

# The Boulder Patch (North Alaska, Beaufort Sea) and its Benthic Algal Flora

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**ABSTRACT.** We describe the benthic algal flora within the Boulder Patch, a unique and relatively isolated assemblage of cobbles and boulders in the Alaskan Beaufort Sea, on the basis of a compilation of opportunistic in situ collections made from 1977 to 2006. The Boulder Patch is a shallow (4–7 m) High Arctic kelp community containing 78 benthic algal species, all of which represent approximately one-half of the pan-Arctic benthic flora (140 species) including one recognized cyanophyte (*Calothrix scopulorum*), one dinophyte (*Rufusiella foslieana*), 26 green algae, 25 brown algae, and 25 red algal species. Two brown algae are Arctic endemics, and 41 of the 78 Boulder Patch species also occur in the North Pacific Ocean and southeast Alaska. Both endemic species occur widely in the Arctic Ocean and extend into the northern North Atlantic Ocean. All 78 Boulder Patch species occur widely in the northeast Atlantic Ocean. No recognizable endemic species from the boreal/subarctic Pacific and Atlantic Oceans are present in the Boulder Patch. Only four species, two of which are closely related and host-specific, show a poleward shift from the boreal to the High Arctic environment. The algal composition of the Boulder Patch and characterization of these algal communities represent an invaluable baseline in which to assess future change in an Arctic system that is undergoing rapid warming. Our baseline analysis of the benthic flora of the Boulder Patch reveals a habitat characterized by an unexpected high diversity and unique phylogeography for a relatively isolated benthic algal assemblage of the north polar ocean.

**Key words:** Boulder Patch, Alaskan Beaufort Sea, Arctic benthic algae, Arctic phylogeography

**RÉSUMÉ.** Nous décrivons la flore algale benthique faisant partie de la Boulder Patch, un assemblage unique et relativement isolé de galets et de rochers de la mer de Beaufort alaskienne. Cette description s'appuie sur la compilation de collections opportunistes recueillies sur place de 1977 à 2006. La Boulder Patch est un varech peu profond (de 4 à 7 m) de l'Extrême-Arctique qui contient 78 espèces d'algues benthiques, représentant environ la moitié de la flore benthique panarctique (140 espèces), dont une cyanophyte reconnue (*Calothrix scopulorum*), une dinophyte (*Rufusiella foslieana*), 26 algues vertes, 25 algues brunes et 25 espèces algales rouges. Deux algues brunes sont endémiques à l'Arctique, et 41 des 78 espèces de la Boulder Patch se retrouvent également dans l'océan Pacifique Nord et dans le sud-est de l'Alaska. Les deux espèces endémiques se trouvent souvent dans l'océan Arctique et s'étendent jusque dans le nord de l'Atlantique Nord. Les 78 espèces de la Boulder Patch sont fortement répandues dans le nord-est de l'océan Atlantique. Aucune espèce endémique reconnaissable des segments boréaux et subarctiques des océans Pacifique et Atlantique ne sont présents dans la Boulder Patch. Seulement quatre espèces, dont deux sont très proches et spécifiques à un hôte, montrent un déplacement vers le pôle, du milieu boréal au milieu de l'Extrême-Arctique. La composition algale de la Boulder Patch et la caractérisation de ces communautés algales représentent une précieuse base de référence permettant d'évaluer les changements à venir dans un système arctique où le réchauffement se produit rapidement. L'analyse de notre base de référence de la flore benthique de la Boulder Patch révèle un habitat caractérisé par une grande diversité inattendue et par une phytogéographie unique pour un assemblage algal benthique relativement isolé de l'océan polaire nordique.

**Mots clés :** Boulder Patch, mer de Beaufort alaskienne, algues benthiques de l'Arctique, phytogéographie de l'Arctique

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## INTRODUCTION

The Arctic Ocean system is currently experiencing unprecedented change that is well documented in the public media and scientific primary literature. The extraordinary decline in Arctic sea ice in 2012, down to 3.41 million km<sup>2</sup>,

reflects an 18% decline from the previous low set in 2007, dropping the Arctic ice cap to nearly half the 1979–2000 average minimum (NSIDC, 2012). Sea ice has been declining by 12% per decade, a rate that far exceeds the worst-case scenario projected by IPCC (IPCC, 2007; Comiso et al., 2008; Melnikov, 2009; Müller et al., 2009; Wassmann,

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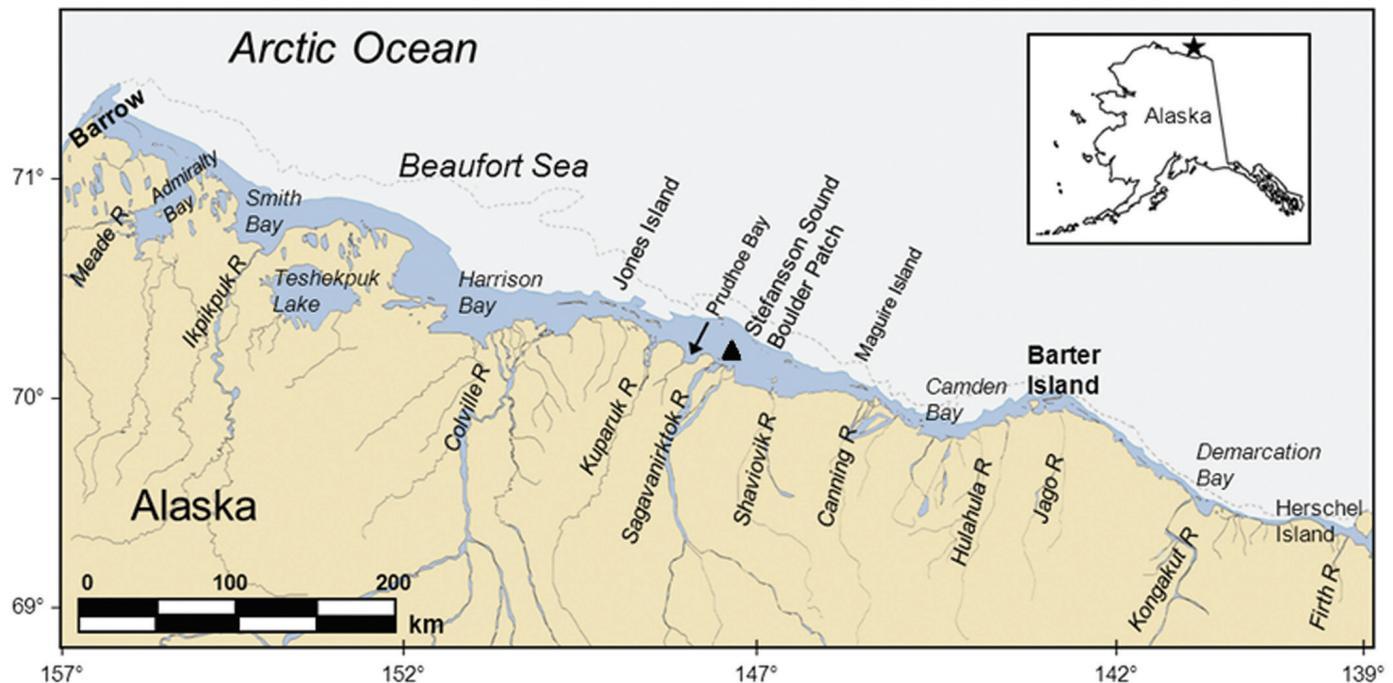


FIG. 1. The Alaska Beaufort Sea coast, showing the linked river-estuarine-lagoon system of the eastern shelf. Triangle denotes the location of the Boulder Patch, east of Prudhoe Bay.

2011; Stroeve et al., 2012; Wiggins, 2012). The loss of sea ice, in concert with warming of seawater (ACIA, 2004; McBean, 2005), is expected to lead to northward migration of macroalgae (and marine organisms in general) currently found in the boreal and subarctic North Atlantic and North Pacific Oceans (Müller et al., 2009). Mounting evidence suggests that these physical changes are influencing the growth, reproduction rates, and spatial distributions of many Arctic organisms, including fish (Perry et al., 2005), birds (Vibe, 1967; Hamilton et al., 2003; Irons et al., 2008), polar bears (Stirling and Parkinson, 2006; Pagano et al., 2012), and invertebrates (Konar and Iken, 2005; Ambrose et al., 2006; Berge et al., 2009). Unequivocally, expression of Arctic marine ecosystem change with accompanying biological alteration is no longer a hypothesis. Disparate disciplines provide uncontroversial documentation of continued change in the polar marine environment.

In this paper, we present the first complete and exhaustive compilation of the benthic flora in the Alaskan Beaufort Sea. Our records are largely based on the relatively unique and isolated marine algal flora in an area designated as the Boulder Patch in Stefansson Sound, near Prudhoe Bay (Fig. 1; Dunton et al., 1982). Objectives of this study are to (1) provide a thorough baseline record of the benthic algal species present in the Boulder Patch to permit future evaluations that address long-term compositional shifts in response to changes in regional climate, (2) present a synopsis of species' biogeographic affinities to assess the origins of this unique flora in the Boulder Patch, and (3) to link the occurrences of species with some of the adaptive mechanisms displayed by various species to survive in the Arctic environment.

#### DESCRIPTION OF THE BOULDER PATCH AND NEARBY SHORE AREAS

The Boulder Patch encompasses a benthic community located ca. 6–8 km off the north Alaskan coast within a roughly 125 km<sup>2</sup> section of Stefansson Sound (70.2556° N, 148.3384° W; Fig. 2). Unlike the soft-sediment bottom present throughout most of the north Alaskan coast and the Beaufort Sea in general, the Boulder Patch bottom is a rare occurrence of localized gravel, cobbles, and small boulders (generally < 1 m diameter). These localized rock accumulations, the result of Pleistocene glacial deposits (Dunton et al., 1982), now provide habitat for attached vegetation and a diverse fauna (Dunton and Schonberg, 2000). Most of the seaweeds of the Boulder Patch are highly dependent on a solid substratum, resulting in an attached algal community that is comparable to those reported in the North Atlantic and Canadian Arctic Islands. Along-shore currents in the Boulder Patch area are sufficiently strong to maintain the Boulder Patch as a non-depositional environment, despite its immediate proximity to the Sagavanirktok River Delta (Dunton et al., 1982).

Consequently, although the Boulder Patch is subject to high turbidity and periods of sedimentation during the summer open-water period, currents prevent significant long-term accumulation of sediments, thereby providing opportunities for the settlement and colonization of rock surfaces by epilithic invertebrates and algae. Patches of sublittoral cobbles and boulders, which vary greatly in density and cover on the seabed, produce an oasis of unexpected species diversity and biomass in an otherwise stressful and unsuitable habitat for marine macroalgae and sessile

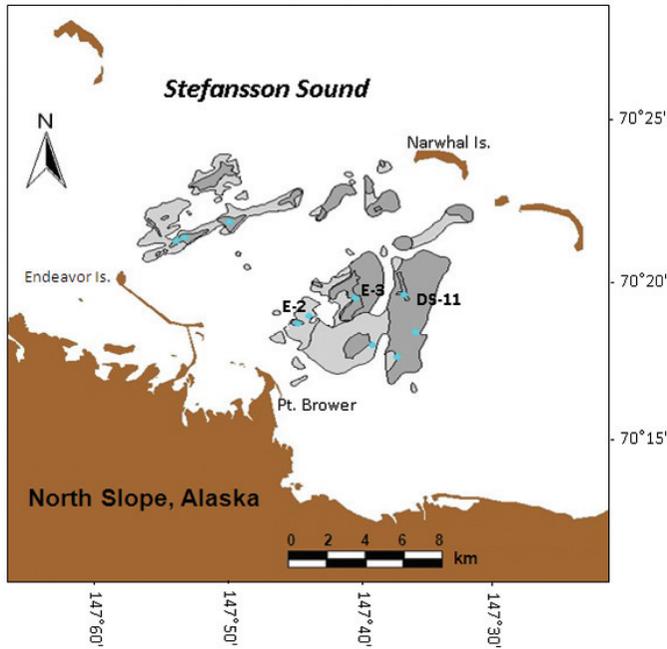


FIG. 2. Location of fixed long-term monitoring stations in the Boulder Patch (denoted in blue) in Stefansson Sound. Algal collections were focused at three stations (DS-11, E-3, E-2). Grey shaded areas represent Boulder Patch extent based on geologic surveys conducted in 1980 and 1997 (Toimil and England, 1980; Coastal Frontiers and LGL, 1998). Dark grey represents areas of boulder cover greater than 25%, and light grey, those with cover between 10% and 25%.

invertebrates. As a consequence, the character of the Boulder Patch kelp community can vary considerably as a function of rock cover (Fig. 2), depth, distance from shore, and location in Stefansson Sound. In areas of high rock cover (> 25%), the overall epilithic community appears diverse and highly colorful, whereas in areas of low rock cover (< 10%), its attractiveness is low in terms of color or texture, giving an impression of species impoverishment.

The Boulder Patch is entirely sublittoral (4–7 m) and mostly free of extreme ice abrasion owing to shelter of low relief by offshore islands. However, this is a perennially harsh environment for phytobenthos colonization and proliferation. The Boulder Patch is characterized by seasonally lower salinities, dramatically low light conditions and periods of intense turbidity and sedimentation. It is comparable to other Arctic sublittoral habitats such as heads of fjords and portions of bays in proximity to glacial discharge. In all such areas, low light, low salinity, and suspended sediments are dominant features that limit algal diversity and biomass. Ambient light on the seabed in the Boulder Patch is minimal for macroalgal photosynthesis, even during summer open-water periods when the sun is above the horizon 24 hrs/day (Dunton, 1990). Annual light availability in the north Alaskan sublittoral is controlled by seasonal high-latitude light oscillations and long periods of heavy ice cover that restrict photosynthesis mainly to the relatively short (3–4 month) open-water period. Light transmission during the short ice-free season is further inhibited by turbid freshwater incursions from local rivers in early summer, followed

by sediment resuspension from wind-generated waves and turbulence throughout the summer months. As a result, the local flora must have sufficiently low-light requirements to persist under such low-water transparencies. For example, *Laminaria solidungula*, a species of kelp whose physiological requirements are well documented (Chapman and Lindley, 1980; Henley and Dunton, 1995; Borum et al., 2002; Krause-Jensen et al., 2007) requires only  $38 \text{ mol m}^{-2} \text{ s}^{-1}$  of irradiance to reach photosynthetic saturation in the Boulder Patch (Dunton and Jodwalis, 1988), considerably lower than the requirements of many macroalgae and nearly all kelp (Gómez et al., 2009; Wiencke et al., 2009).

Bottom-water temperature at the Boulder Patch sites ranges from  $-1.80^\circ\text{C}$  in winter to  $4.0^\circ\text{C}$  in summer, and bottom salinities range from 14 to 25 in summer and 30 to 35 in winter (Sellmann et al., 1992). Water temperatures and salinities do not differ appreciably from those recorded in other Arctic inshore regions (Just, 1970; Rysgaard et al., 2003). It is therefore unlikely that either water temperature or salinity is responsible for the relative floristic impoverishment apparent in the Boulder Patch community compared to other Arctic kelp beds. Ice cover in the Boulder Patch generally lasts from eight to nine months, and shore freeze-up occurs between late September and early October. Reduced light transmission, due to dirty, sediment-laden ice, represents the major ecological influence of ice cover. The presence of offshore islands and shoals precludes frequent ice scour in Stefansson Sound. Over three decades, only a few instances of ice scour have been observed at a variety of locations in the Boulder Patch (K. Dunton, pers. obs.).

## MATERIALS AND METHODS

In situ collection by divers of attached algae in the Boulder Patch began in 1978 (Dunton et al., 1982) and continued through summer 2012, although a majority (more than 95%) of sampling took place between 1978 and 2006 (Dunton et al., 2009). Ten sublittoral stations were occupied in Stefansson Sound at various times over this period at depths ranging from 4.6 to 6.4 m (Fig. 2), but most samples were collected at three stations (DS-11, E-3, and E-2) in late July and early August 1978–83, 1987–88, 1992, and 2004–06 and under the ice at DS-11 in March and April 1978–81 and 1992. Diving safety concerns limited the scope of sampling to the area within a 50 m radius of each sublittoral station's geographic center point. Additional collections were made opportunistically in other years (e.g., 2011 and 2012), but these were limited in scope and targeted specific species for taxonomic study. Samples were obtained under a variety of conditions, from ice-covered (1.8 m thick ice) to open-water periods during summer. Collections and observations were often made at marked locations or along semi-permanent transect lines, which allowed us to note species occurrence, reproductive periodicity, and in some instances, seasonal thallus growth. Unfortunately, the fact

that samples were collected at irregular intervals over three decades within a limited radius of each identified station does not permit a statistical approach to addressing questions of change. However, personal observations made over nearly three decades indicated a static species composition, with perhaps minor changes in species numbers for larger species. Only the algal collections associated with the BIOS Project (Cross et al., 1987), conducted in northern Baffin Island from 1980 to 1983, approximate a similarly thorough picture of the seaweed flora in a High Arctic marine embayment.

In our study, fresh algae collected by divers were normally sorted, rinsed of debris, and mounted on labeled herbarium paper in the field, but specimens collected in August 1987 (ice free) and March 1992 (beneath winter ice cover) were visually inspected in an Alaskan shore laboratory with the aid of Wild light microscopes (M5 dissection and M20 compound) prior to preservation. All algal collections from the Boulder Patch were studied with the same optics by R. Wilce at the University of Massachusetts, Amherst. Specimens were preserved in 5% seawater/formalin, or dried on herbarium paper. Specimens of calcareous red crusts and crustose brown algae were maintained intact on their respective substrate (pebbles or cobbles).

A majority of the Boulder Patch collection is catalogued and maintained at the University of Massachusetts herbarium, Amherst, Massachusetts. Attempts to quantify the relative occurrence of three calcareous crust species were based on their presence on cobble collected throughout the tenure of this study. The taxonomy and nomenclature used conform to the current Algae Base binomials (Guiry and Guiry, 2012). Owing to the observed persistence of morphological form over two consecutive years in the Narwhal Island tidal lagoons, species designation of the ulvophytes follows Bliding (1963) and Hayden et al. (2003).

Collections of more ephemeral shallow-water species from Stefansson Sound shorelines and uppermost sublittoral habitats were made at two islands that border the northern and southern boundaries of the Boulder Patch. Nearest the coast is Endeavor Island (Fig. 2), a man-made oil production island at Endicott that is ringed with interlocking concrete slabs. The island face provides a littoral solid substratum in 3–4 m depth located about 1 km from the southernmost and inshore boundary of the Boulder Patch. The concrete slab substratum at the edge of Endeavor Island is further protected from ice scour and erosion by large woven polypropylene sacs of gravel and rock that also provide a stable surface for attached ephemeral benthic algae. Offshore and seaward of the Boulder Patch, we collected algae from Narwhal Island, which is part of the McClure Island barrier island chain that prevents deep-draft ice from entering Stefansson Sound. Narwhal Island is highly exposed to water and ice movements and projects a long barrier into the outer part of Stefansson Sound. Pebbles are the only solid substratum on its barren shorelines, but the island contains two shallow (< 1.0 m), semi-permanent tidal lagoons (Fig. 3) that support benthic macroalgae.



FIG. 3. Narwhal Island showing the location of two long-lasting, tidal lagoons (arrows). Only several algal species and a few species of microfauna remain viable with the onset of winter in these highly stressful Arctic environments. Photograph taken in August 1978.

## RESULTS

### *Representative Flora of the Stefansson Sound Boulder Patch and Adjacent Areas*

A total of 78 species (Tables 1–3) including one cyanobacterium (*Calothrix scopulorum*) and one member of the Dinophyta (*Rufusiella foslieana*) were identified over the course of this study. Of the Boulder Patch flora, 26 species belong to the Chlorophyta, 25 species to the Ochrophyta, and 25 are members of the Rhodophyta. Two species, *Ralfsia ovata* and *Laminaria solidungula*, are considered endemic to the Arctic. All species are recognized from the pan-Arctic flora (ca. 140 species, R. Wilce, unpubl. records). Forty-one species also occur in the North Pacific Ocean and southeastern Alaska (Gabrielson et al., 2012). The Boulder Patch species list includes many well-recognized boreal algal species (Taylor, 1957; Wilce, 1959; Mathieson and Hehre, 1982; Pedersen, 2011), although many boreal algal species in the Arctic, including those in the Boulder Patch, exhibit dwarf morphologies. Several species are cited on the basis of a single collection or several widely dispersed collections. In this category *Phaeophila dendroides*, *Stylo-nema alsidii*, *Furcellaria lumbricalis* with accompanying *Chlorochytrium inclusum*, and the alternate life history form of *C. inclusum*, *Spongomorpha congregata* (a putative sexual stage), are strikingly representative. The single collections of *P. dendroides* and *Stylo-nema alsidii* from the Boulder Patch represent the first records of these two boreal species in an Arctic ecosystem. Collection of *P. dendroides* and *S. alsidii* in the Beaufort Sea also completes a species continuum for both, connecting their distributional range from the boreal Atlantic Ocean to the North Pacific Ocean. Appearance of *S. alsidii*, *F. lumbricalis*, *C. inclusum*, *P. dendroides*, and *Eugomontia sacculata* in the Boulder Patch extends the known northern limit of these species.

Sampling efforts on Narwhal Island revealed a mixture of green and a single brown algal species in the lagoons, despite the obvious severity of these shallow-water environments, which are completely frozen during the nine-month ice-covered period. Each lagoon blooms annually

TABLE 1. Chlorophyta: (26 species, plus two alternate life history forms with recognized binomials) and Cyanobacteria (1 species) present in Boulder Patch and environs. Algal species present in the North Pacific Ocean and southeast Alaska (22) are denoted with an (\*); all are known from the northeast Atlantic Ocean. Those found from Kongsfjorden, Svalbard, by Hop et al. (2012) are noted for occurrence comparison.

Chlorophyta	Boulder Patch	Narwhal Island	Endicott	Svalbard
<i>Acrosiphonia arcta</i> (L.W. Dillwyn) L. Gain*	X			X
<i>Acrosiphonia flagellata</i> F.R. Kjellman				X
<i>Acrosiphonia incurva</i> F.R. Kjellman				X
<i>Acrosiphonia sonderi</i> (F.T. Kützing) F.T. Kützing				X
<i>Blidingia marginata</i> (J. Agardh) P. Dangeard*		X		
<i>Blidingia minima</i> (C. Nägeli ex F.T. Kützing) H. Kylin*		X		
<i>Chaetomorpha ligustica</i> (F.T. Kützing) F.T. Kützing*	X	X		
<i>Chaetomorpha linum</i> (O.F. Müller) F.T. Kützing*		X	X	
<i>Chaetomorpha melagonium</i> (F. Weber and D. Mohr) F.T. Kützing*	X	X	X	
<i>Chlorochytrium dermatocolax</i> Reinke	X			
<i>Chlorochytrium inclusum</i> F.R. Kjellman*, alternate with <i>Spongomorpha congregata</i>	X			
<i>Chlorochytrium schmitzii</i> L.K. Rosenvinge	X			
<i>Codiolum gregarium</i> A. Braun*, alternate with <i>Urospora wormskioldii</i>	X			
<i>Eugomontia sacculata</i> P. Kornmann*	X		X	
<i>Gloeocystis scopulorum</i> A. Hansgrig in M. Foslie		X		
<i>Monostroma obscurum</i> (F.T. Kützing) J. Agardh				X
<i>Phaeophila dendroides</i> (P.L. Crouan and H.M. Crouan) Batters*	X			
<i>Pringsheimiella scutata</i> (J. Reinke) M. Marchewinka*				X
<i>Pseudopringsheimia confluens</i> (K.L. Rosenvinge) N. Wille*	X			
<i>Spongomorpha congregata</i> F.T. Kützing	X			X
<i>Syncoryne reinkei</i> R. Nielsen and P.M. Pedersen				X
<i>Ulothrix flacca</i> (L.W. Dillwyn) G. Thuret in A. Le Jolis*	X			X
<i>Ulothrix implexa</i> (F.T. Kützing) F.T. Kützing*	X	X	X	X
<i>Ulva flexuosa</i> (Wulfen) J. Agardh	X	X		
<i>Ulva intestinalis</i> L.*				X
<i>Ulva prolifera</i> (O.F. Müller) H.S. Hayden, J. Blomster, A.C. Maggs, P.C. Silva, M.J. Stanhope and R. Waaland		X	X	
<i>Ulva torta</i> (J.C. Mertens) V.A. Trevisan*		X		
<i>Ulva rigida</i> J. Agardh*	X			
<i>Ulvaria obscura</i> (K.T. Kützing) P. Gayral ex C. Bliding*	X			X
<i>Ulvella repens</i> (N. Pringsheim) R. Nielsen, C.J. O'Kelly, and B. Wysor*	X			X
<i>Ulvella viridis</i> (Reinke) R. Nielsen, C.J. O'Kelly, and B. Wysor*		X		
<i>Ulvella wittrockii</i> (N. Wille) R. Nielsen, C.J. O'Kelly, and B. Wysor*		X		
<i>Urospora elongata</i> (K.L. Rosenvinge) O. Hagem			X	
<i>Urospora penicilliformis</i> (A.W. Roth) J.E. Areschoug		X	X	
<i>Urospora wormskioldii</i> (J.C. Mertens ex J.W. Hornemann) L.K. Rosenvinge*		X	X	
Cyanobacteria:				
<i>Calothrix scopulorum</i> C. Agardh*	X		X	

with large populations of loose-lying mat and crust forming cyanobacteria, attached green algal species (*Ulva* spp., *Ulothrix flacca*, *U. implexa*, *Urospora wormskioldii*), and a common filamentous brown alga (*Pylaiella littoralis*). The foregoing species and others are predictable components of north Alaskan coastal lagoons, brackish ponds, and tidal embayments (Collins, 1927; Kent, 1975). Despite the absence of firm substratum in the small tidal lagoon, other than small pebbles, algae have occurred ubiquitously in these lagoons since our work in Stefansson Sound began in 1978. The lagoons are brackish and relatively warm, as noted in August 2011, when we recorded a temperature of 13.2°C and a salinity of 14. Although the exposed north- and northwest-facing outer coasts of Narwhal Island are composed entirely of pebbles and small cobbles, abrasion from ice and substratum movement along this highly dynamic shoreline prevent even short-lived macroalgal colonization. Collections of more ephemeral benthic algal species from semi-permanent tidal lagoons (Fig. 3) on Narwhal Island included *Pylaiella littoralis*, *Urospora*

*wormskioldii*, *U. penicilliformis*, *Ulothrix implexa*, *Codiolum gregarium*, and *Calothrix scopulorum* (one of several unidentified cyanobacteria). The algal vegetation attached to the concrete bulwarks and gravel-filled sacs that buffer Endeavor Island consisted of eight species (Tables 1 and 2) that included several filamentous green algae and clumps of *Pylaiella littoralis*. These species first appear on the solid substratum in late July, after the disappearance of winter ice, and are likely lost with the onset of winter ice and storms by November.

#### Characteristic Features of the Boulder Patch Macroalgal Community

At first glance, the dull browns of *Laminaria solidungula* (Fig. 4) and *Saccharina latissima* and the deep reds of *Dilsea socialis* and *Coccotylus truncatus* are the most evident features of the seabed in the Stefansson Sound Boulder Patch. Even perennial thalli of the common *Phycodryas rubens* and *Odonthalia dentata* are almost a chocolate

TABLE 2. Ochrophyta: (25 species) and Dinophyta (1 species) present in Boulder Patch and environs. Arctic endemics (2) are noted in boldface. Algal species present in the North Pacific Ocean and southeast Alaska (18) are denoted with an (\*); all are known from the northeast Atlantic Ocean. Those found from Kongsfjorden, Svalbard, by Hop et al. (2012) are also noted for floral occurrence comparison.

Ochrophyta	Boulder Patch	Narwhal Island	Endicott	Svalbard
<i>Alaria esculenta</i> (L.) R.K. Greville	X			X
<i>Battersia arctica</i> (W.H. Harvey) S.G. Draisma, W.F. Prud'homme, & H. Kawai*	X			X
<i>Chaetopteris plumosa</i> (H.G. Lyngbye) F.T. Kützing	X			X
<i>Chorda filum</i> (L.) J. Stackhouse				X
<i>Chordaria flagelliformis</i> (O.F. Müller) C. Agardh*				X
<i>Desmarestia aculeata</i> (L.) J.V. Lamouroux*	X			X
<i>Desmarestia viridis</i> (O.F. Müller) J.V. Lamouroux*	X			X
<i>Dictyosiphon foeniculaceus</i> (G. Hudson) R.K. Greville				X
<i>Ectocarpus siliculosus</i> (L.W. Dillwyn) H.C. Lyngbye				X
<i>Elachista fucicola</i> (T. Velley) J.E. Areschoug*	X			X
<i>Eudemes virescens</i> (Carmichael ex M.J. Berkeley) J. Agardh*	X			X
<i>Fucus distichus</i> L.*				X
<i>Halosiphon tomentosus</i> (H.G. Lyngbye) E. Jaasund				X
<i>Haplospora globosa</i> F.R. Kjellman				X
<i>Hincksia ovata</i> (F.R. Kjellman) P.C. Silva*	X			
<i>Laminaria digitata</i> (G. Hudson) J.V. Lamouroux				X
<b><i>Laminaria solidungula</i></b> J. Agardh*	<b>X</b>			<b>X</b>
<i>Laminariocolax tomentosoides</i> (W.G. Farlow) H. Kylin*	X			
<i>Leptonematella fasciculata</i> (J. Reinke) P.C. Silva*	X			
<i>Lithoderma fatiscens</i> (J.E. Areschoug) emend. M. Waern	X			
<i>Myrionema corunnae</i> C. Sauvageau				X
<i>Mikrosyphar polysiphoniae</i> P. Kuckuck				X
<i>Petalonia fascia</i> (O.F. Müller) O. Kuntze*	X			X
<i>Petroderma maculiforme</i> (R. Wollny) P. Kuckuck*	X			
<i>Phaeostroma pustulosum</i> P. Kuckuck	X			
<i>Pogotrichum filiforme</i> J. Reinke				X
<i>Pseudolithoderma extensum</i> (P.L. and H.M. Crouan) S. Lund				X
<i>Pseudolithoderma rosenvingii</i> (M. Waern) S. Lund	X			X
<i>Punctaria tenuissima</i> (C. Agardh) R.K. Greville*	X			
<i>Pylaiella littoralis</i> (L.) F.R. Kjellman*	X			X
<b><i>Ralfsia ovata</i></b> L.K. Rosenvinge	<b>X</b>			
<i>Saccharina latissima</i> (L.) C.E. Lane, C. Mayes, L. Dreuhl, and G.W. Saunders*	X			X
<i>Saccorhiza dermatodea</i> (B. de la Pylae) J. Agardh				X
<i>Scytosiphon lomentaria</i> (H.G. Lyngbye) H.F. Link*	X			
<i>Sorapion kjellmanii</i> (N. Wille) L.K. Rosenvinge	X			
<i>Sphaceloderma caespitula</i> (H.G. Lyngbye) S.G. Draisma, W.F. Prud'homme & H. Kawai*	X			
<i>Stictyosiphon tortilis</i> (C. Gobi) J. Reinke*	X			X
Dinophyta:				
<i>Rufusiella foslieana</i> (A. Hansgrig) T. Christensen		X	X	

reddish color except for the annual terminal growth segments. Short thallus tips (< 1.0 cm) are bright red to pinkish and stand in complete contrast to the otherwise muted colors of the supporting axes. Occasional dwarfed thalli of *Ulvaria obscura*, bright green in many other habitats, are subdued and often virtually indistinct as a green alga. Conspicuous green algae are mostly absent except for *Chaetomorpha melagonium*. Minuscule green epiphytes and endophytes, detectable only with the aid of optics, represent the majority of the Boulder Patch Chlorophyta. All Boulder Patch species appear to perennate. Most species are long lasting and exhibit thalloid, crustose, or filamentous forms. Others, such as chlorophytes, filamentous browns, and some unicells, regenerate from overwintering fragments. Annual Arctic algal species appear largely absent in the Boulder Patch.

Three dominant life forms are immediately apparent in the Boulder Patch: (1) a large, mostly homogenous kelp population, (2) a seemingly ubiquitous crustose algal population, and (3) clumps of delicate or coarse thalloid reds and

browns, often long-lasting, loose-lying populations. Most of the thalloid individuals belong to *Coccotylus truncatus*, *Phycodryis rubens*, *Dilsea socialis*, and the brown alga *Desmarestia aculeata*. Few species are readily identifiable in situ, and the majority of species are infrequent and cryptic, hidden in the silt bottom cover, or form loose-lying algal populations. Three kelp species (*Laminaria solidungula*, with two lesser co-dominants, *Saccharina latissima* and *Alaria esculenta*) are invariably present. Some bottom areas are largely covered with numerous dark, sediment-laden, leathery, decumbent blades of *L. solidungula* (Fig. 4). The great abundance of *L. solidungula* in an unusually stressed Arctic sublittoral environment adds support to its distinction as one of the few Arctic algal endemics. Although abundant and gregarious in other areas of the Cold Boreal and Arctic, *S. latissima* has a spotty occurrence in the Boulder Patch (Dunton et al., 1982; Dunton, 1985). Similarly, *A. esculenta* occurs with even less frequency than pan-Arctic *S. latissima* and *L. solidungula*, and occurs in the Boulder Patch as fairly infrequent, mostly solitary thalli (Dunton et al., 1982).

TABLE 3. Rhodophyta: (25 species) present in Boulder Patch and environs. Algal species present in the North Pacific Ocean and southeast Alaska (10) are denoted with an (\*); all are known from the northeast Atlantic Ocean. Those found from Kongsfjorden, Svalbard by Hop et al. (2012) are noted for occurrence comparison.

Rhodophyta	Boulder Patch	Narwhal Island	Endeavor	Svalbard
<i>Ahnfeltia plicata</i> (G. Hudson) E.M. Fries	X			
<i>Callophyllis cristata</i> (C. Agardh) H. Kützing*	X			X
<i>Ceratocolax hartzii</i> L.K. Rosenvinge	X			
<i>Chromastrum mahumetanum</i> (G. Hamel) H. Stegenga and A.S. Mulder	X			
<i>Clathromorphum compactum</i> (F.R. Kjellman) M. Foslie	X			
<i>Coccotylus truncatus</i> (P. S. Pallas) M.J. Wynne and J.N. Heine*	X			
<i>Cystoclonium purpureum</i> (G. Hudson) E. Batters				X
<i>Devaleraea ramentaceum</i> (L.) M.D. Guiry*	X			X
<i>Dilsea socialis</i> (A. Postels and F. Ruprecht) L.P. Perestenko	X			
<i>Euthora cristata</i> (C. Agardh) J. Agardh *	X			X
<i>Grania efflorescens</i> (J. Agardh) H. Kylin	X			X
<i>Hildenbrandia rubra</i> (C. Sommerfelt) G. Meneghini				X
<i>Furcellaria lumbricalis</i> (G. Hudson) J.V. Lamouroux	X			
<i>Harveyella mirabilis</i> (P.F. Reinsch) F. Schmitz and J. Reinke*	X			
<i>Kvaleya epilaeve</i> W.H. Adey and C.P. Serapani	X			
<i>Odonthalia dentata</i> (L.) H.C. Lyngbye	X			X
<i>Palmaria palmata</i> (L.) F. Weber and D.M. Mohr*	X			X
<i>Phycodryas rubens</i> (L.) E. Batters	X			X
<i>Phymatolithon foecundum</i> (F.R. Kjellman) L. Düwel and S. Wegeberg*	X			X
<i>Phymatolithon tenue</i> (L.K. Rosenvinge) L. Düwel and S. Wegeberg *	X			
<i>Polysiphonia arctica</i> J. Agardh	X			X
<i>Polysiphonia elongata</i> (G. Hudson) K. Sprengel				X
<i>Polysiphonia fucoides</i> (G. Hudson) R.K. Greville				X
<i>Ptilota gunneri</i> P.C. Silva, C. Maggs and L.M. Irvine				X
<i>Ptilota serrata</i> F.T. Kützing*	X			
<i>Rhodochorton purpureum</i> (J. Lightfoot) L.K. Rosenvinge				X
<i>Rhodomela confervoides</i> (G. Hudson) P.C. Silva (Annual)	X			X
<i>Rhodomela lycopodioides</i> (L.) C. Agardh* (Perennial)	X			
<i>Rhodophysema kjellmanii</i> (S. Lund) G.W. Saunders and S. L. Clayden				X
<i>Rubrointrusa membranacea</i> (P. Magnus) S.L. Clayden and G.W. Saunders*	X			X
<i>Scagelia pylaisaei</i> (J.F. Montagne) M.J. Wynne*	X			X
<i>Stylonema alsidii</i> (G. Zanardini) K. Drew*	X			
<i>Wildemania miniata</i> (C. Agardh) M. Foslie				X

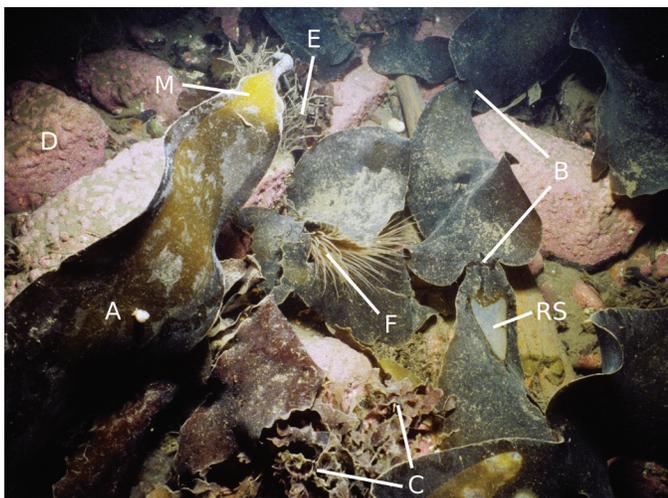


FIG. 4. *Laminaria solidungula* population at DS-11 in the Boulder Patch (6 m), with associated biota. (A) *L. solidungula* with reproductive sori (RS); note the meristematic area at the base of the blade (M), and the annual blade segments (B); (C) *Coccotylus truncatus*; (D) Nodular *Phymatolithon foecundum*; note the prevalence of coralline crusts on rock substratum; (E) *Rhodomela lycopodioides*; (F), the tube dwelling anemone *Cerianthus*.

Crustose coralline red algae and fleshy brown algae accompany a remarkable assemblage of benthic invertebrate fauna on the rock substratum in the Boulder Patch

(Dunton and Schonberg, 2000). The occurrence of calcareous red and brown crusts is typical of the crustose vegetation of most other Arctic sublittoral inshore habitats (Wilce, 1994; Glud et al., 2009; Konar and Iken, 2005). Three species of coralline algae, *Phymatolithon foecundum*, *P. tenue*, and *Clathromorphum compactum*, are the major space occupiers in the Boulder Patch. Collectively, these species covered 60% of the hard substratum in 80% of in situ observations (Konar and Iken, 2005; Fig. 4). Although both *P. foecundum* and *P. tenue* are most important in terms of substratum cover, analysis of over 50 cobbles reveals that *P. foecundum* (Fig. 4) has by far the greatest occurrence and cover, exhibiting a minimum 3:1 ratio in species presence to *P. tenue*. In the competition for substratum, *C. compactum* is more successful than *P. tenue*, but less successful than *P. foecundum*. When present, reproductive sori help to distinguish each coralline crust species in situ (Adey, 1966; R. Wilce, pers. obs.). Occasionally, *Elachista fucicola*—normally epiphytic on species of *Fucus* and *Ascophyllum nodosum*, neither of which is present in the Boulder Patch—occurred on coralline red algal substratum.

Of the encrusting brown algae, and in order of abundance, *Ralfsia ovata*, *Sorapion kjellmanii*, and *Lithoderma fatiscens* occur most frequently. The remaining brown crustose species (*Petroderma maculiforme* and

*Pseudolithoderma extensum*) are considered only occasional. All of the five brown crustose species occur throughout the Canadian Arctic and West Greenland, and most also occur in the Subarctic. Only endemic *R. ovata* develops populations that are primarily Arctic in occurrence. The life-history stratagem that permits *R. ovata* to form only its distinctive plurilocular organs remains unknown. Numerous representatives of *R. ovata*, collected at the Boulder Patch during both ice covered and open-water summer season, fail to contain unilocular sporangia. Interestingly, unilocular sporangia are present on specimens of the type collection from Godthaab (Nuuk), West Greenland (July 1890), noted by Rosenvinge (1893).

The Boulder Patch algal community contains several loose-lying forms of algae that are typically recognized as attached thalloid and leafy red and brown algal species. Six species are conspicuous, long lasting, and readily identifiable in situ: *Coccotylus truncatus*, *Odonthalia dentata*, *Phycodrys rubens*, *Rhodomela lycopodioides*, *Dilsea socialis*, and *Desmarestia aculeata*. Only the red algal genera *Dilsea*, *Coccotylus*, and *Phycodrys* develop attached populations of appreciable size. The remaining Boulder Patch species, though present, are generally infrequent and at times inconspicuous. Only two Arctic endemic species (*Ralfsia ovata* and *Laminaria solidungula*) were recognized in the Boulder Patch. Both species have pan-Arctic distributions. It is likely that many Boulder Patch species have boreal origins from both the North Atlantic and North Pacific Oceans. A third Arctic endemic species (*Turnerella pennyi*), commonly found throughout the central Arctic Ocean and west Greenland, is missing from the Boulder Patch. Inexplicably, this species is present in the collections from the initially discovered boulder substratum along the north Alaskan coast near Point Barrow (Mohr et al., 1957; R. Wilce, initial I.D., 1956). None of the algae identified from the Boulder Patch are identifiably of Pacific Ocean origin (Dunton, 1992; Tables 1–3). However, North Pacific Ocean and Bering Sea algal species could spread northward since some (e.g., *Bossiella cretacea*, *Halosaccion glandiforme*, *Pterosiphonia hamata*) are already found at Port Clarence, northwest Alaska (Kjellman, 1889; Dunton, 1992; R. Wilce, unpubl. data), just south of the Bering Strait. It is also remarkable that only three (*Turnerella pennyi*, *Laminaria solidungula* and *Ralfsia ovata*) of the recognized 20–22 Arctic endemic species (R. Wilce, unpubl. records) are documented from the north Alaskan coast (from Point Barrow to Stefansson Sound).

A single thallus (4.5 cm) of *Furcellaria lumbricalis* was collected at station E3 on 23 August 1987. This thallus occurred with an accompanying endophyte of *Chlorochytrium inclusum* and accompanying *Spongomorpha congregata* filaments. *F. lumbricalis*, an accepted boreal species, has not previously been cited from an Arctic environment. Kjellman (1883:158) distinguished *Polyides* (as *Polyides rotundus* (Huds.) Greville) from *Furcellaria* by the character of its tetraspores and cites the northernmost occurrence of *F. lumbricalis* as from “the coast of

Spitsbergen.” The Boulder Patch specimen *F. lumbricalis* was juvenile and lacked even incipient tetraspores. Generic distinction was based on the internal structure of the erect thallus, the medulla composed of both distally oriented filaments and branching rhizoids (e.g., Rosenvinge, 1917; Dixon and Irvine, 1977; Guiry and Guiry, 2012). Holdfast features of *Furcellaria* specimens, also helpful in generic identity with *P. rotunda*, remain unresolved.

## DISCUSSION

Although much of our knowledge of the Boulder Patch kelp bed community is based on its productivity, benthic community composition, and trophic structure, the biogeographic characteristics of the flora may help us explain the evolution of the Arctic Ocean during the Pleistocene epoch (Dunton, 1992). There has been no detailed description of the Boulder Patch flora, yet such information is critical to documenting long-term changes in Arctic marginal seas during the Anthropocene. For instance, it is curious that so few central Arctic and northwestern Greenland algal taxa dominate the vegetation (Pedersen, 2011). Many species are cryptic or reduced in size, which are traits indicative of rigorous, stressful Arctic environments. Other taxa are present in unusually small populations. Others normally present in the Arctic littoral and the shallow sublittoral (25%–30%) are absent from the Boulder Patch community. Most Boulder Patch species (94%–97%) occur in the northeast Atlantic Ocean from Svalbard and northern Norway south to Britain and Ireland (Rueness, 1977; Hardy and Guiry, 2003; Hop et al., 2012). How different is the algal composition of the Boulder Patch flora from that of other Arctic floras? To address this question, we listed the algae most recently cited from west Svalbard by Hop et al. (2012). We found that the floras had considerable similarities (ca. 56% of the species in Svalbard are found in the Boulder Patch, Tables 1–3) that reflect both the uniqueness and the Arctic character of each flora. Differences in species number and type are likely attributable to (1) the northeast Atlantic Ocean boreal component in the Svalbard flora, which includes several typically littoral/upper sublittoral species and other species that have only recognized boreal/subarctic occurrence, (2) the presence of a number of shallow-water and littoral species in Svalbard not present in the Boulder Patch, and (3) the longer period of collection in the Boulder Patch compared to that of the 2012 Svalbard study. The absence of intertidal and upper sub-littoral vegetation in the Boulder Patch (and on the Alaskan Beaufort Sea coast in general) further reduced the number of species we recorded here; absent species include various species of filamentous green algae, *Fucus distichus* spp. *evanescens*, *Chordaria flagelliformis*, and at least two *Polysiphonia* species. Silt-covered rock substratum in the Boulder Patch also likely deters attachment of crustose species, including *Myrionema coronnae*, *Mikrosyphar polysiphoniae*, and *Hildenbrandia*

*rubra*, present in the Svalbard flora (Wessels et al., 2004; Hop et al., 2012).

Absence of many typical subarctic/boreal and High Arctic species in the Boulder Patch flora cannot be attributed to ice scour since such physical disturbances are relatively rare in Stefansson Sound. However, even in the most ice-scoured habitats, ice serves only to reduce populations, not to eliminate them entirely. Low-incident light in the Boulder Patch sublittoral for much of the year and seasonal sedimentation are perhaps most limiting for colonization of benthic algae. At this point, our knowledge of the suite of environmental variables limiting algal diversity at the Boulder Patch remains incomplete.

Several crusts (*Lithothamnion glaciale* and *L. tophi-forme*) and fleshy crusts (e.g., *Haemescharia polygyna*, *Rhodophysemodopsis hyperborea*) that occur throughout the North Atlantic and Arctic Oceans are surprisingly missing from the Boulder Patch. These red algal crusts clearly do not exhibit circumArctic distributions. Similarly, *Agarum clathratum* and *Saccharina longicuris*, as well as a cadre of small thalloid and filamentous species, are also absent from the Boulder Patch flora. These species are common throughout much of the Canadian Arctic and West Greenland. Additional species absent from both the inshore and the littoral Boulder Patch include the green algal clumps of *Spongomorpha arctica*, an association of *Chordaria/Petalonia/Scytosiphon*, a *Sphacelaria/Battersia* turf, *Stictyosiphon tortilis*, *Halosiphon tomentosus*, the Arctic endemic *Platysiphon verticillatus*, *Punctaria glacialis*, and the ubiquitous yellowish tufts of *Devaleraea ramentacea* and *Fucus evanescens*. The common Arctic red alga *Ptilota serrata* is occasionally present, but each of the above-listed species, except for *P. verticillatus*, has disjunct North Atlantic and North Pacific distributions. Clearly, high turbidity from suspended sediments, the lack of hard substratum, brackish conditions, and ice scour are limiting the presence of the above-listed species along the Alaskan nearshore coast and shallow waters.

#### *The Algal Crusts: A Distinguishing Feature of the Arctic Benthos?*

Coralline crusts are keystone species in all Arctic sublittoral areas thus far studied (Wilce, 1994, pers. obs.; Roberts et al., 2002; Adey and Hayek, 2011; Teichert et al., 2012). Future assessments of crust populations in the Boulder Patch may drastically improve our understanding of ecosystem structure and possible change in the Arctic sublittoral flora and fauna (Borum et al., 2002; Brown et al., 2011). Five species of brown algal crusts, representing five different genera, directly compete with coralline crusts and benthic invertebrates for space. Konar and Iken (2005) noted that coralline crusts were the major occupiers of space in the Boulder Patch, with epilithic benthic invertebrates following in abundance. While brown crusts were not considered by Konar and Iken (2005), these crustose algae are also significant competitors for space in the Boulder Patch

environment. However, the relative importance of brown crustose algae as space occupiers remains unknown. Identification of most crustose browns to the generic and specific levels is possible only through the study of viable material in a laboratory setting.

#### *Benthic Algal Adaptation to the Arctic Marine Environment*

Although numerous ecophysiological studies have examined boreal and Arctic algal species, few studies to date have studied these algal species in situ (Chapman and Craigie, 1977; Dunton and Schell, 1986; Rysgaard and Glud, 2007). In situ studies of *Laminaria solidungula* have shown that at low temperatures, this species develops novel physiological adaptations to light limitation, which include initiating new frond growth, completing more than 90% of its annual linear growth, and releasing meiospores in darkness during the nine-month ice-covered period (Dunton and Schell, 1986; Dunton and Jodwalis, 1988). Another Arctic endemic species, *Platysiphon verticillatus*, shows specific reproductive adaptation to this harsh environment through formation of overwintering cysts (R. Wilce, pers. obs.). Subsequent field and laboratory observations may reveal other adaptive mechanisms employed by Arctic macroalgal species to survive under extreme temperature and light conditions.

The exceptional Arctic specimen of *Furcellaria lumbricalis* was observed emergent from the bottom sediments at station E3 on 23 August 1987. A distinctive cuff of many green epiphytic/endophytic and filamentous cells of what appeared to be *Chlorochytrium* was apparent near the distal portion of the unbranched (juvenile stage) of the specimen. Several unanswered questions remain, including the definitive identification of the host specimen presumed to be *Furcellaria lumbricalis* and the character of some aspects of the life history of the green algal endophyte that forms the cuff. Historical collections of *F. lumbricalis* from northern areas were likely made from a subarctic environment; all are from localities distant from the Boulder Patch. For example, Kjellman (1883:158) noted that he had “failed to find this species in the Polar Sea,” but he cited records of the species (without collection data) from Svalbard, Norway, and Novaya Zemlya, Russia (Kjellman, 1877). Others have recorded *F. lumbricalis* in northern Norway (Jaasund, 1965; Rueness, 1977); Newfoundland, Canada (South and Tittley, 1986); and Svalbard, Norway (Vinogradova, 1995). Propagule movement of this boreal species from one or more boreal sites of *Furcellaria* occurrence to Stefansson Sound is enigmatic. Whether the endophytic *C. inclusum* within the *Furcellaria* host in the Boreal and Subarctic is multicellular is unknown, but such an association has not previously been documented in the Arctic. In the boreal environment, the *Furcellaria/Chlorochytrium* association is common, but with the endophyte (*C. inclusum*) only as a unicell (Jaasund, 1965; Chihara, 1969). Fortunately, germinating *Chlorochytrium* cells (Fig. 5a–d) contained the alternate filamentous stage of *C. inclusum*, *S. congregata* (Fig. 5e–h), aiding

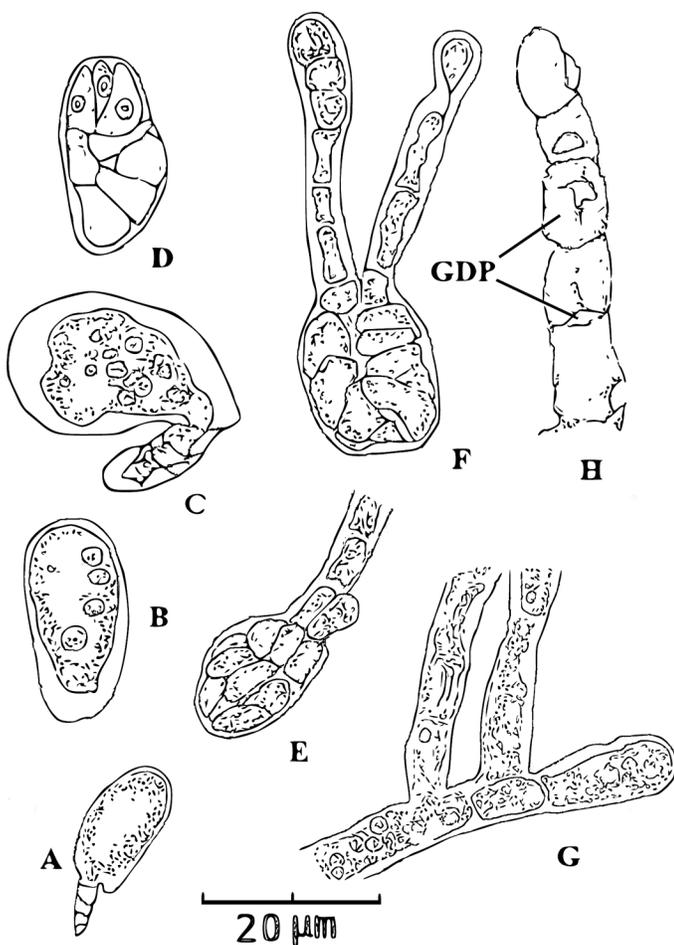


FIG. 5. *Spongomorpha congregata/Chlorochytrium inclusum* life history stages. (A–C) *C. inclusum* cells prior to cell division with net-like plastid and several pyrenoids; (D) multicellular *C. inclusum*; (E–F) juvenile *S. congregata* filaments attached to multicellular *C. inclusum*; (G) fragment of branched *S. congregata*. Note the net-like plastid with several conspicuous pyrenoids and the characteristic branch initiation; (H) fragment of reproductive *S. congregata* filament with evident presumed gametangial discharge pores (GDP), which suggest a putative gametophytic stage in the species life history.

in the identification of the reproductive *Spongomorpha* filaments (Fig. 5h). Although annual species of benthic algae are largely absent in the Boulder Patch, both boreal *Chlorochytrium inclusum* and *Spongomorpha congregata* have recognized annual periodicities (Sussmann and DeWreede, 2001). Species occurrence and initiation of motile cells occur seasonally, and both are affected by temperatures, which vary from year to year. *Acrosiphonia arcta* and *A. spiralis*, related species from British Columbia, Canada, failed to produce motile cells at temperatures close to 15°C but formed gametes between 5.0° to 10.0°C in culture (Sussmann et al., 1999; Sussmann and DeWreede, 2001). Moreover, a long-day regime was required for the initiation and germination of the gametophytic filaments (Hudson, 1974). Boulder Patch *Chlorochytrium* and *Spongomorpha* reside at 4–6 m depths and generally do not experience temperatures greater than 5.0°C. It is therefore likely that in the Arctic, lower temperatures and extended light periods during July and August elicit the abbreviated life cycle described above.

The heteromorphic life history of *Chlorochytrium inclusum* and *Spongomorpha congregata* includes a unicellular, putative diploid state that is a common endophyte in the outer cortex of boreal *Furcellaria lumbricalis* and foliose red algae, including *Dilsea socialis* (Jónsson, 1962; Kornmann, 1964, 1972; Jaasund 1965; Chihara, 1969; Hudson, 1974). Typically, nuclei of the *Chlorochytrium* stage are known to undergo both meiotic and mitotic nuclear divisions followed by the liberation of quadriflagellate motile cells that initiate the gametophytic, filamentous stage of *S. congregata* (Sussmann and DeWreede, 2001). The Boulder Patch *Chlorochytrium* stage of *S. congregata* is atypical and thus far unique in its novel production of a cell aggregate of 6–10 walled cells within the initial *Chlorochytrium* cell (Fig. 5d–f). Meiosis is assumed to occur during the first divisions of a putative diploid nucleus in the unicellular stage of the endophyte (Chihara, 1969; Kornmann, 1972; Sussmann and DeWreede, 2001). Each protoplast within the *Chlorochytrium* sporangium identified in this collection has a rigid cell wall and a net-like chloroplast with numerous pyrenoids, typical of the gross cytology of cells of the filamentous stage of this species. The most apically positioned cells of the *Chlorochytrium* sporangium are first to initiate development of the branched filamentous stage of *Spongomorpha* (Fig. 5d–e). We suggest that other sporangial cells, more basally positioned, over time will give rise to additional gametophytic filaments. The suggested absence of haploid motile cells from the *Chlorochytrium* sporangium in this Boulder Patch population is unknown in the life histories of boreal North Atlantic and North Pacific Ocean populations of *Acrosiphonia* and *Spongomorpha* species. Elimination of the haploid zoospore stage in the life history of Arctic *Chlorochytrium/Spongomorpha* reduces propagule dispersal and attachment chance, and it diminishes the amount of time required to complete the species life history. Elimination of the motile stage from the putative diploid *Chlorochytrium* cell in the life history represents an adaptive strategy to the Arctic short light period in the sublittoral environment. Only fortuitous collections of the Arctic endophyte with critical laboratory study will confirm this hypothesis.

Longevity of the two morphological forms in the *Spongomorpha* life history in the Boulder Patch is assumed on the basis of decades of empirical observations in Arctic waters. *Spongomorpha congregata* is commonly attached or free-floating in tide pools and shallow coastal sub-arctic boreal waters; in Arctic habitats, it is infrequently observed in small populations as loose-lying algal filaments. Evidence of discharged Boulder Patch *Spongomorpha* gametangia in late August suggests gamete fusion and the formation of a diploid *Chlorochytrium* cell in late July and early August. This time period immediately precedes the formation of sea ice and subsequent prolonged period of darkness. The *Chlorochytrium* unicell is also a common endophyte in several red algal species (*Dilsea socialis*, *Turnerella pennyi*, and *Phycodrys rubens*) in polar waters.

Yet another possible form of adaptation to the Arctic marine environment is represented by a microscopically observed association of the red alga *Rubrointrusa membranacea* (Magnus) Clayden and Saunders and benthic Arctic hydroid *Sertularia* sp. When freshly collected, the hydroid was reddish and extensively covered with what appeared as a red film. Red algal filaments and algal plastids are especially evident in the larger cells of internodal portions of the host. Pit connections are evident, but cell fusion was not observed. Records of *R. membranacea* show that Kuckuck (1897) and Jaasund (1965) described a similar association at Helgoland (North Sea) and northern Norway, respectively. Kuckuck (1897) and Clayden and Saunders (2010) thoroughly characterized the species and its association from laboratory analyses.

*Rubrointrusa membranacea* occurs widely in boreal to subarctic environments and from several locations in the sub-Antarctic. This species is always contained within the outer chitinous layer of a marine sertularian hydroid. The small size of the exposed erect filaments distinguishes *R. membranacea* specimens in the Boulder Patch from those in subarctic and boreal environments. The endozoic association and its diminutive tetrasporic filaments likely represent an advantageous adaptation to low incident light, which is further reduced in quality and quantity by the hydrozoan exosarc cover. Clearly, the hydroid habitat offers a form of shelter and protection from abrasion and grazers. Additional benefits of the host organism, such as excreted nitrogenous compounds and the presence of chitin, are currently undescribed.

#### *The Boulder Patch Macroalgae: A Sentinel for Change in Arctic Coastal Waters*

Climatic warming, which is especially pronounced in polar regions, will likely alter the physical and chemical properties of Arctic coastal waters (Hop et al., 2012). However, by the close of 2012, the impact of these changing physical environments on the composition of the Boulder Patch algal community had not yet become apparent. It is probable that several relatively conspicuous subarctic and boreal thalloid species will experience range shifts (e.g., *Chordaria flagelliformis*, *Petalonia fascia*, *Saccorhiza dermatodea*, *Agarum clathratum*, *Saccharina longicruris*). But only four species documented in this study (*Phaeophila dendroides*, *Eugomontia sacculata*, *Furcellaria lumbricalis*, and *Stylonema alsidii*) are clearly unexpected subarctic or boreal invaders into an Arctic environment. At this time, there is no compelling evidence of a considerable poleward movement of species from either the North Atlantic or the North Pacific Oceans. Some faunal species, such as the green sea urchin (*Strongylocentrotus droebachiensis*), reported in west and northeast Greenland (Blicher et al., 2007), Franklin Bay, Amundsen Gulf, and the Canadian archipelago (Brown and Belt, 2012), appear to be completely missing from the Boulder Patch and eastern Beaufort Sea benthos (K. Dunton, pers. obs). Current

urchin populations of the eastern Canadian archipelago in Ragged Channel of northern Baffin Island are small on the basis of visual inspection, but the effect of their presence on the attached vegetation is apparent (R. Wilce, pers. obs.). This herbivore has the potential to dramatically influence the biomass and diversity of future algal populations throughout the Arctic marine environment. With the exception of a few prominent algal species, primary producers from the Arctic inshore environment are largely underrepresented in the algal literature. This study provides the first comprehensive account of attached Arctic algae in the Beaufort Sea, which complements qualitative studies that pertain mostly to the benthic North Atlantic flora (Kjellman, 1883; Taylor, 1957; Lee, 1980; Cross et al., 1987; Brown et al., 2011). The Boulder Patch and other sublittoral rocky bottoms across the Arctic coast from near Point Barrow (Konar and Iken, 2005; Mohr et al., 1957) to Camden Bay (Fig. 1) (Dunton et al., 1982) represent ideal locations to monitor the ecological effects of environmental change (Müller et al., 2009). Records of biological data from these sites provide an unmatched baseline of the biotic (algal and faunal) composition, structure, and function of a Beaufort Sea coastal habitat. These data serve as an invaluable resource for assessing the long-term environmental impacts from both natural and anthropogenic disturbances (Hodgson and Sergy, 1987). The current study provides accurate floristic details from the central Beaufort Sea coast based on collections made over several decades and prior to the onset of dramatic losses in ice cover. Our observations describe an algal flora with distinct biogeographic affinities that ultimately reflect the circulation patterns and character of a High Arctic system poised for change.

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