rhodophyta) from the west coast of North America: the *Pyropia lanceolata* species complex updated. PhytoKeys, **52**: 1–22. doi:10.3897/phytokeys.52.5009.

Lindstrom, S.C., Lemay, M.A., Starko, S., Hind, K.R., and Martone, P.T. 2021. New and interesting seaweed records from the Hakai area of the central coast of British Columbia, Canada: Chlorophyta. Bot. Mar. **64**: 343–361. doi:10.1515/bot-2021-0038.

McDevit, D.C., and Saunders, G.W. 2009. On the utility of DNA barcoding for species differentiation among brown macroalgae (Phaeophyceae) including a novel extraction protocol. Phycol. Res. **57**: 131–141. doi:10.1111/j.1440-1835.2009.00530.x.

McDevit, D.C., and Saunders, G.W. 2017. A molecular investigation of Canadian scytosiphonaceae (Phaeophyceae) including descriptions of *Planosiphon* gen. nov. and *Scytosiphon promiscuus* sp. nov. Botany, **95**: 653–671. doi:10.1139/cjb-2017-0042.

McHenry, J., Okamoto, D.K., Filbee-Dexter, K., et al. 2024. A blueprint for national assessments of the blue carbon capacity of kelp forests applied to Canada's coastline. bioRxiv. doi:10.1101/2024.04.05.586816.

Montecinos, A.E., Couceiro, L., Peters, A.F., Desrut, A., Valero, M., and Guillemin, M.-L. 2017. Species delimitation and phylogeographic analyses in the *Ectocarpus* subgroup *Siliculosi* (Ectocarpales, Phaeophyceae). J. Phycol. **53**: 17–31. doi:10.1111/jpy.12452.

MPA Network BC Northern Shelf Initiative. 2023. Network Action Plan. p. 324.

Mystikou, A., Asensi, A.O., DeClerck, O., Müller, D.G., Peters, A.F., Tsiamis, K., and Küpper, F.C. 2016. New records and observations of macroalgae and associated pathogens from the Falkland Islands, Bot. Mar. **59**: 105–121. doi:10.1515/bot-2015-0071.

Nelson, W.A., and DeWreede, R.E. 1989. Reproductive phenology of *Analipus japonicus* (Harv.) Wynne (Phaeophyta) in the eastern North Pacific. Jpn. J. Phycol. **37**: 53–56.

Parente, M.I., and Saunders, G.W. 2019. A molecular survey of *Ralfsia* sensu stricto (Ralfsiales: Phaeophyceae) in Canada uncovers three new species: *R. robertii* sp. nov., *R. tenebris* sp. nov., and *R. unimaculata* sp. nov. Botany, **97**: 135–147. doi:10.1139/cjb-2018-0138.

Parente, M.I., Fletcher, R.L., Neto, A.I., Tittley, I., Sousa, A.F., Draisma, S., and Gabriel, D. 2010. Life history and morphological studies of *Punctaria tenuissima* (Chordariaceae, Phaeophyceae), a new record for the Azores. Bot. Mar. **53**: 223–231. doi:10.1515/BOT.2010.030.

Perestenko, L.P., and Zakhodnova, T.A. 2007. The genus *Desmarestia* (Phaeophyta, Desmarestiaceae) in the Far Eastern Seas of Russia. Bot. J. **93**: 1112–1127+ 4 pls [In Russian].

Peters, A.F. 2003. Molecular identification, distribution and taxonomy of brown algal endophytes, with emphasis on species from Antarctica. *In* Proceedings of the 17th International Seaweed Symposium, NY. pp. 293–302.

Peters, A.F., and Ramírez, M.E. 2001. Molecular phylogeny of small brown algae, with special reference to the systematic position of *Caepidium antarcticum* (Adenocystaceae, Ectocarpales). Cryptogam. Algol. **22**: 187–200. doi:10.1016/S0181-1568(01)01062-5.

Peters, A.F., van Oppen, M.J.H., Wiencke, C., Stam, W.T., and Olsen, J.L. 1997. Phylogeny and historical ecology of the Desmarestiaceae (Phaeophyceae) support a southern hemisphere origin. J. Phycol. **33**: 294–309. doi:10.1111/j.0022-3646.1997.00294.x.

Peters, A.F., Mann, A.D., Córdova, C.A., Brodie, J., Correa, J.A., Schroeder, D.C., and Cock, J.M. 2010a. Genetic diversity of *Ectocarpus* (Ectocarpales, Phaeophyceae) in Peru and northern Chile, the area of origin of the genome-sequenced strain. New Phytol. **188**: 30–41. doi:10.1111/j.1469-8137.2010.03303.

Peters, A.F., Van Wijk, S.J., Cho, G.Y., Scornet, D., Hanyuda, T., Kawai, H., and Boo, S.M. 2010b. Reinstatement of *Ectocarpus cruoaniorum* Thuret in Le Jolis as a third common species of *Ectocarpus* (Ectocarpales, Phaeophyceae) in Western Europe, and its phenology at Roscoff. Phycol. Res. **58**: 157–170. doi:10.1111/j.1440-1835.2010.00574.x.

Peters, A.F., Couceiro, L., Tsiamis, K., Küpper, F.C., and Valero, M. 2015. Barcoding of cryptic stages of marine brown algae isolated from incubated substratum reveals high diversity in acinetosporaceae (Ectocarpales, Phaeophyceae). Cryptogam. Algol. **36**: 3–29. doi:10.7872/crya.v36.iss1.2015.3.

Puillandre, N., Lambert, A., Brouillet, S., and Achaz, S. 2012. ABGD, automatic barcode gap discovery for primary species delimitation. Mol. Ecol. **21**: 1864–1877. doi:10.1111/j.1365-294X.2011.05239.x.

Ratnasingham, S., and Hebert, P.D.N. 2007. BOLD: the barcode of life data system. Mol. Ecol. Notes, **7**: 355–364. doi:10.1111/j.1471-8286.2007.01678.x.

Santiañez, W.J.E., and Kogame, K. 2017. Transfer of *Petalonia filiformis* (Batters) Kuntze to the genus Planosiphon McDevit and G.W. Saunders (Scytosiphonaceae, Phaeophyceae). Notul. Algar. **40**: 3.

Santiañez, W.J.E., Macaya, E.C., Lee, K.M., Cho, G.Y., Boo, S.M., and Kogame, K. 2018. Taxonomic reassessment of the Indo-Pacific scytosiphonaceae (Phaeophyceae): *Hydroclathrus rapanuii* sp. nov. and *Chnoospora minima* from Easter Island, with proposal of *Dactylosiphon* gen. nov. and *Pseudochnoospora* gen. nov. Bot. Mar. **61**: 47–64. doi:10.1515/bot-2017-0089.

Saunders, G.W. 2005. Applying DNA barcoding to red macroalgae: a preliminary appraisal holds promise for future applications. Philos. Trans. R. Soc. B Biol. Sci. **360**: 1879–1888. doi:10.1098/rstb.2005.1719.

Saunders, G.W. 2008. A DNA barcode examination of the red algal family Dumontiaceae in Canadian waters reveals substantial cryptic species diversity. 1. The foliose *Dilsea–Neodilsea* complex and *Weeksia*. Botany, **86**: 773–789. doi:10.1139/B08-001.

Saunders, G.W. 2014. Long distance kelp rafting impacts seaweed biogeography in the Northeast Pacific; the kelp conveyor hypothesis. J. Phycol. **50**: 968–974. doi:10.1111/jpy.12237.

Saunders, G.W. 2024. NEAS Keys to the benthic marine algae of the Northwest Atlantic and Canadian Arctic from Long Island Sound to Cambridge Bay, 3rd edition, with the description of eight new species. NEAS Contribution Number 3.

Saunders, G.W., and McDevit, D.C. 2013. DNA barcoding unmasks overlooked diversity improving knowledge on the composition and origins of the Churchill algal flora. BMC Ecol. **13**(9): 23.

Saunders, G.W., and McDevit, D.C. 2014. A DNA barcode survey of Haida Gwaii kelp (Laminariales, Phaeophyceae) reveals novel ecological and distributional observations and *Saccharina druehlii* sp. nov. Botany, **92**: 821–826. doi:10.1139/cjb-2014-0119.

Scagel, R.F., Gabrielson, P.W., Garbary, D.J., Golden, L., Hawkes, M.W., Lindstrom, S.C., and Widdowson, T.B. 1989. A synopsis of the benthic marine algae of British Columbia, southeast Alaska, Phycological Contribution No. 3. Reprinted 1993. Washington and Oregon. University of British Columbia, Vancouver. p. 532.

Setchell, W.A., and Gardner, N.L. 1924. Phycological Contributions, VII. Univ. Calif. Publ. Bot. **13**: 1–13.

Silva, P. C., Basson, P. W., and Moe, R. L. 1996. Catalogue of the Benthic Marine Algae of the Indian Ocean. University of California Press, Berkeley. pp. xiv + 1259.

Smith, G.M. 1944. Marine Algae of the Monterey Peninsula, California. Stanford, Calif. p. 622.

Starko, S., Gomez, M.S., Darby, H., Demes, K.W., Kawai, H., Yotsukura, N., and Martone, P.T. 2019. A comprehensive kelp phylogeny sheds light on the evolution of an ecosystem. Mol. Phylogenet. Evol. **136**: 138–150. doi:10.1016/j.ympev.2019.04.012.

Starko, S., Bringloe, T.T., Soto Gomez, M., Darby, H., Graham, S.W., and Martone, P.T. 2021. Genomic rearrangements and sequence evolution across brown algal genomes. Genome Biol. Evolut. **13**: 14. doi:10.1093/gbe/evab124.

Starko, S., Timmer, B., Reshitnyk, L., et al. 2024a. Local and regional variation in kelp loss and stability across coastal British Columbia. Mar. Ecol. Progr. Ser. **733**: 1–26. doi:10.3354/meps14548.

Starko, S., van der Mheen, M., Pessarrodona, A., Wood, G.V., Filbee-Dexter, K., Neufeld, C.J., and Wernberg, T. 2024b. Impacts of marine heatwaves in coastal ecosystems depend on local environmental conditions. Global Change Biol. **30**: e17469. doi:10.1111/gcb.17469.

Steneck, R.S., Graham, M.H., Bourque, B.J., Corbett, D., Erlandson, J.M., Estes, J.A., and Tegner, M.J. 2002. Kelp forest ecosystems: biodiversity, stability, resilience and future. Environ. Conserv. **29**: 436–459. doi:10.1017/S0376892902000322.

Sunday, J.M., Pecl, G.T., Frusher, S., Hobday, A.J., Hill, N., Holbrook, N.J., and Bates, A.E. 2015. Species traits and climate velocity explain geographic range shifts in an ocean-warming hotspot. Ecol. Lett. **18**: 944–953. doi:10.1111/ele.12474.

Teagle, H., Hawkins, S.J., Moore, P.J., and Smale, D.A. 2017. The role of kelp species as biogenic habitat formers in coastal marine ecosystems. J. Exp. Mar. Biol. Ecol. **492**: 81–98. doi:10.1016/j.jembe.2017.01.017.

Tseng, Y.-H., Ding, R., and Huang, X. 2017. The warm blob in the Northeast Pacific–the bridge leading to the 2015/16 El Niño. Environ. Res. Lett. **12**: 054019. doi:10.1088/1748-9326/aa67c3.

Wade, R.M., Gabrielson, P.W., Hind, K.R., Shivak, J., Hughey, J.R., Ohtsu, S., and Martone, P.T. 2023. Resolving some of the earliest names for *Corallina* species (Corallinales, Rhodophyta) in the North Pacific by sequencing type specimens and describing the cryptic *C. hakodatensis* sp. nov. and *C. parva* sp. nov. J. Phycol. **59**: 221–235. doi:10.1111/jpy.13299.

Watson, J.C., Hawkes, M.W., Lee, L.C., and Lamb, A. 2021. The dynamics and geographic disjunction of the kelp *Eisenia arborea* along the west coast of Canada. Bot. Mar. **64**: doi:10.1515/bot-2021-0040.

Wernberg, T.S., and Filbee-Dexter, K. 2019. Missing the marine forest for the trees. Mar. Ecol. Progr. Ser. **612**: 209–215. doi:10.3354/meps12867.

Wernberg, T.S., Bennett, R.C., Babcock, T., de Bettignies, K., Cure, M., Depczynski, F., et al. 2016. Climate driven regime shift of a temperate marine ecosystem. Science, **353**: 169–172. doi:10.1126/science.aad8745.

Wernberg, T., Thomsen, M.S., Baum, J.K., Bishop, M.J., Bruno, J.F., Coleman, M.A., and Vanderklift, M.A. 2024. Impacts of climate change on marine foundation species. Annu. Rev. Mar. Sci. **16**: 18.1–18.36. doi:10.1146/annurev-marine-042023-093037.

Whalen, M.A., Starko, S., Lindstrom, S.C., and Martone, P.T. 2023. Heatwave restructures marine intertidal communities across a stress gradient. Ecology, **104**; e4027. doi:10.1002/ecy.4027.

White, R.H., Anderson, S., Booth, J.F., Braich, G., Draeger, C., Fei, C., and West, G. 2023. The unprecedented Pacific Northwest heatwave of June 2021. Nat. Commun. **14**(727): 20. doi:10.1038/s41467-023-36289-3.

Wynne, M.J. 1987. Records and notes on Alaskan marine algae. II. Contr. Univ. Michigan Herbarium 16. pp. 223–232.